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Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion

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Abstract With multiple species introductions and rapid global changes, there is a need for comprehensive invasion models that can predict community responses. Evidence suggests that abiotic constraint, propagule pressure, and biotic resistance of resident species each determine plant invasion success, yet their interactions are rarely tested. To understand these interactions, we conducted community assembly experiments simulating situations in which seeds of the invasive grass species *Phragmites australis* (Poaceae) land on bare soil along with seeds of resident wetland plant species. We used structural equation models to measure both direct abiotic constraint (here moist vs. flooded conditions) on invasion success and indirect constraint on the abundance and, therefore, biotic resistance of resident plant species. We also evaluated how propagule supply of *P. australis* interacts with the biotic resistance of resident species during invasion. We observed that flooding always directly reduced invasion success but had a synergistic or antagonistic effect on biotic resistance depending on the resident species involved. Biotic resistance of the most diverse resident species mixture remained strong even when abiotic conditions changed. Biotic resistance was also extremely effective under low propagule pressure of the invader. Moreover, the presence of a dense resident plant cover appeared to lower the threshold at which invasion success became stable even when propagule supply increased. Our study not only provides an analytical framework to quantify the effect of multiple interactions relevant to community assembly and species invasion, but it also proposes guidelines for innovative invasion management strategies based on a sound understanding of ecological processes.

Keywords Community assembly · Ecological restoration · Freshwater wetland · *Phragmites australis* · Structural equation model

Introduction

Biological invasion can be viewed as a community reassembly process for which the outcome depends on multiple interacting factors (Byun et al. 2013; Catford et al. 2009; Sax et al. 2007). In invasion ecology, the need to predict that outcome has led to the search for general principles that could guide community conservation, management, and/or restoration (Heger and Trepl 2003; Kettenring and Adams 2011). Improving predictions of community dynamics, however, remains a challenge. Experimental and analytical frameworks designed to understand and predict the outcome of invasion must take into account not only

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biotic and abiotic determinants of invasion success individually, but also their interactions (Holle and Simberloff 2005; Perelman et al. 2007; Thomsen et al. 2006b). With multiple species introductions and rapid global changes likely to affect both resident and invading species (Bellard et al. 2013), the need to develop comprehensive invasion models is becoming even more pressing.

Plant invasion is a multi-phase process (introduction, colonization, naturalization, etc.; Dietz and Edwards 2006), and the colonization phase determines whether an invasive species will ultimately establish at a site. For sexually reproducing invaders such as the grass species *Phragmites australis*, seeds can facilitate long-distance spread and rapid colonization of disturbed sites (Belzile et al. 2010), but seedlings often also represent the most vulnerable stage of plant development (Weisner and Ekstam 1993). Therefore, the colonization phase offers a critical window of opportunity when site or community management can be most efficient if invasive plant control or community restoration are the goals. To achieve these objectives using approaches based on ecological principles, such as by modifying abiotic conditions and/or by establishing invasion-resistant communities, a good understanding of processes determining the establishment success of invasive species is required.

When anthropogenic or natural disturbances provide opportunities for species recruitment into a community, species will often compete for the available space or resources. Biotic interactions may lead to biotic resistance (Levine et al. 2004), where invading species will be sorted out based on their competitive abilities. The diversity–resistance hypothesis (Elton 1958) predicts that species-rich communities will be more resistant to invasion, and experimental studies generally support this hypothesis (Frankow-Lindberg 2012; Frankow-Lindberg et al. 2009; Hector et al. 2001; Knops et al. 1999; Naeem et al. 2000). Not only species richness, however, but also functional group composition in a community can determine the likelihood that a particular invader will colonize a site (Byun et al. 2013; Pokorny et al. 2005). Biotic resistance can reduce the abundance of some invaders, but may not eliminate them entirely (Levine et al. 2004) as recipient communities are rarely saturated with species (Sax et al. 2007; Tilman 1997). It may, however, keep invaders below the nuisance level, thereby reducing the need for extensive interventions.

Biotic resistance may be enhanced by abiotic conditions that filter out intolerant invaders and/or allow the establishment of an invasion-resistant community (Gleason 1926; Melbourne et al. 2007; Weiher and Keddy 1995). Conversely, invaders may be favored by any change in abiotic conditions that are detrimental to resident species, such as extreme climatic events (Collinge et al. 2011; Goldstein and Suding 2014). Biotic resistance will also be modulated by propagule pressure (Miller et al. 2013; Thomsen et al. 2006b). Propagule pressure refers to both the number of individual invaders released and the frequency of releasing events to a single location (Lockwood et al. 2005). It remains unclear whether an invader derives increasing benefits from increasing propagule pressure or whether saturation occurs in a community at a certain propagule threshold (Lockwood et al. 2005). There is therefore considerable interest in relating propagule pressure to invasion success and, even more importantly, to test whether this relationship varies with the seed density of other plant species involved in the community reassembly process or with biotic resistance (Brown and Fridley 2003).

To develop a predictive invasion model, detailed information on how all of these abiotic and biotic factors interact under a given set of conditions is required (Herborg et al. 2007; Leung et al. 2012). Although several studies have considered interacting factors in the invasion process (Eschtruth and Battles 2009; Holle and Simberloff 2005; Miller et al. 2013; Perelman et al. 2007; Thomsen et al. 2006b), the results have been inconsistent, with propagule pressure overwhelmingly determining invasion success in some cases (Eschtruth and Battles 2009; Holle and Simberloff 2005), while in other cases abiotic constraints/habitats (Miller et al. 2013; Thomsen et al. 2006b) or biotic factors predominate (Davies et al. 2011). The relative importance of these factors also depends on the scale of the investigation (Perelman et al. 2007). Fortunately, recent advances in analytical tools, such as structural equation models (Grace et al. 2010), make it possible to test competing hypotheses on interactions and causal relationships among multiple factors in a variety of ecosystems (Whalen et al. 2012). These advances could help improve our ability to predict the outcome of complex invasion processes.

The aim of this study was to quantify the interplay between abiotic constraint, propagule pressure, and biotic resistance in the critical colonization phase of the invasion process. Our target invader is *P. australis* (Cav.) Trin. ex Steud., a widely spread grass (Poaceae) with at least one introduced lineage in North America (haplotype M in this case) (Kettenring et al. 2012; Meyerson et al. 2010; Saltonstall 2002). The introduced *P. australis* is aggressively invading wetlands and anthropogenic linear habitats such as roadside or agricultural ditches (Brisson et al. 2010; Maheu-Giroux and de Blois 2007; Moody and Mack 1988). We conducted two experiments simulating a situation in which *P. australis* seeds land on bare soil along with other wetland plant species, a common occurrence in the field following disturbances. For the species–environment experiment, we expected biotic resistance (measured as the decrease in invasion success of *P. australis*) to vary depending on the identity and diversity of the other resident wetland plants involved in the assembly process. We also tested a series of hypotheses on the ways by which abiotic conditions (here moist vs. flooded conditions) modulate biotic resistance. For the propagule experiment, we evaluated the effects of interactions between propagule pressure of *P. australis* and seed density of resident wetland plants in determining biotic resistance.

Materials and methods

We conducted two outdoor pot experiments at the Montreal Botanical Garden (Quebec, Canada): (1) a species–environment experiment in 2010 and (2) a propagule experiment in 2011. Fertile clay soil was collected from natural wetlands for use in both experiments and sterilized with a steam pasteurizer at 76 °C for 4 h to kill any viable seeds and prevent unwanted contamination. The pots (diameter 25.4 cm, height 30.5 cm) were immersed in water using large plastic containers (six pots per container). In the species–environment experiment, water was maintained at a constant level with an automatic water gauge device at either 5 cm below soil surface in the pot (hereafter referred to as 'moist conditions') or 5 cm above soil surface (hereafter referred to as 'flooded conditions'). Bricks were used to raise the pots to the height required for moist conditions [Electronic Supplementary Material (ESM) 1].

Species selection

Anaerobic tolerance should be a good indicator of resistance to flooding, which was the main abiotic constraint in our experiment. Similar to several other species, the anaerobic tolerance of *P. australis* varies according to its developmental stages, with relatively low tolerance at seedling stage but increasing tolerance with age (Engloner 2009; Mauchamp et al. 2001). To test biotic resistance in the experiments we chose five other wetland plant species commonly found in the area and covering a range of anaerobic tolerance levels at maturity (hereafter referred to as 'resident species'; ESM 2): *Typha latifolia* L. (Typhaceae), which has high anaerobic tolerance; *Panicum virgatum* L. (Poaceae) and *Scirpus cyperinus* (L.) Kunth (Cyperaceae), both with intermediate tolerance; *Eutrochium maculatum* (L.) E.E. Lamont (Asteraceae) and *Lolium multiflorum* Lam. (Poaceae), which have the lowest anaerobic tolerance of all species tested at maturity. This range in anaerobic tolerance allowed us to test hypotheses on the interplay between biotic resistance and abiotic conditions, based on the assumption that differences in anaerobic tolerance among species determine in part their response to abiotic constraints (here their cover in moist vs. flooded conditions) and therefore could modulate their biotic resistance under different environmental conditions. We used accepted species name as reported in VASCAN, the Database of Vascular Plants of Canada (Desmet and Brouillet 2013).

Prior to the experiments, seeds of *P. australis* were collected from mature colonies of the exotic genotype thriving in roadside ditches in Dundee, Quebec, Canada (45°05′50.6″N, 74°24′36.4″W). Seeds of *T. latifolia* were collected from a naturally established colony at the Montreal Botanical Garden, and seeds of other resident species were purchased from seed suppliers and had been harvested from an identified ecotype in natural habitats in North America. We standardized seed viability among species by applying pure live seed rates as determined by our own test (for *P. australis* and *T. latifolia*) or from information provided by the suppliers for the other species.

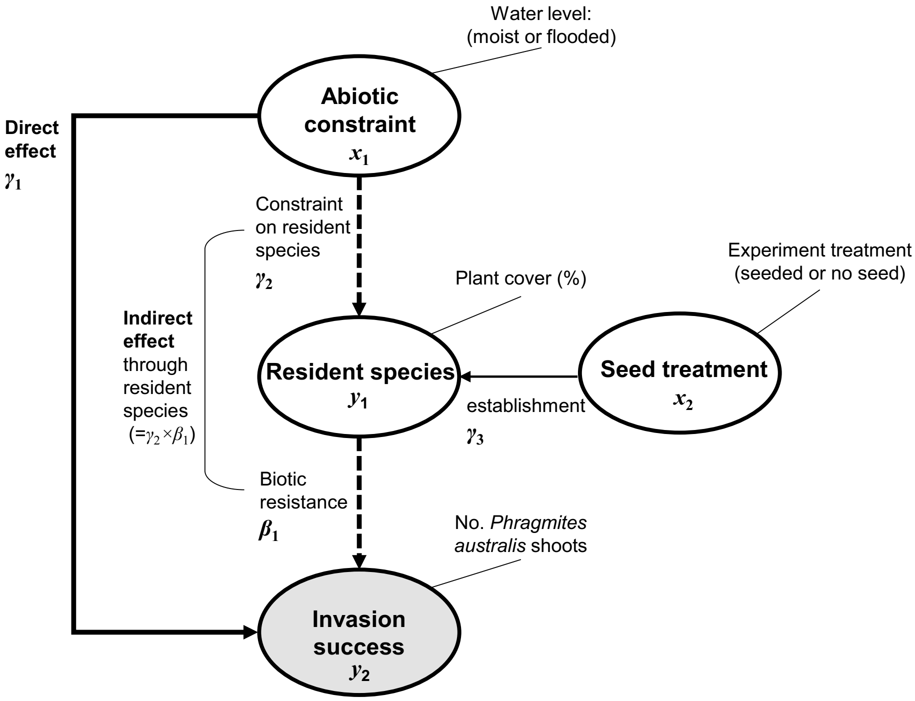
Species–environment experiment

In the species–environment experiment, we applied a two-way factorial design to test both the main and interaction effects of treatments. For each water level (either moist or flooded), we planted seeds, varying species composition as follows: Control (only *P. australis*), two-species mixtures (each of the five resident species individually + *P. australis*), and a six-species mixture (all five resident species + *P. australis*) based on an additive competition design (Connolly et al. 2001). Each treatment was replicated three times in a randomized complete block design (one replicate per block) for a total of 42 experimental units. Seed density of the resident species was fixed at 140 pure live seeds per pot regardless of the number of resident species; it was equally distributed among all five resident species (28 seeds per species) in the case of the six-species mixture. We used the same sowing density (140 pure live seeds) for *P. australis* for a total of 280 pure live seeds per pot. This corresponds to roughly 4,000 seeds m^{-2}, which is within the range of seedbanks from natural wetlands (Galatowitsch and van der Valk 1996). All seeds, including those of *P. australis*, were cold-stratified at 3 °C until sown. This experiment was run from May to October 2010.

Propagule experiment

In the propagule experiment, we evaluated the interaction between propagule supply of *P. australis* and biotic resistance of resident species by varying the seeding density of both *P. australis* and the resident species, while water level and resident species identity were fixed. Increasing propagule pressure from *P. australis* should increase invasion success, while increasing resident species cover should increase biotic resistance and therefore decrease invasion success. We used a mixture of *T. latifolia* and *L. multiflorum* in equal proportion for the resident species because these species had shown good resistance to invasion in the first

Fig. 1 Diagram showing proposed causal relationships among factors hypothesized to affect *Phragmites australis* invasion success in the species–environment experiments. Abiotic constraint (flooding) can have both direct (*solid line*) and indirect (*dashed lines*) effects on invasion success. Resident plant species may offer biotic resistance. See Table 1 and "Materials and methods" for details of the structural equation models



experiment. Water level was kept at the intermediate level (2 cm below soil surface) to minimize abiotic constraint. The different treatments for the seeding density of *P. australis* were 30, 90, 300, or 900 seeds; for the two resident species, they were no seed, 90, or 450 seeds. All species were sown in pots (diameter 15.2 cm, height 12.7 cm) using a factorial design. Seeding density treatments were replicated three times for a total of 36 experimental units, and the pots were allocated in a randomized complete block design. This experiment was run from May to October 2011.

Data collection

At the end of the growing season for both experiments, we counted the number of *P. australis* shoots to quantify invasion success. We also measured cover (%) of the resident species using the point intercept method with a 40-cell mesh. Plant cover was considered to be an appropriate measure to compare species with different life forms and sizes, and it was used, in this case, to relate the abundance of a resident species to its biotic resistance (i.e., the effect of resident species on invasion success) in structural equation models. For the six-species mixture, plant cover included all resident species.

Data analyses

Two-way analysis of variance (ANOVA) was used to test the main effect of each treatment as well as their interaction effect. The generalized linear mixed model with REML for the ANOVA test was applied, taking into account random block effect (Bolker et al. 2009). When significant main effects were found, we compared means using Tukey's HSD multiple comparison test. In all analyses, the assumptions of normality of residuals and homoscedasticity were checked, and response variables were log-transformed to meet the assumption if necessary. In addition, we used regression analysis to test the relationship between cover of resident species and number of *P. australis* shoots.

In the species–environment experiment, structural equation models (SEMs; Grace 2006; Grace et al. 2010, 2012) were used to test further hypotheses about causal relationships, as we found significant correlations among factors in two-way ANOVA. Structural equation models allow untangling of the direct and indirect effects of water level and resident species cover on invasion success (see Fig. 1 and next section for details). To illustrate, flooding can have an effect on an invader as well as on the cover of resident species. The former is considered in our models as a direct effect of flooding on invasion success, whereas the latter, by reducing or increasing the cover of resident species, can be considered as an indirect effect on invasion success through biotic resistance. Different chains of causal relationships, given different combinations of direct and indirect effects, correspond to alternative hypotheses on mediation patterns.

We built the models using the *sem* function in the *lavaan* R package with maximum likelihood, then compared goodness of model fit using AICc (corrected Akaike information criterion) and Akaike weight in a model selection approach (Burnham et al. 2002; Johnson and Omland 2004). We calculated AICc and Akaike weights using *aictab.lavaan* functions in the *lavaan* package. In general, a lower AICc means a better model fit (significant when ΔAICc > 2). Akaike weights (w_I) can be viewed as the probability that model I is the best model given a set of competing model candidates (Johnson and Omland 2004). After choosing the best model, we estimated standardized value of covariance on each connection of interests (dotted line in our model system; Fig. 1). We used JMP© software (SAS Institute, Cary, NC) for the classical statistical tests (ANOVA and regression analysis) and for drawing figures. We used R software (www.r-project.org) to build the structural equation models and to compare models' goodness of fit.

Structural equation models with hypotheses

A structural equation model typically involves multiple equations each representing hypotheses about causal relationships and mediation patterns in a system.

Let's assume that a response variable y_1 is influenced by another variable x_1:

$x_1 \rightarrow y_1$ or $y_1 = f(x_1)$

In addition, x_1 may also affect another response variable of interest y_2 directly, or indirectly through y_1. In this case, we will say that the response of y_2 is determined by both the direct effect of x_1 and indirect effect of x_1 mediated by y_1.

$x_1 \rightarrow y_1 \rightarrow y_2$ or $y_2 = f(x_1, y_1)$

Structural equations are expressed in classical simple linear models to express different pathways of causal relationships.

$$y_1 = \alpha_1 + \gamma x_1 + \zeta_1$$

$$y_2 = \alpha_2 + \gamma x_1 + \beta y_1 + \zeta_2$$

Our species–environment experiment is more complex, with the main response variable being invasion success (y_2: number of shoots of *P. australis*). The mediator variable, resident plant cover (y_1), provides an indication for biotic resistance (i.e., the effect of resident species on invasion success). Both can depend on water level [x_1; 0 (moist) or 1 (flooded)] and whether or not resident species were sown [x_2: 0 (no seed/control) or 1 (seeded)]. Equations reflect the fact that both direct and indirect effects can be significant (partial mediation), that only direct effects are significant (no mediation), or that only indirect effects are significant (complete mediation). We built and tested separate models for each species mixture type and compared the results for the different resident species mixtures.

SEM 1 (partial mediation model; Eq. 1)

Hypotheses *Phragmites australis* invasion success depends on abiotic constraints (water level) both on the invader and on resident species. Hence biotic resistance depends on abiotic conditions and may vary with resident species' response to water level (presumably related to their anaerobic tolerance).

$$\begin{aligned} y_1 &= \alpha_1 + \gamma_2 x_1 + \gamma_3 x_2 + \zeta_1 \\ y_2 &= \alpha_2 + \gamma_1 x_1 + \beta_1 y_1 + \zeta_2 \end{aligned} \tag{1}$$

where y_1 = resident plant cover (%); y_2 = number of shoots of *P. australis* (invasion success); x_1 = water levels (moist or flooded); x_2 = seed treatments (no seed or seeded); γ_1 = correlation coefficient between water level (x_1) and invasion success (y_2) as an indicator for direct flooding effect on invasion; γ_2 = correlation coefficient between water levels (x_1) and resident plant cover (y_1) as an indicator for flooding effect on resident plants; γ_3 = correlation coefficient between seed treatments (x_2) and resident plant cover (y_1); β_1 = correlation coefficient between resident plant cover (y_1) and invasion success (y_2) as an indicator for biotic resistance; ζ (zetas) are residuals (see also Fig. 1).

SEM 2 (no mediation model; Eq. 2)

Hypotheses *Phragmites australis* invasion success depends on abiotic constraints (water level) on the invader and on biotic resistance from the resident species. The performance of the latter, however, does not depend on abiotic conditions (in SEM Eq. 1, either $\gamma_2 = 0$ or $\beta_1 = 0$).

$$\begin{aligned} y_1 &= \alpha_1 + \gamma_3 x_2 + \zeta_1 \\ y_2 &= \alpha_2 + \gamma_1 x_1 + \beta_1 y_1 + \zeta_2 \end{aligned} \tag{2}$$

SEM 3 (complete mediation model; Eq. 3)

Hypotheses *Phragmites australis* invasion success depends only on biotic resistance to invasion as determined by abiotic constraints. There is no direct effect of water level on the invader (in SEM Eq. 1, $\gamma_1 = 0$)

$$\begin{aligned} y_1 &= \alpha_1 + \gamma_2 x_1 + \gamma_3 x_2 + \zeta_1 \\ y_2 &= \alpha_2 + \beta_1 y_1 + \zeta_2 \end{aligned} \tag{3}$$

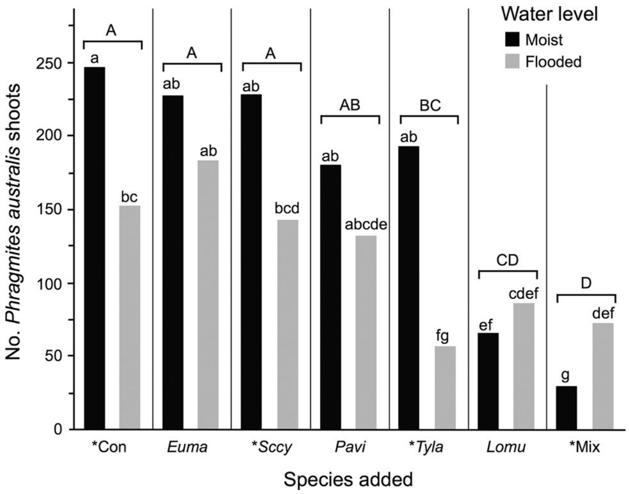


Fig. 2 Effect of biotic resistance from resident species on *P. australis* invasion success at two water levels. *Con* Control (no resident species added), *Mix* mixture [all five resident species added (*Euma Eutrochium maculatum*, *Sccy Scirpus cyperinus*, *Pavi Panicum virgatum*, *Tyla Typha latifolia*, *Lomu Lolium multiflorum*). Species treatments with the *same uppercase letter* do not significantly differ from each other (Tukey's HSD test, $P > 0.05$). Combinations of water level/species treatments with the *same lowercase letter* do not significantly differ from each other (Tukey's HSD test, $P > 0.05$). *Asterisks* indicate significant differences between water levels within each species treatment (contrast test, $P < 0.05$)

Results

Species–environment experiment

Abiotic constraints and biotic resistance interactively determined *P. australis* invasion success (Fig. 2). Both water level and resident species treatments were significant (two-way ANOVA test on log-transformed y: main effect of water level $F_{1,32} = 21.94$, $P < 0.001$; resident species treatments $F_{6,32} = 14.96$, $P < 0.001$). *P. australis* invaded less in flooded [average number of *P. australis* shoots per pot ($\bar{y}$) = 121] than in moist conditions ($\bar{y} = 176$). *P. australis* invasion was lowest with the six-species mixture ($\bar{y} = 50$), followed by the two-species mixtures of *L. mutiflorum* ($\bar{y} = 75$), *T. latifolia* ($\bar{y} = 124$), *P. virgatum* ($\bar{y} = 155$), *S. cyperinus* ($\bar{y} = 185$), and *E. maculatum* ($\bar{y} = 204$) in that order. There was a significant interaction effect between water level and resident species treatments and *P. australis* invasion (log-transformed y; $F_{6,32} = 4.22$, $P = 0.003$). While *L. multiflorum* resisted *P. australis* invasion much better in moist than flooded conditions, *T. latifolia* resisted the invasion better in flooded than in moist conditions. *P. australis* invasion success decreased as resident species cover increased in a linear relationship both in moist ($F_{1,22} = 52.62$, $P < 0.001$; Eq. 4) and in flooded ($F_{1,22} = 31.30$, $P < 0.001$; Eq. 5) conditions (ESM 3).

$$y_2 = 251.9 - 2.54 \cdot y_1 \tag{4}$$

$$y_2 = 156.0 - 1.55 \cdot y_1 \tag{5}$$

where y_1 stands for resident species cover (%) and y_2 stands for number of *P. australis* shoots per pot. *P. australis* invasion success was negatively correlated with resident species cover in moist conditions (Pearson correlation coefficient $r = -0.83$) and in flooded conditions ($r = -0.76$). In a further ANOVA test, both water level and species composition significantly affected resident species cover (log-transformed y; main effect of water level $F_{1,32} = 28.63$, $P < 0.001$; species $F_{6,32} = 155.7$, $P < 0.001$) with significant interactions (log-transformed y; $F_{6,32} = 33.58$, $P < 0.001$). Resident species with low anaerobic tolerance, such as *L. multiflorum* and *E. maculatum*, were more abundant in moist than in flooded conditions, while *T. latifolia*, with high anaerobic tolerance, was more abundant in flooded than in moist conditions. The abundance of *P. virgatum* and, interestingly, of resident species growing in the six-species mixture did not vary significantly with water level.

The SEM results for the different species mixtures are compared in Table 1. For most two-species mixtures, the partial mediation model (SEM 1; having both a direct effect of abiotic constraints on invasion success and an indirect effect via resident species cover) was the best model (with lowest AICc). In the cases of the two-species mixture with *P. virgatum* and the six-species mixture, the null mediation model (SEM 2; only direct effect on *P. australis*, no mediation) had the lowest AICc, but its goodness of fit was not significantly better than that of SEM 1 (ΔAICc < 2). While the direct effect of flooding on *P. australis* invasion was significantly and consistently negative, flooding had different effects on biotic resistance depending on the resident species in the two-species mixtures (Fig. 3). For example, while biotic resistance from *L. multiflorum* reduced *P. australis* invasion success ($\beta = -0.85$), flooding also reduced *L. multiflorum* cover ($\gamma_2 = -0.19$). The indirect flooding effect on invasion, mediated by its effect on *L. multiflorum* cover, was estimated to be 0.16 ($= -0.19 \times -0.85$). Therefore, flooding prevented biotic resistance from *L. multiflorum*. In contrast, flooding increased *T. latifolia*'s abundance ($\gamma_2 = 0.32$), while biotic resistance from *T. latifolia* reduced invasion ($\beta = -0.48$). The indirect flooding effect on invasion, mediated by its effect on *T. latifolia* cover, was estimated to be -0.15 ($=0.32 \times -0.48$). Therefore, flooding enhanced *T. latifolia*'s biotic resistance. For *P. virgatum* and the six-species mixture, flooding effect ($\gamma_2 = -0.02$ and -0.03, respectively) on their abundance was marginal; their biotic resistance was not significantly influenced by water level in this study. For

Table 1 Selection of the best structural equation models (SEM 1–3) for the species–environment experiment

Models	k^a	*Lolium*	*Typha*	*Panicum*	*Scirpus*	*Eutrochium*	Mixture
SEM 1	8	**372**, **0.83***	**439**, **0.82***	**371**, **0.16**	**410**, **0.84***	**415**, **0.84***	**430**, **0.20**
SEM 2	7	375, 0.17	442, 0.18	**369**, **0.84***	414, 0.16	418, 0.16	**428**, **0.75***
SEM 3	7	386, 0.00	451, 0.00	382, 0.00	424, 0.00	426, 0.00	433, 0.05

The models test hypotheses on the direct and indirect effects of flooding on invasion success of *Phragmites australis* given the resident species present. The mixture refers to all five resident species. SEM 1: partial mediation—both direct flooding effect and indirect flooding effects through resident species. SEM 2: null mediation—direct effect only. SEM 3: complete mediation—indirect effect only. Asterisks indicate best model for a given species treatment with corrected Akaike information criterion (AICc) and Akaike weight shown (in that order). Models in bold are not significantly different from the best model for that treatment (Δ AICc < 2)

[a] k = number of model parameters

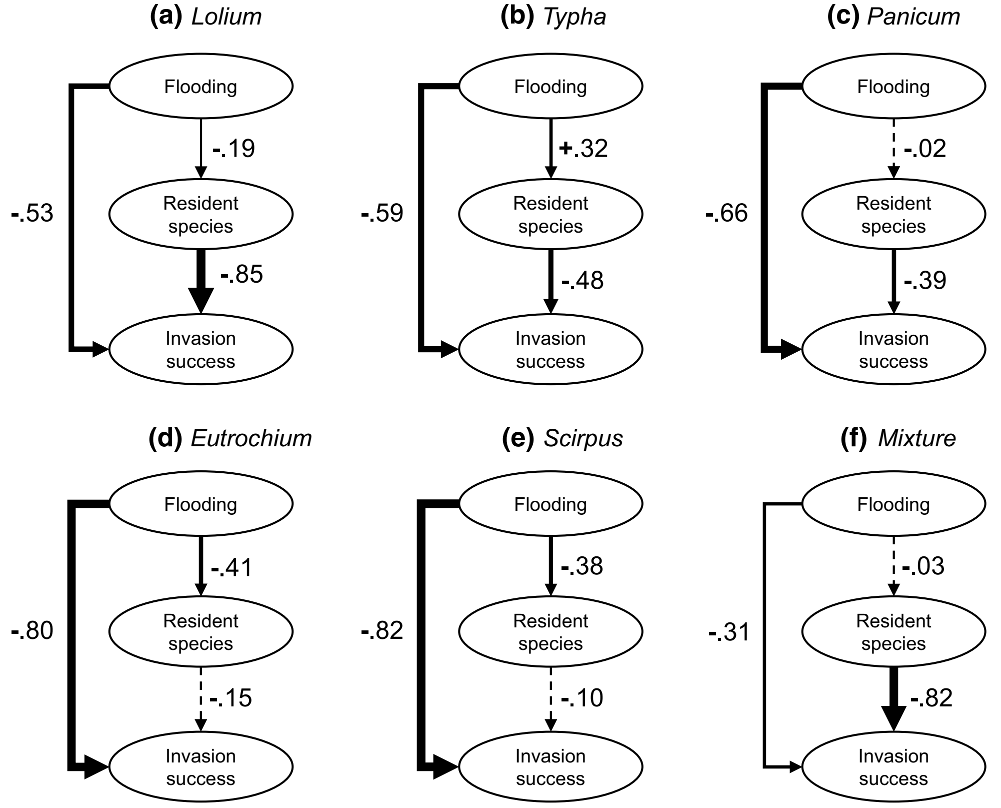


Fig. 3 Structural equation model results (SEM 1: partial mediation; see Table 1 for details) for *Lolium multiflorum* (**a**), *Typha latifolia* (**b**), *Panicum virgatum* (**c**), *Scirpus cyperinus* (**d**), *Eutrochium maculatum* (**e**) and mixture of all species (**f**). *Numbers* Standardized parameter values for the relationship of covariance, with the *sign* indicating a positive (+) or negative (−) effect. *Solid lines* Significant effect (*t* test, $P < 0.05$), *bar width* magnitude of effect, *dashed lines* non-significant effect ($P > 0.05$)

E. maculatum and *S. cyperinus*, flooding reduced their abundance ($\gamma_2 = -0.41$ and -0.38), as for *L. multiflorum*, but their biotic resistance was marginal or ineffective ($\beta = -0.15$ and -0.10). In these cases, *P. australis* invasion success was controlled mostly by the direct flooding effect on *P. australis*—i.e., neither by mediation nor biotic resistance. All resident species mixtures could thus be arranged along gradients of response to flooding and biotic resistance (ESM 4).

Propagule experiment

Both the propagule supply of *P. australis* and seeding density of resident species had significant effects on invasion success (Fig. 4; two-way ANOVA test: propagule pressure $F_{3,22} = 14.03$, $P < 0.001$; seeding density of resident species $F_{2,22} = 38.21$, $P < 0.001$). *P. australis* invasion success increased with propagule supply, but decreased with seeding rate of resident plants. In addition, there were

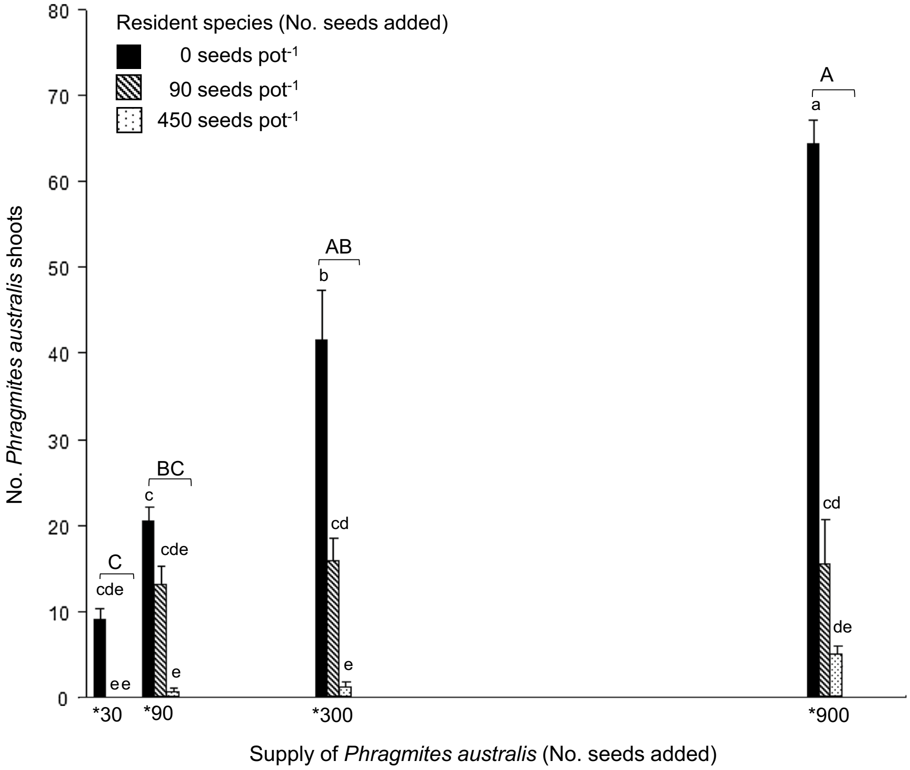


Fig. 4 Effect of propagule supply of *P. australis* on invasion success at three seeding densities of resident species. Propagule supply treatments with *same uppercase letter* do not significantly differ from each other (Tukey's HSD test, $P > 0.05$). Combinations of propagule supply/seeding density treatments with *same lowercase letter* do not significantly differ from each other (Tukey's HSD test, $P > 0.05$). *Asterisks* indicate significant differences among seeding densities of resident plants within each propagule supply treatment (contrast test, $P < 0.05$)

significant interactions between propagule supply and seeding density of resident plants ($F_{6,22} = 7.46$, $P < 0.001$). The effect of seeding density of resident plants on the relationship between propagule supply and invasion success suggests that there are clear benefits in investing in a dense cover of resident species, especially under low propagule pressure (ESM 5a, b). Biotic resistance stopped invasion when propagule supply was the lowest (30 seeds pot^{-1}) and reduced invasion even under high propagule pressure when a resident plant cover was present compared to no cover. Conversely, invasion success increased with propagule pressure most rapidly—and to its highest level—when there was no cover.

Discussion

Our study examined how biotic resistance, abiotic constraint, and propagule pressure interactively regulate *P. australis* invasion and identified synergetic or antagonistic processes relevant to community assembly and management. We found that biotic resistance varied with the identity and diversity of wetland plant species in the community and was also modulated by abiotic conditions, in relation to resident species traits or propagule pressure. Structural equation models support a partial mediation hypothesis in which *P. australis* invasion success depends on abiotic constraints (water level) both on the invader and on resident species.

The strength of biotic resistance to invasion is determined by various components of a community, including the identity of the dominant species (Emery and Gross 2007; Sheley and James 2010), species diversity (Fargione and Tilman 2005; van Ruijven et al. 2003), functional group identity (Byun et al. 2013; Fargione et al. 2003), and functional diversity (Pokorny et al. 2005). Direct indicators of biotic resistance are also provided by resident species' performance traits or community-wide fitness, such as plant size (Schamp and Aarssen 2010), plant cover (this study; Gerhardt and Collinge 2003), height (Gaudet and Keddy 1988), or biomass (Gaudet and Keddy 1988; Lulow 2006; Rinella et al. 2007). Interestingly, total plant cover of the six-species mixture was relatively stable in both the flooded and moist conditions. In this mixture, niche partitioning (or complementarity) among species each of which adapted to certain conditions or with different traits contributed to maintaining community-wide abundance even when conditions changed. Such community-wide stability could secure invasion resistance, evoking the insurance hypothesis (Byun et al. 2013; Ives et al. 2000; Loreau et al. 2001; Tilman et al. 2006).

Biotic resistance was partially modulated by flooding. Abiotic constraints and biotic resistance have been shown to determine invasibility when conditions vary in terms of water depth (Collinge et al. 2011; Gerhardt and Collinge 2003), sediment salinity (Dethier and Hacker 2005), or soil nutrients (Goldstein and Suding 2014). We provide additional quantitative evidence that biotic resistance and abiotic constraints work synergistically (or antagonistically) to control invasion depending on species traits in the species pool. In stressful or harsh environments, abiotic constraints alone can determine the fate of invaders (Chytrý et al. 2008; Dethier and Hacker 2005; Wang et al. 2006), as shown by the lower abundance of *P. australis* in flooded conditions compared to moist conditions in this study. Abiotic stress, however, can also determine the abundance of resident wetland plants and, therefore, indirectly modulate their potential to offer biotic resistance. Most resident species were less abundant when flooded, except for *T. latifolia*. The outcome of strong abiotic filtering has been shown to result in trait underdispersion and phylogenetic clustering during community reassembly (Adler et al. 2013; Procheş et al. 2008). The direct benefit of biotic resistance on invasion is expected to be more significant in benign or intermediate conditions that favor a broad range of species (Gerhardt and Collinge 2003; Naeem et al. 2000; Perelman et al. 2007; Thomsen et al. 2006a, b), namely, the moist conditions in our case. In these conditions, species can express their differential potential for invasion resistance depending on species traits and can therefore be ranked from most to least resistant to invasion accordingly.

The ability to predict the outcome of the interplay between abiotic constraints and biotic resistance on biological invasion in any given set of conditions rests on a good knowledge of the functional ecology of the species. Our experiments illustrate the important role of fitness-related traits (how well a species adapts to given abiotic constraints) in determining the ability of a species to resist invasion. Sharing information about species through databases of functional traits, such as TRY (Kattge et al. 2011), should facilitate the rigorous testing of specific predictions about community responses to invasion (Heger and Trepl 2003).

The invasion success of *P. australis* increased with propagule pressure, but there may be a threshold, or at least a saturation tendency, beyond which additional *P. australis* seeds will not necessarily increase invasion proportionally. Interestingly, our results suggest that biotic resistance from a resident plant cover could lower that threshold, with potential benefits in terms of community dynamics and control. The decision to invest or not in the restoration of a competitive cover may depend on how these benefits are perceived. For example, reducing invasion success early in community assembly may have long-term benefits in terms of the frequency and cost of control interventions if invader populations stabilize at manageable levels. Dense communities typically offer fewer opportunities for invaders to establish than sparse or disturbed ones (Lindig-Cisneros and Zedler 2002). Density could therefore be just as important as the species richness of the resident community in determining invasibility, particularly in the early establishment phase (Brown and Fridley 2003; Meiman et al. 2009; Reinhardt Adams and Galatowitsch 2008). Under the highest propagule pressure, biotic resistance offered by a dense cover of resident plants (450 seeds pot^{-1}) reduced invasion by 93 % on average compared to the control. Lindig-Cisneros and Zedler (2002) reported that a dense plant cover consisting of six species in the canopy cover and one species in the matrix cover reduced invasion of *Phalaris arundinacea* (reed canary grass) by 98.1 %, compared to 77 % under sparse cover. Other studies have found a significant interaction between abiotic constraint and propagule pressure, suggesting that alleviating abiotic constraint/stress promotes seed establishment under a given level of propagule pressure (Adler et al. 2013; Thomsen et al. 2006b). Overall, in our study, biotic resistance reduced invasion success significantly and effectively; biotic resistance alone, however, does not guarantee complete suppression of recruitment. Under high propagule pressure, raising the water level may further prevent invasion, as shown in our study, providing that some of the resident species in the mixture can tolerate the changes in abiotic conditions—hence the importance of species diversity.

Introduced *P. australis* is considered to be an invasive species in many wetland ecosystems in North America, and efforts to eradicate it are ongoing, often at high costs and with repeated interventions. Very few experimental studies so far have rigorously evaluated the role of resident plant communities in preventing or delaying reinvasion when control measures have been taken or when a wetland is disturbed. In these cases, our study shows that the outcome of community reassembly and invasion success will depend on the interactions between wetland plant identity/diversity, abiotic conditions, and propagule pressure. The ability of a species to provide biotic resistance will vary with abiotic conditions and, therefore, mixtures of species are more likely to provide more reliable resistance services in fluctuating environmental conditions—a common situation in wetlands—than monocultures. The positive effect of propagule pressure on invasion success may be offset by dense communities of invasion-resistant species that occupy available niches. Although complete eradication through biotic resistance is unlikely, avoiding or delaying the establishment of a dense *P. australis* cover could be beneficial. Finally, while species selection depends on the ecosystem under consideration, we believe that the principles outlined in this study are sufficiently robust to provide insights on community assembly and invasion process in any system.

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References

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJ (2013) Trait-based tests of coexistence mechanisms. Ecol Lett 16:1294–1306. doi:10.1111/ele.12157

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Glob Chang Biol 19:3740–3748. doi:10.1111/gcb.12344

Belzile F, Labbé J, LeBlanc M-C, Lavoie C (2010) Seeds contribute strongly to the spread of the invasive genotype of the common reed (Phragmites australis). Biol Invasions 12:2243–2250. doi:10.1007/s10530-009-9634-x

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135. doi:10.1016/j.tree.2008.10.008

Brisson J, de Blois S, Lavoie C (2010) Roadside as invasion pathway for common reed (*Phragmites australis*). Invasive Plant Sci Manag 3:506–514. doi:10.1614/ipsm-09-050.1

Brown RL, Fridley JD (2003) Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. Oikos 102:15–24. doi:10.1034/j.1600-0706.2003.12191.x

Burnham KP, Anderson DR, Burnham KP (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Byun C, de Blois S, Brisson J (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. J Ecol 101:128–139. doi:10.1111/1365-2745.12016

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15:22–40. doi:10.1111/j.1472-4642.2008.00521.x

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J Appl Ecol 45:448–458. doi:10.1111/j.1365-2664.2007.01398.x

Collinge SK, Ray C, Gerhardt F (2011) Long-term dynamics of biotic and abiotic resistance to exotic species invasion in restored vernal pool plant communities. Ecol Appl 21:2105–2118. doi:10.1890/10-1094.1

Connolly J, Wayne P, Bazzaz FA (2001) Interspecific competition in plants: how well do current methods answer fundamental questions? Am Nat 157:107–125. doi:10.1086/318631

Davies KF, Cavender-Bares J, Deacon N (2011) Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. Divers Distrib 17:35–42. doi:10.1111/j.1472-4642.2010.00721.x

Desmet P, Brouillet L (2013) Database of Vascular Plants of Canada (VASCAN): a community contributed taxonomic checklist of all vascular plants of Canada, Saint Pierre and Miquelon, and Greenland. PhytoKeys 25:55–67. doi:10.3897/phytokeys.25.3100

Dethier MN, Hacker SD (2005) Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. Ecol Appl 15:1273–1283. doi:10.1890/04-0505

Dietz H, Edwards PJ (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology 87:1359–1367. doi:10.1890/0012-9658(2006)87[1359:rtcpcd]2.0.co;2

Elton CS (1958) The ecology of invasions by animals and plants, 2000 edn. University of Chicago Press, Chicago

Emery SM, Gross KL (2007) Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology 88:954–964. doi:10.1890/06-0568

Engloner AI (2009) Structure, growth dynamics and biomass of reed (*Phragmites australis*)—a review. Flora 204:331–346. doi:10.1016/j.flora.2008.05.001

Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol Monogr 79:265–280. doi:10.1890/08-0221.1

Fargione JE, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. Ecol Lett 8:604–611. doi:10.1111/j.1461-0248.2005.00753.x

Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Natl Acad Sci USA 100:8916–8920. doi:10.1073/pnas.1033107100

Frankow-Lindberg BE (2012) Grassland plant species diversity decreases invasion by increasing resource use. Oecologia 169:793–802. doi:10.1007/s00442-011-2230-7

Frankow-Lindberg BE, Brophy C, Collins RP, Connolly J (2009) Biodiversity effects on yield and unsown species invasion in a temperate forage ecosystem. Ann Bot 103:913–921. doi:10.1093/aob/mcp008

Galatowitsch SM, van der Valk AG (1996) The vegetation of restored and natural prairie wetlands. Ecol Appl 6:102–112

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334:242–243. doi:10.1038/334242a0

Gerhardt F, Collinge SK (2003) Exotic plant invasions of vernal pools in the Central Valley of California, USA. J Biogeogr 30:1043–1052. doi:10.1046/j.1365-2699.2003.00911.x

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7. doi:10.2307/2479933

Goldstein L, Suding K (2014) Applying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. Biol Invasions 16:191–203. doi:10.1007/s10530-013-0513-0

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, New York

Grace JB, Anderson TM, Olff H, Scheiner SM (2010) On the specification of structural equation models for ecological systems. Ecol Monogr 80:67–87. doi:10.1890/09-0464.1

Grace JB, Schoolmaster DR, Guntenspergen GR, Little AM, Mitchell BR, Miller KM, Schweiger EW (2012) Guidelines for a graph–theoretic implementation of structural equation modeling. Ecosphere 3:73. doi:10.1890/es12-00048.1

Hector A, Dobson K, Minns A, Bazeley-White E, Lawton JH (2001) Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. Ecol Res 16:819–831. doi:10.1046/j.1440-1703.2001.00443.x

Heger T, Trepl L (2003) Predicting biological invasions. Biol Invasions 5:313–321. doi:10.1023/B:BINV.0000005568.44154.12

Herborg L-M, Jerde CL, Lodge DM, Ruiz GM, MacIsaac HJ (2007) Predicting invasion risk using measures of introduction effort and environmental niche models. Ecol Appl 17:663–674. doi:10.1890/06-0239

Holle BV, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86:3212–3218. doi:10.1890/05-0427

Ives AR, Klug JL, Gross K (2000) Stability and species richness in complex communities. Ecol Lett 3:399–411. doi:10.1046/j.1461-0248.2000.00144.x

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108. doi:10.1016/j.tree.2003.10.013

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. J Appl Ecol 48:970–979. doi:10.1111/j.1365-2664.2011.01979.x

Kettenring KM, de Blois S, Hauber DP (2012) Moving from a regional to a continental perspective of *Phragmites australis* invasion in North America. AoB Plants 2012:pls040. doi: 10.1093/aobpla/pls040

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293. doi:10.1046/j.1461-0248.1999.00083.x

Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, LlusiÀ J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, MÜLler SC, Nadrowski K, Naeem S, Niinemets Ü, NÖLlert S, NÜSke A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, OrdoÑEz J, Overbeck G, Ozinga WA, PatiÑO S, Paula S, Pausas JG, PeÑUelas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negret B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana JF, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY—a global database of plant traits. Glob Chang Biol 17:2905–2935. doi:10.1111/j.1365-2486.2011.02451.x

Leung B, Roura-Pascual N, Bacher S, Heikkila J, Brotons L, Burgman MA, Dehnen-Schmutz K, Essl F, Hulme PE, Richardson DM, Sol D, Vila M, Rejmanek M (2012) TEASIng apart alien species risk assessments: a framework for best practices. Ecol Lett 15:1475–1493. doi:10.1111/ele.12003

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989. doi:10.1111/j.1461-0248.2004.00657.x

Lindig-Cisneros R, Zedler JB (2002) Relationships between canopy complexity and germination microsites for *Phalaris arundinacea* L. Oecologia 133:159–167. doi:10.1007/s00442-002-1020-7

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228. doi:10.1016/j.tree.2005.02.004

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808. doi:10.1126/science.1064088

Lulow ME (2006) Invasion by non-native annual grasses: the importance of species biomass, composition, and time among California native grasses of the central valley. Restor Ecol 14:616–626. doi:10.1111/j.1526-100X.2006.00173.x

Maheu-Giroux M, de Blois S (2007) Landscape ecology of *Phragmites australis* invasion in networks of linear wetland. Landsc Ecol 22:285–301. doi:10.1007/s10980-006-9024-z

Mauchamp A, Blanch S, Grillas P (2001) Effects of submergence on the growth of *Phragmites australis* seedlings. Aquat Bot 69:147–164. doi:10.1016/S0304-3770(01)00135-8

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

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol Lett 10:77–94. doi:10.1111/j.1461-0248.2006.00987.x

Meyerson LA, Viola DV, Brown RN (2010) Hybridization of invasive *Phragmites australis* with a native subspecies in North America. Biol Invasions 12:103–111. doi:10.1007/s10530-009-9434-3

Miller AL, Diez JM, Sullivan JJ, Wangen SR, Wiser SK, Meffin R, Duncan RP (2013) Quantifying invasion resistance: the use of recruitment functions to control for propagule pressure. Ecology 95:920–929. doi:10.1890/13-0655.1

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. J Appl Ecol 25:1009–1021

Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108. doi:10.1034/j.1600-0706.2000.910108.x

Perelman SB, Chaneton EJ, Batista WB, Burkart SE, LeÓN RJC (2007) Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. J Ecol 95:662–673. doi:10.1111/j.1365-2745.2007.01255.x

Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ (2005) Plant functional group diversity as a mechanism for invasion resistance. Restor Ecol 13:448–459. doi:10.1111/j.1526-100X.2005.00056.x

Procheş Ş, Wilson JRU, Richardson DM, Rejmánek M (2008) Searching for phylogenetic pattern in biological invasions. Glob Ecol Biogeogr 17:5–10. doi:10.1111/j.1466-8238.2007.00333.x

Reinhardt Adams C, Galatowitsch SM (2008) The transition from invasive species control to native species promotion and its dependence on seed density thresholds. Appl Veg Sci 11:131–138. doi:10.3170/2007-7-18335

Rinella MJ, Pokorny ML, Rekaya R (2007) Grassland invader responses to realistic changes in native species richness. Ecol Appl 17:1824–1831

Saltonstall K (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proc Natl Acad Sci USA 99:2445–2449. doi:10.1073/pnas.032477999

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471. doi:10.1016/j.tree.2007.06.009

Schamp B, Aarssen L (2010) The role of plant species size in invasibility: a field experiment. Oecologia 162:995–1004. doi:10.1007/s00442-009-1499-2

Sheley RL, James J (2010) Resistance of native plant functional groups to invasion by medusahead (*Taeniatherum caput-medusae*). Invasive Plant Sci Manag 3:294–300. doi:10.1614/Ipsm-D-09-00056.1

Thomsen MA, Corbin JD, D'Antonio CM (2006a) The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California. Plant Ecol 186:23–35. doi:10.1007/s11258-006-9109-4

Thomsen MA, D'Antonio CM, Suttle KB, Sousa WP (2006b) Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. Ecol Lett 9:160–170. doi:10.1111/j.1461-0248.2005.00857.x

Tilman D (1997) Community invasibility, recruitment limitation and grassland biodiversity. Ecology 78:81–92

Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632. doi:10.1038/nature04742

van Ruijven J, de Deyn GB, Berendse F (2003) Diversity reduces invasibility in experimental plant communities: the role of plant species. Ecol Lett 6:910–918. doi:10.1046/j.1461-0248.2003.00516.x

Wang Q, Wang C, Zhao B, Ma Z, Luo Y, Chen J, Li B (2006) Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats. Biol Invasions 8:1547–1560. doi:10.1007/s10530-005-5846-x

Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74:159–164

Weisner SEB, Ekstam B (1993) Influence of germination time on juvenile performance of *Phragmites australis* on temporarily exposed bottoms—implications for the colonization of lake beds. Aquat Bot 45:107–118. doi:10.1016/0304-3770(93)90017-q

Whalen MA, Duffy JE, Grace JB (2012) Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. Ecology 94:510–520. doi:10.1890/12-0156.1