

## RESEARCH ARTICLE

# Generalization alters the probability of plant community invasion

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**ABSTRACT** The effects of native plant species diversity on community susceptibility to invasion are currently unclear. While species rich communities are often thought to be more robust to invasion as a consequence of high redundancy in mutualistic interactions, a positive association between native and exotic species richness is often observed. In animal-pollinated plants, higher plant species richness may dilute pollinator visitation to individuals, especially in the face of a limited pollinator pool. The presence of showy exotic plants at low densities in such communities can facilitate the pollination of natives by attracting generalist pollinators to the community, potentially halting their own invasion. Here we model the invasion of a resident plant community with the goal of examining whether allocation to floral display in an invasive plant affects the outcome of competition for pollination with a native species on a disturbed landscape, and whether the diversity of pollinator sharing species in a community influences the resistance to invasion. We find evidence for an optimal resource trade-off between floral and seed allocation in exotic plants, as invaders with low floral allocation do not attract enough visits for full seed set, while high investment in floral attraction results in lower seed set. Increased pollinator sharing in the resident community increases the probability of invasion, because the invader usurps pollinator visits from natives that share a common pollinator pool.

**KEYWORDS** competition, density, exotic species, facilitation, floral display, invasion, pollen limitation, seed-flower trade-offs, seed limitation

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## Introduction

The relationship between native species richness and exotic species richness has provided a paradox, as both positive and negative associations between the two have been observed

in nature (Sax and Brown 2000). At a local scale, species-rich communities can be robust to invasion due to a high degree of niche complementarity or a redundancy in mutualistic interactions (Lyons and Schwartz 2001, Kaiser-

Bunbury et al. 2010, Davies et al. 2011). Yet, positive correlations between native and exotic species richness have been reported in aquatic and terrestrial communities (Levine 2000, Sax 2002). This unexpected pattern could be explained by features of environmental quality that favour both natives and exotics, such as soil carbon and nitrogen or mean temperature and precipitation (Stohlgren et al. 1999, Levine 2000). This finding has sparked debate as to the relative importance of abiotic factors, such as disturbance, versus the presence and identity of native species in the community in the likelihood of the establishment of invasives (e.g., Memmott and Waser 2002, Strauss et al. 2006, Cadotte et al. 2010, Davies et al. 2011).

Plant communities have a high proportion of animal-pollinated species (90% Ollerton et al. 2011), and, on average, most of these visiting species are generalists (Waser et al. 1996). Generalist pollinators may allow exotic species to establish because they can pollinate many incoming species (Chittka and Schurkens 2001, Aizen et al. 2007, Lopezaraiza-Mikel et al. 2007). Two interrelated relationships have surfaced that may be important in how plant species richness affects the relative success of exotics. First, the lower mean conspecific density observed in species rich communities (Stirling and Wilsey 2001) and how it may operate to lower the probability of pollen delivery (Knight 2003, Knight et al. 2005). Second, the rise in pollinator sharing that is observed with species richness (Jordano 1987, Lázaro et al. 2009, Mitchell et al. 2009). Whether these two patterns affect pollen delivery in the face of an impending invasion, depends on the level of pollinator specialization within the community and this relationship has not been explored with respect to how it may affect the invasion of an exotic species.

Apart from the dynamics brought on by characteristics of the native (or 'resident') community, the floral display of invasives themselves can readily affect the outcome of pollination competition or facilitation. Accumulating evidence indicates that, once established, invasives tend to usurp generalist

pollinators from native species within communities (Chittka and Schurkens 2001, Brown et al. 2002, Bjerknes et al. 2007, Lopezaraiza-Mikel et al. 2007, Morales and Traveset 2009). On the other hand, some studies have indicated that pollinator visitation rates increase with increased floral resources (Ghazoul 2006), such that invasives might recruit additional pollinators to a community. These facilitative interactions, where a showy invasive species acts as a "magnet" species, have also been documented (Molina-Montenegro et al. 2008, Muñoz and Cavieres 2008, Jakobsson et al. 2009, Da Silva et al. 2013). Floral traits may be especially critical to the success of showy invaders in terms of achieving pollinator visitation when populations are just establishing. These mating dynamics can produce positive frequency dependence, whereby the growth of the exotic species will accelerate, theoretically leading to more rapid competitive exclusion of the native species (Zhou and Zhang 2006) compared to when these mating dynamics are ignored in competition models (Chesson and Warner 1981, Mouquet et al. 2002).

The effect of sharing pollinators with invasives may depend on the allocation to floral display in the native plant community. Empirical findings support the idea that many animal-pollinated invasive species have showy flowers and high allocation to floral displays as compared to their native counterparts (Grabas and Lavery 1999, Chittka and Schurkens 2001, Brown et al. 2002). These showy floral displays presumably allow exotic species to invade native pollination networks by attracting a large number of generalist pollinators (Aizen et al. 2008, Harmon-Threatt et al. 2009, Burns et al. 2011). While increased floral display will increase the visitation rates and may be advantageous in terms of intraspecific competition for mates, trade-offs between resources invested in display versus seed production have been observed for several species (Vaughton and Ramsey 1998, Worley and Barrett 2000, Lehtila and Brann 2007). Contrasting the marginal returns on investment in floral display in the context of interspecific competition for pollination and seed germination sites remains an

understudied avenue of plant community ecology (Kettle et al. 2011). In other words, the success of any given species may relate less to its pollen limitation and more to the seeds produced relative to its local competitors.

While pollen limitation is often viewed as a factor that reduces seed production, we provide an examination of how various contributions to seed production affect the outcome of interspecific seed competition. In particular, we examine the importance of investment in pollinator attraction in both native and invasive plant species on the potential for an invasive to establish in a disturbed community (Willson and Rathcke 1974, Podolsky 1992). Within this basic framework, we examine how invasive and native population densities, ecological disturbance, floral display, pollinator competition, and community species richness predict the long-term outcome of incipient invasions. Our model jointly investigates the invasibility of native communities with varying degrees of pollinator sharing. Specifically, we ask the following questions: (1) Does the amount of disturbance alter the growth rate of native populations in such a way as to affect whether invasives facilitate or compete for pollinator visits with native species? (2) Does the relative investment in floral display by invasives alter the probability of successful establishment? (3) How does the degree of pollinator sharing (i.e., level of generalization) in the community alter the establishment of an invasive? We ask these questions using a model that incorporates pollen limitation, flower-seed resource trade-offs, and floral constancy.

## Methods

### *The model community*

We developed a model that examines the competition dynamics between common natives and rare exotics with varying floral display and pollinator sharing between resident species. Initially, the model focuses on the pollination and seed production of individuals from a single-flowered 'resident' native plant species growing in a monoculture. Pollinator attraction is seen as an

essential component of plant fitness as no autogamous selfing occurs. Because there is only one species to visit, we assume that each pair of consecutive pollinator visits results in conspecific pollen transfer and ovule fertilization.

We envision the landscape as being subdivided into sites equivalent to the size of an individual plant, with each space being either empty ( $E_t$ , signifying disturbed, bare ground) or occupied by a resident plant species ( $R_t$ ). Thus, the density of sites occupied by resident plants is  $R_t$ , and the density of empty sites is  $E_t = 1 - R_t$ . We assume that in an undisturbed community, plants will exploit all sites, and empty spaces therefore signify disturbance within the community. The level of disturbance present in a community can range from 0 (where the resident community is intact) to 1 (where all native plant individuals have disappeared), so  $0 \leq E_t \leq 1$ .

Classic pollen limitation theory is employed to examine the trade-off between seed production and floral display (as in Haig and Westoby 1988, Vamosi and Otto 2002, Ashman et al. 2004). Following Ashman et al. (2004), we assume that the optimal allocation to floral display reflects a balance between the benefits accrued from recruiting pollinators (a saturating function of floral display) and the cost incurred by devoting these resources to seed development (i.e., a trade-off between flowers and seeds). We deviate from this classic pollen limitation theory with regards to the mechanics of the flower-seed trade-off. We posit that trade-offs, while present, may not occur as previously imagined between ovules and attractive parts of the flowers (petals, sepals, and nectar rewards). Rather, empirical evidence suggests that increasing the allocation to floral attraction may actually result in a corresponding increase in the number of ovules (Primack 1987, Robertson et al. 1994, Fenster and Carr 1997), potentially due to genetic constraints (Burd et al. 2009, Friedman and Barrett 2011). Thus, we allow the allocation to ovules to increase with increases in floral display and model the trade-off at the level of resources remaining to develop fertilized ovules into seeds. This trade-off may incorporate more biological realism as empirical studies have

found trade-offs between allocation to flowers versus vegetative structures (shoots/leaves), and a decrease in allocation to leaves would likely result in fewer resources for seed production (Delph 1990, Worley and Harder 1996, Thompson and Eckert 2004). This positive relationship between ovule and flower production sets our model apart from previous studies (e.g., Vamosi and Otto 2002). The resources devoted to seed maturation in each plant are thus represented as  $S_R$ , and  $1-S_R$  represents resource allocation to attractive petals and ovules. We assume that ovule volume remains constant and that any increases in resources are converted into increased ovule number.

Following this resource allocation framework, we model the number of ovules ( $O_R$ ) as  $O_R = d(1-S_R)$  and the number of seeds ( $\sigma_R$ ) as  $\sigma_R = \rho S_R$ , where  $d$  and  $\rho$  represent conversion constants representing the per-ovule and per-seed resource cost. Floral attractiveness ( $A_R$ ) is assumed to follow a linear relationship with  $S$ , influenced by another conversion factor  $c$ , which takes into account the resources required for each “unit” of attraction:  $A_R = 1 + c(1-S_R)$ . Thus, even the smallest flower is assumed to have non-zero attractiveness, i.e.,  $A_R \geq 1$ . It is important to note that our deviation from the standard flower size/seed trade-off presents different expectations for how investment in floral attractiveness results in the potential for pollen limitation. For instance, while a plant may divert 20% of its resources from seeds in favour of attraction, the result would be many more ovules than seeds and therefore a larger degree of pollen limitation. Here we explore a range of naturally occurring seed:ovule cost ratio values ( $\rho/d$ ) between 0.5-0.8 (Holland and Chamberlain 2007).

A single generalist pollinator species, equally efficient at pollinating all species in the community, services our initial virtual plant community. We simplify pollen movement by assuming that each successful visit sequence by a pollinator consists of two consecutive visits to two compatible conspecific plants in the community (as in Sargent and Otto 2006).

**Table 1:** Summary of key variables in the model

| Parameter | Meaning   | Default value |
|-----------|---|---------------|
| R         | Proportion of resident natives in the community                             |               |
| E         | Proportion of empty sites in the community, reflecting level of disturbance |               |
| I         | Proportion of invaders in the community                                     |               |
| N         | Number of native species sharing pollinators in the community               |               |
| S         | Resources allocated to seed maturation                                      |               |
| $\rho$    | Conversion constant for per-seed energy cost                                | $\rho/d=0.65$ |
| O         | Resources allocated to ovules   |               |
| D         | Conversion constant representing per-ovule energy cost                      | $\rho/d=0.65$ |
| $\sigma$  | Seed production for a species in the community                              |               |
| A         | Realized attractiveness of floral display                                   |               |
| $A_c$     | Overall floral attractiveness of the community                              |               |
| C         | Conversion constant of resource allocation to attraction                    | 1             |
| V         | Total number of two-plant visit sequences                                   |               |
| B         | Pollinator abundance index  | 50            |
| W         | Pollinator floral constancy   |               |
| P         | Probability of pollination success  |               |
| $\mu$     | Mortality rate  | 1             |
| $\chi$    | The probability that at least one seed is dispersed to a site               |               |
| $\gamma$  | Additional proportion of resources devoted to flowers in the invader        | 0.2           |
| k         | Maximal seed production asymptote   |               |

Pollinator recruitment to a plant community depends on both the attractiveness of the plant community and the regional abundance of pollinators. Plant community attractiveness takes into account the density of each plant species within the community and its species' allocation to attractiveness, so the attractiveness of a community composed entirely of native residents is  $A_c = RA_R$ . The total number of two-plant visit sequences ( $V$ ) recruited to the community is  $V = BA_c$ , where  $B$  represents the abundance of pollinators in the general vicinity. We assume here that disturbance is local and that healthy pollinator populations are available within the area ( $B = 100$ ).

As floral density increases, a saturating negative-exponential relationship with pollination probability is expected (Rathcke 1983, Knight et al. 2005). While this maximum floral visitation is hypothesized to decrease as floral density increases due to pollinator saturation (Rathcke 1983), we presume that seed set does not grow beyond the point of maximum visitation. Pollination success ( $P$ ) then follows a Poisson distribution with mean  $V$ . Therefore, the probability of a plant receiving zero visitors is equal to  $e^{-V}$  and the probability of successfully receiving a pollination visit is equal to:

$$P_R = 1 - e^{-BA_c} \quad (1)$$

This function adds an upper limit on how many pollinator visits result in increases in fitness after which further investment in floral display accrues no advantage. Seed production  $\sigma$  will increase with the number of pollinated ovules until the point where all available ovules have been fertilized, or the plant has no remaining resources to allocate to seed production. This point represents the maximal seed production asymptote  $k$  (as in Ashman et al. 2004), in this case equal to  $k_R = P(1-S_R)dS_R\rho$ .

To calculate how many seeds will germinate in unoccupied sites, we need to estimate the probability that plants vacate a site through mortality ( $\mu$ ), and the probability of seed dispersal to a site. We assume that seed density in

a site is independent of its previous state (i.e., there is no dispersal limitation, unlike Vamosi et al. (2007)), so that the probability of dispersal to a site is based entirely on the density of adults ( $R_t$ ) and the number of seeds produced ( $\sigma_R$ ). The seed densities in resident and empty sites are all proportional to  $R_t\sigma_R$ . The dispersal of seeds is assumed to follow a Poisson distribution, such that the probability that at least one individual is dispersed to any given site is  $\chi = 1 - e^{-\sigma_R}$ . The above processes yield the following discrete-time equation, with both persisting resident individuals and newly recruited resident individuals contributing to the resident population in the next generation:

$$R_{t+1} = (1 - \mu)R_t + \chi(E + \mu R_t) \quad (2)$$

Here, recruitment occurs when resident seeds germinate into empty sites that were previously unoccupied or that became vacant through mortality in the previous time step, as long as a single seed disperses to that site.

#### *Invasion of the model community*

Next we examine these population dynamics when an initially rare exotic species ( $I$ ) enters the resident community following disturbance, by considering a third occupation state in our community: in addition to empty (disturbed) sites ( $E_t$ ), and sites containing resident natives ( $R_t$ ), sites may now also contain an invader ( $I_t$ ).  $I_t$  is the density of the invader species, making the density of empty sites  $E_t = 1 - R_t - I_t$ . Densities of  $R_t$  and  $I_t$  range from 0 (when a species is extinct) to 1 (when a species occupies all sites), so that  $0 \leq R_t, I_t, E_t \leq 1$  and  $R_t + I_t + E_t = 1$ . Resident individuals still devote  $S_R$  resources to seed maturation and  $(1-S_R)$  resources to floral structures (petals + ovules) while  $S_I$  and  $(1-S_I)$  indicate the resources the invading species devotes to seeds and floral structures, respectively. To take into account the possibility of differing seed:flower resource ratios in invading plants, we examine the dynamics of a variable  $\gamma$  that represents an additional proportion of resources devoted to flowers in the invader as compared to resident

species, such that  $1 - S_i = 1 - S_R + \gamma S_R$  (making the allocation to seeds in invaders  $S_i = S_R (1 - \gamma)$ ). Thus, in the invaded community,  $A_c$  represents the mean attractiveness based on the density of residents and invaders and their respective floral allocations, or  $A_c = R_i^* A_R + I_i^* A_I$ , such that a showy invader could potentially facilitate the pollination success of a native species in a habitat patch.

Once pollinators are recruited to a patch, seed production ( $\sigma$ ) depends on the proportion of  $V$  foraging bouts to resident ( $R_i$ ) or invader ( $I_i$ ) species resulting in conspecific matings (and thus on floral constancy), and how many ovules are fertilized per successful foraging bout. Visitation to resident individuals depends on their relative frequency  $R_i/(R_i + I_i)$ , weighted by the ratio of their attractiveness compared to the invaders  $A_R/A_I$ . Conspecific matings per visit sequence depend upon two consecutive visits to the same species  $(A_R/A_I \times R_i/(R_i + I_i))^2$ . As more pollinators visit the patch ( $V$  increases), they increasingly visit flowers that have been previously pollinated, such that the mean pollination success  $P_R$  of the resident species mirrors a diminishing returns Poisson process (as in Morgan et al. (2005)):

$$P_R = 1 - e^{-V \left( \frac{A_R}{A_I} \frac{R_i}{R_i + I_i} \right)^2} \quad (3a).$$

Similarly, the mean pollination success through conspecific matings of the invader species,  $P_I$ , is distributed as

$$P_I = 1 - e^{-V \left( \frac{A_I}{A_R} \frac{R_i}{R_i + I_i} \right)^2} \quad (3b)$$

Seed production for resident and invader species ( $\sigma_R$  and  $\sigma_I$ , respectively) increases with pollination, as described for the resident community, until a maximum seed production asymptote ( $k_R$  or  $k_I$ ) is reached. To calculate how many of these seeds germinate in vacant or previously (but no longer) occupied sites, we assume that dispersal ability and mortality are equivalent for all species (as in Hurtt and Pacala (1995)). The probability that a species recruits seeds to a site depends on the seed production for

both species in the community ( $\sigma_R$  and  $\sigma_I$ ) so that the total seed densities in all sites (whether resident, invaded, or empty) are equal to  $R_i \sigma_R + I_i \sigma_I$ . The abundance of seeds at each site is again assumed to follow a Poisson distribution, such that the probability that at least one individual (of either type) occupies site in the next generation (resident, invaded, and empty sites) is  $\chi = 1 - e^{-(R_i \sigma_R + I_i \sigma_I)}$ .

Seed competition for vacant sites operates as a simple lottery competition, with, for example, the fraction  $R_i^* \sigma_R / (R_i^* \sigma_R + I_i^* \sigma_I)$  representing the probability that a resident species wins a site. The above processes yield the following discrete-time equations

$$R_{i+1} = (1 - \mu) R_i + \chi E_i \frac{R_i \sigma_R}{R_i \sigma_R + I_i \sigma_I} + \left( \mu \chi \frac{R_i \sigma_R}{R_i \sigma_R + I_i \sigma_I} \right) (R_i + I_i) \quad (4a)$$

$$I_{i+1} = (1 - \mu) I_i + \chi E_i \frac{I_i \sigma_I}{R_i \sigma_R + I_i \sigma_I} + \left( \mu \chi \frac{I_i \sigma_I}{R_i \sigma_R + I_i \sigma_I} \right) (R_i + I_i) \quad (4b)$$

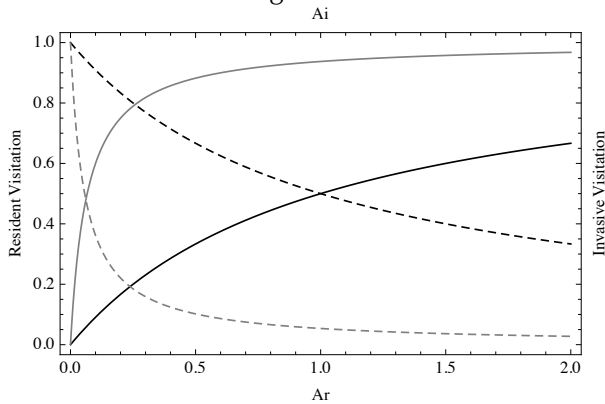
#### *Pollinator sharing and floral constancy in native communities*

Extending these dynamics to a community context, pollination now depends on the floral display of multiple native species and the encounter rates between conspecifics via our generalist pollinator (as in Sargent and Otto 2006). The density of each resident species becomes  $R_i = R_i/N$ , where  $N$  is the number of resident species in the community. The encounter rates depend on the number of species that share the same pollinator ( $N$ ), and the floral constancy of that pollinator ( $w$ ). We assume that all resident species have the same seed:flower trade-off, and that constant pollinators follow-up with a visit to the same species with a probability of one. Thus, equations 3a and 3b become:

$$P_R = 1 - e^{-V \left( \left( \frac{A_R}{A_I} \frac{R_i}{R_i + I_i} \right)^2 (1-w) + \left( \frac{A_R}{A_I} \frac{R_i}{R_i + I_i} \right) w \right)} \quad (5a)$$

$$P_I = 1 - e^{-V \left( \left( \frac{A_I}{A_R} \frac{I_I}{R_I + I_I} \right)^2 (1-w) + \left( \frac{A_I}{A_R} \frac{I_I}{R_I + I_I} \right)^w \right)} \quad (5b)$$

We also carried out an invasion analysis where we examined the conditions under which a rare introduced species, with a different investment in pollinator attraction, could ‘invade’ a community of resident species (as in Vamosi et al 2007). Specifically, we ask under what conditions is the (non-zero) equilibrium of the resident community unstable after the rare invading species is introduced, following Otto and Day (2007). Here, we assume that each resident species is set at the evolutionary stable state for floral display (see above) and that the novel pollinator and density conditions brought on by disturbance or introduction of the invasive happen instantaneously (i.e., there is no evolution of floral display in our model, as in Vamosi et al. 2007). While we expect that such evolutionary dynamics probably do occur and are important in communities, the present investigation aims to uncover the relative importance of factors involved in the initial ecological sorting that can occur in the first few generations after disturbance.



**Figure 1:** Results of a stability analysis examining the stability of a resident species with a particular investment in floral display. As the relative attractiveness of the resident ( $A_r$ , x-axis) increases, more pollinators are attracted to the resident (solid lines) versus the invasive ( $A_i$ , dashed lines). When the resident is relatively common (grey lines,  $R = 0.15$ ), visitation to the resident becomes greater than visitation to the invasive (where the two lines cross) at a relatively low level of investment in floral display. Conversely, the resident must invest more heavily to achieve greater visitation when it is relatively rare (black lines,  $R = 0.01$ ). Other parameter values:  $I = 0.01$ .

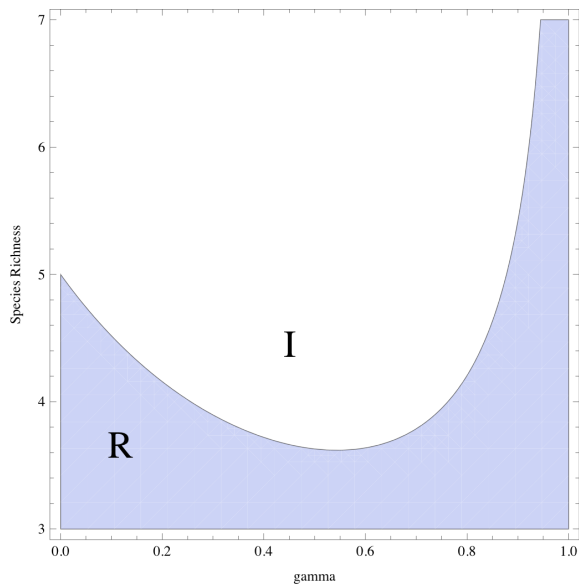
## Results

### *Seed limitation and the Haig-Westoby equilibrium*

Interestingly, we find that altering trade-offs such that they occur between attractive structures and seeds, rather than between attractive structures and ovules, has only a modest effect on the Evolutionarily Stable Strategy (ESS) of allocation to attraction (see Supplementary Material). Extending this ESS framework to a native and an invasive species competing for pollination shows that increasing attractiveness in invasive species will increase visitation to invading species (Figure 1). However, by employing a flower-seed trade-off in our simulations, we demonstrate that while an attractive invader can cause native residents to experience pollen limitation, whether increased visitation results in increased population growth depends on the environment (i.e., the density of native residents), such that an invasive species will never establish in communities of dense resident monocultures (Figure 2). In effect, what they gain in pollination competition, they lose in seed competition.

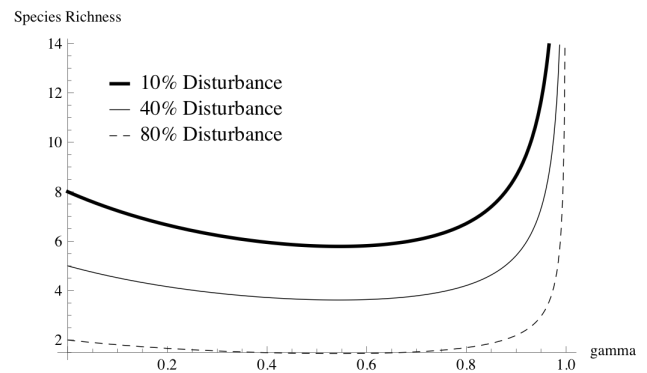
### *Invasion of the model community*

Because we assume that invasives are initially at a numerical disadvantage compared to residents, the preceding analysis suggests that the additional investment in floral attractive structures compared to the residents will be greater than zero (i.e.,  $\gamma > 0$ ). Two main factors substantially changed whether an invasive could establish: pollinator sharing in species-rich communities and the level of disturbance (Figure 3). When we add additional resident species sharing finite visits from the pollinator pool (increasing  $N$ ), we find that invasives have greater population growth than the resident community over a greater amount of examined parameter space (Figure 2). The trade-off in successful competition for pollinators versus seed germination sites is reflected in an optimal level of  $\gamma$ , below which pollinators are attracted to the residents versus the invasive. When  $\gamma$  is relatively high, however, visitation to the invasive becomes greater but they then suffer the costs of low investment in seed production.



**Figure 2.** The curve of equal colonization of resident (*R*) and invader (*I*) plant species, where the growths of the two populations are equivalent against the additional investment in attractive structures of the invasives compared to the residents ( $\gamma$ , or  $\gamma$ ). The area below the curve represents conditions where resident (*R*) plant species are more successful than invaders, whereas the area above the curve shows conditions where invasion (*I*) is likely. Invaders devoting a low or very high proportion of floral resources to attraction become seed limited and may only invade when pollinator sharing is high (i.e., the native community has a high species richness and consequently a high degree of pollinator sharing).

Increased disturbance levels increase the probability of invasion (Figure 3). As the frequency of disturbance increases, invasion becomes possible over a greater parameter space. For example, at a disturbance level of 80% of sites, invasion can occur even in monotypic patches with only moderate additional investments in attractiveness (Figure 3). The decrease in the average seed output of a monotypic patch acts the same as decreasing the attractiveness of the native community, depressing pollinator recruitment and seed production of the resident community (Figure 4). Because pollination success is dependent on a species' relative density in the community, high disturbance reduces the resident's pollination success to be equivalent to that of the invader. Invaders that invest heavily in pollinator attraction could presumably facilitate pollination of the resident population for a short period of time, but will ultimately decline in abundance.



**Figure 3.** The ability of invaders to invade a community increases as the level of disturbance also increases. Below the lines indicate parameter space where the residents are stable, whereas parameter space above the lines indicates where invasion is possible. As disturbance increases, invasion is possible over more parameter space.

## Discussion

By jointly examining pollination and seed competition, we find that showy invasive species experience diminishing returns in a landscape with disturbance. In our model the advantage of a larger floral display reaches a limit related to the regional abundance of pollinators (Hegland and Totland 2008, Forrest and Thomson 2009) such that seed yield declines with increasing floral display beyond that which produces the optimal number of seeds (Geber 1985, Andersson 1988, Cruzan et al. 1988, Schmid-Hempel and Speiser 1988, Robertson 1992). We find that optimal floral display for invasion is potentially influenced by the flower-seed trade-off when seed competition is examined in conjunction with competition for pollinators. Pollinator sharing between native species further facilitates invasion, potentially contributing to the patterns of correlation observed between native and nonnative species richness (Sax and Brown 2000). The effects of increased pollinator sharing can also reflect the low quality pollen (increased heterospecific pollen) that is received by generalist plants yet we did not include this aspect into the present model. We find the effects of increased pollinator sharing can be offset if native plants are showy (i.e., sufficient visits will be attracted to fertilize all ovules). Surprisingly, we know little regarding whether resource allocation to floral structures is greater in plant specialists.



Zygomorphic species (thought to be more specialized (Sargent 2004)) are more often self-compatible (Rosas-Guerrero et al. 2011) and may devote fewer resources to floral structures (Goodwillie et al. 2010). Our results suggest that generalists on the other hand may invest more heavily in floral display to succeed in competitions for pollinators. These results are consistent with previous studies indicating that specialists exhibit lower degrees of pollen limitation (Hegland and Totland 2008, Davila et al. 2012). In summary, native communities with fewer pollinator-sharing species were robust to invasion in our numerical simulations. Because of the negative relationship between the density of each constituent species and species richness, higher species richness allows invasive species to have visitation rates that are nearly equivalent to each resident species.

Disturbance and pollinator sharing were the two main factors affecting the likelihood of invasion. The finding that disturbance affords invaders with opportunities for success is perhaps not surprising. Burke and Grime (1996), using an experimental approach, found that community invasibility was largely determined by the amount of bare ground created (one of their “disturbance” treatments). In our simulations, this scenario is modeled by increasing the number of empty sites compared to residents, thereby reducing the numerical advantage of resident communities, such that increased disturbance facilitates the colonization of invaders. However, the influence of pollinator sharing on invasibility further allows exotic species to invade and outcompete residents. Specialization of pollinators or floral constancy could thus act to make species-rich communities more robust to invasion (as seen in Muir and Vamosi 2015). The ecosystem function of specialists may lie in stabilizing native species richness from invasion.

#### *Attraction allocation of invaders*

Our model allows for the presence of invasive species to offer both advantages and disadvantages to the pollination dynamics of native communities. However, perhaps because

we did not model changes in pollinator behaviour that may accompany changes in the community composition (such as constancy; Hersch & Roy 2007), we did not find facilitation by invasives to have a large influence on pollination of natives. We did, however, factor in that the presence of an invasive species could cause additional pollinators to be recruited to the area, which is consistent with empirical studies (Moragues and Traveset 2005, Lopezaraiza-Mikel et al. 2007). Yet because our model made visitation dependent on the attractiveness of the individual, we still found that additional pollinators could disproportionately visit the invasive and thus have the effect of creating an overall decrease in visitation rates to native species. Thus, additional allocation to floral display served to increase invasive visitation more so than facilitate that of the residents, which is consistent with what has been shown in field experiments (Chittka and Schergens 2001). However, while increased investment in floral display facilitated colonization to a point, it eventually resulted in seed limitation of invaders, which lead to a decrease in colonization potential. This highlights an important point that is often neglected in studies of pollen limitation and pollinator visitation: such studies often concentrate on whether a particular species has higher seed-set in the presence or absence of an invader, while failing to consider whether it makes more seeds *relative* to the invading species. In other words, invaders may “steal” pollinators, but if this comes at the expense of seed production, it will not translate into successful establishment.

When trade-offs between seed production and flower production are present, producing more seeds than competing species can be accomplished by (1) devoting more resources to fruit maturation and aborting fewer fertilized ovules and (2) devoting more resources to attraction and fertilizing more ovules. Our joint examination of pollen and seed limitation reveals that the optimal allocation to attraction depends on the relative density of invaders and native species, as well as the species richness of the native species. We envision that there is a correlation between flowers and ovules, such that

ovule number increases as flowers become larger (or more numerous) as a consequence of floral allometry (Primack 1987, Robertson et al. 1994, Fenster and Carr 1997). However, resources for fruit maturation decline with flower (or inflorescence) size. In reality, trade-offs among flower, ovule and fruit production are even more complex than how we have modeled them here (Cao et al. 2011), and future investigations of more complex trade-off functions are certainly warranted. Nonetheless, we feel that the trade-off, as presented here, represents a good balance between simplicity and accuracy. Perhaps most importantly, our trade-off function is supported by empirical studies (Fenster and Carr 1997; Vaughton and Ramsey 1998). We find that pollen limitation is more likely in plants that invest heavily in floral display, consistent with previous studies (Knight et al 2005; Burd et al. 2009). Yet, while attractive species are more likely to be pollen-limited, they may receive more visits and hence produce more seeds than their competitors.

#### *Community metrics and invasion*

Other studies have examined the interactions between plant investment in display and community invasibility from the perspective of plant-pollinator networks (Aizen et al. 2007, Bartomeus et al. 2008). Because most communities do not have a single pollinator species providing service to every plant species, our model is analogous to an examination of the invasion of a single “node” of plants that share pollinators within a larger plant-pollinator network, where pollinators share preferences for particular types of flowers. In this context, the invasion of a “node” may not relate to the collapse of the entire native community. We find that these more generalized nodes in native communities are more at risk of invasion and adding more specialized pollinators to our model would likely decrease the parameter space where invasion is possible. Indeed, a biotically-pollinated exotic will not invade if it cannot recruit any native pollinators, and so pollinator sharing at some level is integral to the invasion process (Morales and Traveset 2009). While species richness is often reported to buffer communities (Levine and

D’Antonio 1999, Levine 2000), here we find that communities that are connected through a generalized plant-pollinator network are more susceptible to invasion. Finally, Aizen et al. (2008) found that as an invasion proceeds, the invasive species appears to act as a vacuum for pollinator mutualists, such that remaining native species appear to become more specialized in their suite of pollinator interactions (i.e., the connectance among native species declines in invaded communities). While we do not model this situation explicitly, if pollinator sharing declines as an invasion proceeds, this may offer native communities a form of rescue.

#### **Conclusions and Future Directions**

Our results call into question whether species diversity alone functions to make plant communities prevent plant invasions. We find instead that species-rich plant communities that consist of higher levels of specialization are robust against showy invasive species (Dorado et al. 2011). Plant species richness is often correlated with a higher degree of pollinator sharing and a lower level of floral constancy, as pollinators incorporate more plant species into their diet (Sjodin 2007, Vamosi et al. 2014). We also note that similarities in floral traits of constituent members of a plant community may offer a way to predict the degree of pollinator sharing and which “nodes” in a plant-pollinator communities are most likely to be negatively affected by establishing non-native plants (Chamberlain et al. 2014).

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