

Propagule pressure cannot always overcome biotic resistance: the role of density-dependent establishment in four invasive species

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Summary

Successful invasions result from species functional traits interacting with the receiving community. Some have proposed that propagule pressure, or the size and number of introductions, can overcome high invasion resistance. However, few studies empirically investigate the relationship among functional traits, community composition, and propagule pressure. Here, we empirically examined how propagule pressure influenced the invasive success of four species in four resident communities (bare ground, grass-only, forb-only, and full resident community). The four species represented both small- and large-seeded grasses and forbs, and propagule sizes (the number of individuals in an introduction event) ranged from 16 to 160 000 seeds m⁻². Invasion probability varied among species and communities and was strongly influenced by the propagule size. The large-seeded species had the

highest invasion success in all communities, while the grasses did as well or better, respectively, in the grass-only and bare ground communities. However, contrary to existing assumptions, we found that the establishment probability of individual seeds decreased exponentially with increasing propagule size. Therefore, increased propagule pressure was subjected to severely diminishing returns on invasiveness. Thus, while propagule pressure played a role in determining invasion success, it was not always able to overcome communities with high invasion resistance, particularly for species that experienced strong density-dependent inhibition. The role of propagule pressure in invasion is more complex than previously thought and may present important trade-offs for bet-hedging colonisation strategies.

Keywords: functional traits, invasion cliff, invasion pressure, propagule pressure, seed size.

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Introduction

Successful invasion of new locations depends on biotic and abiotic characteristics of both the invader and the receiving community (Rejmánek *et al.*, 2005; Barney & Whitlow, 2008). Invasibility, or the susceptibility of a location to invasion, is determined by plant community composition (Fridley *et al.*, 2007),

available establishment sites (Duncan *et al.*, 2009), resource availability (Davis *et al.*, 2000), herbivore and pathogen load (Mitchell & Power, 2003), and local climate. These factors interact and vary in time and space, and serve as stringent recruitment filters that introduced species must overcome, if they are to establish successfully (Simberloff, 2009).

All invasions must begin with introduction of viable propagules, with invasion success hypothesised to scale with propagule load and habitat invasibility. Propagule pressure is defined as the size (number of individuals) and number of introductions to a location (Lockwood *et al.*, 2005) and is widely considered a primary determinant of invasion success (Catford *et al.*, 2009; Simberloff, 2009; Jeschke, 2014). In fact, Colautti *et al.* (2006) proposed that propagule pressure serves as the null model explaining invasion of new locations, as species with high propagule pressure are able to overcome limited genetic variation, limited safe sites and environmental and demographic stochasticity (Simberloff, 2009). However, our understanding of the role of propagule pressure and its interactions with species and habitats is limited for most species, especially plants.

Importantly, it is being increasingly recognised that no single explanation exists for biological invasions. Instead, there is a need to integrate information on functional traits, habitat suitability and propagule pressure, to paint a clearer and more realistic picture of the invasion process (Barney & Whitlow, 2008; Davis, 2009). To this end, Davis (2009) developed the concept of 'invasion pressure,' which is the integration of habitat invasibility and propagule pressure (after Leung *et al.*, 2004), and is described by the simple function in which invasion pressure increases exponentially with propagule pressure:

$$Y = (1 - P)^N \quad (1)$$

here, Y is defined as the invasion pressure, or the probability that at least one propagule establishes in a given area, P is invasibility, or the probability of establishment of individual propagules, and N is the number of propagules arriving to a given area in an introduction event (i.e., propagule size). It is important to note here that propagule size is measured as a flux; it is the density of propagules that arrive in a specified area over a specified unit of time.

As described, the invasibility parameter P can be empirically measured and, while it can vary depending on the biotic and abiotic conditions of the receiving habitat, it is assumed to not vary with N . In other words, the probability of an individual propagule establishing in a given environment is constant regardless of the density of propagules. However, as a result of self-thinning and other forms of self-limitation (Westoby, 1984; Duncan *et al.*, 2009), invasibility might be expected to vary with propagule size. As many models, including the original Davis (2009) model, assume no relationship, any non-constant relationship between invasibility and propagule size would

give rise to a more complex relationship between propagule pressure and invasion success than was originally described (Warren *et al.*, 2012). Other, more descriptive models have been developed to describe how invasion pressure might vary with propagule size, taking into account competition for limited suitable recruitment sites of uncertain size and distribution (Poulsen *et al.*, 2007; Duncan *et al.*, 2009).

To generalise Davis' model to allow for a simple model of density dependence, we first assume that the proportion of plants that successfully establish varies as a function of propagule density according to the following equation:

$$P = P'N^D \quad (2)$$

where P' is the establishment probability of a single propagule in a given area and D is a density dependence parameter that determines how P responds to changes in propagule density. Ecologically realistic values of D might be expected to fall between 0 and -1 , in which more negative values of D indicate stronger negative density dependence. When $D = 0$, there is no density dependence among a population of propagules and P is constant for any density of propagules. When $D = -1$, a log-change in N produces an identical log-change in P . In other words, density dependence exactly cancels out the addition of new propagules, so the expected total number of successful establishment individuals is constant for all values of N .

Taking the log of this equation reveals a linear relationship between $\log(P)$ and $\log(N)$:

$$\log(P) = \log(P') + D\log(N) \quad (3)$$

Equation 3 bears a similarity to the linear relationship between log-density and log-biomass that is produced by self-thinning (Westoby, 1984), and in our case, reflects the reduction in establishment probability as a function of propagule density. This also exposes a major limitation of assuming that P varies according to the power function of N : extrapolating to lower densities can yield nonsense values of P . Thus, this equation can only be applied when density-dependent effects are constant over the entire range of propagule sizes being considered. This also means that P' measured in this way is difficult to scale to systems with lower propagule pressure than the lowest sampled propagule pressure in the study where P' was fitted.

When Eqn (2) is combined with Eqn (1), we can estimate the invasion pressure Y according to the following equation:

$$Y = 1 - (1 - P'N^D)^N \quad (4)$$

Because per-capita establishment probability is low, establishment can also be modelled as a Poisson process:

$$Y = 1 - \exp(-P'N^{1+D}) \quad (5)$$

Finally, we can express this in terms of $\log(N)$:

$$Y = 1 - \exp(-\exp[\log(P') + (1 + D)\log(N)]) \quad (6)$$

Equation (6) is the inverse of the complementary log–log link function, which is commonly used in generalised linear models. This is not surprising, as the complementary log–log link was originally developed to describe the probability of establishing a colony of microorganisms from a serial dilution of liquid cultures (Fisher, 1922) in a manner directly analogous to identifying whether a propagule establishes or not at a given density. This has enormous heuristic value; most modern statistical packages are able to fit models using the complementary log–log link, allowing researchers to readily estimate habitat invasibility (P') and the role of density dependence on per-capita establishment (D), using basic statistical packages.

Here we explored the relationship between invading species functional traits (seed size), receiving habitat community composition and propagule size (the number of individuals in an introduction event). We used the models described above to estimate the relationship between per-capita invasibility (P) and propagule size (N) and explored the effect of species functional traits and community composition on these relationships.

Materials and methods

Species

Four common summer annual species were selected given their historically weedy presence in early-successional communities that also represent common grass and broad-leaved species that vary in seed size: *Urochloa platyphylla* (Munro ex C. Wright) R.D. Webster (broadleaf signalgrass), *Digitaria sanguinalis* (L.) Scop. (large crabgrass), *Abutilon theophrasti* Medik. (vel-

vetleaf), and *Amaranthus retroflexus* L. (redroot pigweed). *Urochloa platyphylla* and *D. sanguinalis* are both caespitose grasses, while *A. theophrasti* and *A. retroflexus* are erect broad-leaved species. Seed size and mass are considered important functional traits, as large-seeded invaders establish more frequently than small-seeded plants (Eisenhauer & Scheu, 2008), and these traits are important functional traits in the early stages of invasion. One species within each guild represents a relatively small- and large-seeded invader (Table 1). To reduce experimental complexity but maintain robustness, we opted for a balanced design of one small- and large-seeded broad-leaved and grass. Future studies could expand to test additional species and functional traits.

Plant communities

We manipulated the resident plant community to achieve four target communities that varied in functional composition: bare ground, grass-only community, forb-only community, and full resident community. Following germination of the resident community, but prior to adding our target invaders, we applied either selective (grass and forb communities) or non-selective (bare ground) herbicides, which were subsequently maintained by hand clipping at ground level throughout the experiment.

Propagule size

We varied the number of propagules in a single introduction event (propagule size) using a logarithmic curve to span five orders of magnitude, which included the majority of the range in the original invasion pressure discussion (Davis, 2009) and is ecologically relevant for these species: 1, 10, 100, 1000, 10 000 seeds per 0.25×0.25 m subplot (or 16, 160, 1600, 16 000, 160 000 seeds m^{-2}).

Experimental design

A randomised split-plot design with four replications was established in May 2013 at three locations in Southwest Virginia: one location was at the Glade Road Research Facility in Blacksburg, Virginia

Table 1 Target invasive species and seed functional traits

Species	Common name	Size designation	Seed size (mm)	Seed mass (g) (per 100 seeds)
<i>Abutilon theophrasti</i>	Velvetleaf	Large	3.6	0.981
<i>Amaranthus retroflexus</i>	Redroot pigweed	Small	1.1	0.032
<i>Urochloa platyphylla</i>	Broad-leaved signalgrass	Large	4.4	0.282
<i>Digitaria sanguinalis</i>	Large crabgrass	Small	2.5	0.057

(37.233783N, 80.436542W), while the second and third locations were in two fields at Virginia Tech's Kentland Research Farm in McCoy, Virginia (37.189997N, 80.578075W and 37.190697N, 80.576908W). We chose early-successional post-agricultural fields as the environment to test our objectives, as it provided a relatively consistent resident species composition of annual grasses and forbs that are generally not resource limited. The Glade Road location previously held maize and soybean under annual rotation, with a Groseclose–Urban land complex with a loam to clay loam texture profile. The Kentland Farm fields had a recent cropping history of maize with a winter rye cover crop on a fertile flood plain containing Ross soils and a loam texture profile.

Each replication contained 20 1×1 m plots with a 0.5 m buffer surrounding each plot. Each 1 m^2 plot was subdivided into four 0.25×0.25 m subplots, for a total of 320 subplots (four species \times four communities \times five propagule sizes \times four replications) per site. The relatively small subplot size was chosen due to limited seed availability, which precluded using larger sizes at the same density. We understand the small subplot size has possible implications for safe site limitation and edge effects. Each plot was randomly assigned a propagule size and plant community, and each subplot was randomly assigned a target invader. Seeds were evenly distributed across each subplot on May 20, 2013. The number of emerged individuals (used to calculate establishment probability) and height of the tallest individual were recorded every 2 weeks until late August when all species had flowered.

Analysis

We used a GLMM with a complementary log–log link to estimate effects of invader traits, propagule size, and community composition on invasion pressure (Y), defined as the probability of at least one individual established by the conclusion of the study in August. This model was chosen because of its heuristic value compared with the model shown in Eqn (4), which is its binomially distributed counterpart. We modelled block, nested within location, as a random effect, and location, invading species guild (grass/forb), seed mass (small/large), community (bare ground/grass-only/forb-only/full community), and propagule size (number of seeds introduced) as fixed effects. To limit model complexity, only first- and second-order terms were permitted. Propagule size was natural log-transformed to normalise the residuals and standardised ($\bar{x} = 0$, $s = 1$) to facilitate model convergence. All analyses were performed in R (v3.2). We estimated the modified invasibility parameter P' and density-dependent

parameter D from model-fitted slopes (B_1) and intercepts (B_0). From Eqn (6), $P' = e^{B_0}$ and $D = B_1 - 1$.

Results

Invasion pressure varied strongly with propagule size among guilds and communities (Table 2 and Fig. 1). Across all species, the large-seeded broad-leaved *A. theophrasti* had the highest establishment probabilities in all communities (Fig. 1), with the fewest seeds needed to ensure high establishment probability, sometimes lower by two orders of magnitude compared with the other invaders (Table 3). Interestingly, three of the four invaders had the highest invasion pressure in the grass community, even compared with the competition-free bare ground environment (Fig. 1 and Table 3). This was particularly true for the grasses, which would need orders of magnitude fewer seeds to establish in the grass versus forb communities. In contrast, *A. theophrasti* had near-identical establishment probabilities in both communities (Table 3). Despite the fact that the small-seeded *A. retroflexus* had a seed mass nearly 50% smaller than the small-seeded grass *D. sanguinalis*, the forb had higher invasion probabilities than either grass (Fig. 1). It is clear that mixed communities with both grasses and forbs are more resistant to invasion (i.e., require more seeds to ensure establishment) than single functional group communities (Fig. 1 and Table 3). In our study system, the forb leaf only community was more resistant to invasion than the grass-only community, although in both cases the larger seeded species did better (Table 3). The estimated propagule sizes needed for establishment in Table 3 should be interpreted with caution with values above 10 000, which was the upper limit of the values empirically tested and where the statistical models are extrapolated. Additionally, *A. theophrasti* achieves much higher establishment probabilities and required fewer seeds to achieve establishment than either grass, regardless of community composition; this is probably a function of the very large seed mass (Tables 1 and 3 and Fig. 1).

We used Eqn (6) to estimate the invasibility term, P' , which is the establishment probability of a single propagule. Estimates of P' show clear species and community effects across the range of propagule sizes examined (Fig. 2 and Table 3). In all cases, P' was highest in bare ground plots than in other plots, although P' was also high in the grass-only plots. Forb-only and full-community plots had similarly low P' . Counterintuitively, the two small-seeded species had much higher estimates of P' than large-seeded species, suggesting that small-seeded species may be able to establish at much lower seed densities than large-seeded species.

Table 2 Results of the GLMM of invasion pressure. Log-likelihood tests were performed for each factor. For community type, estimates of each planned contrast are also shown along with z -values and P -values estimated by Laplace approximation. We base our inference on the planned, orthogonal contrasts and report significance of main and interaction effects of community type for reference only

	χ^2	$B \pm SE$	z	P
Site	5.05			0.0801
Community type	146.09			<0.0001
Community (broadleaf)		-1.645 \pm 0.395	-4.16	<0.0001
Community (grass)		-0.175 \pm 0.329	-0.53	0.5944
Community (full)		-1.466 \pm 0.38	-3.85	0.0001
Invader guild (grass/forb)	87.82			<0.0001
Invader seed mass (Lg./Sm.)	53.29			<0.0001
Propagule size (num. seeds)	423.42	1.692 \pm 0.202	8.38	<0.0001
Community \times guild	41.38			<0.0001
Broadleaf \times forb		0.936 \pm 0.388	2.41	0.0158
Grass \times forb		-0.982 \pm 0.343	-2.86	0.0042
Full \times forb		0.419 \pm 0.365	1.15	0.2514
Community \times seed mass	2.50			0.4749
Broadleaf \times small		-0.682 \pm 0.368	-1.85	0.0638
Grass \times small		0.149 \pm 0.348	0.43	0.6687
Full \times small		-0.308 \pm 0.363	-0.85	0.3955
Community \times propagule size	6.68			0.0829
Broadleaf \times prop. size		0.208 \pm 0.23	0.90	0.3658
Grass \times prop. size		0.572 \pm 0.218	2.62	0.0087
Full \times prop. size		-0.08 \pm 0.209	-0.38	0.7003
Guild \times seed mass	15.27			<0.0001
Guild \times propagule size	0.28			0.5992
Seed mass \times propagule size	26.39			<0.0001

The density dependence parameter D was consistently negative for all species and in all communities, and estimates of this parameter were not significantly different among communities or between guilds (Table 2). However, D did vary between large- and small-seeded invaders (Table 3), with small-seeded species experiencing intense density dependence (mean $D = -0.680$) relative to large-seeded species (mean $D = -0.437$). As a result, while small-seeded species had higher establishment probabilities at low planting densities (evidenced by their high P'), large-seeded species had a much higher establishment probability than small-seeded species at high propagule densities. As a result, the large-seeded species *U. platyphylla* and *A. theophrasti* imposed a relatively even invasion pressure over a large range of propagule sizes.

Our mathematical models assumed that the log of the per-capita establishment probability (P) varied linearly with log-propagule size (N). We input estimates of D and P' into Eqn (4) to estimate P given a binomial distribution, and plotted this against observed per-capita emergence (Fig. 2). There did appear to be a negative, linear relationship between log-propagule size (N) and log-individual establishment probability (P). In other words, as more seeds were introduced, the probability of establishment of each individual seed was proportionally reduced with increasing propagule

size, which has been found in a variety of species (Antonovics & Levin, 1980). Because this relationship was linear on the log-log scale, over the range of propagule sizes used in this study, an increase in propagule size led to massive decreases in *per-capita* establishment probability. For *A. theophrasti*, P generally varied by around one order of magnitude between 10 and 10 000 seeds, while all other species often varied by 2–4 orders of magnitude (Fig. 2). Both large-seeded species had lower reductions in P across N . In all cases, P decreased with increasing propagule size and generally more steeply in communities more resistant to invasion. The relationship between N and P was difficult to evaluate statistically due to strong zero inflation (because very low per-capita survival probabilities can only be measured with very high sample sizes).

Following the discovery that P has a negative relationship with N , and is not constant as currently modelled (Leung *et al.*, 2004; Davis, 2009), we modelled the consequences of three scenarios. We compared the modelled invasion pressure when P was allowed to vary under three scenarios: 1) using a constant P (after Davis, 2009); 2 & 3) where P equalled either the maximum or minimum value estimated using Eqn (4) (corresponding to $N = 1$ and 10 000, respectively, from Fig. 2). Under these scenarios, a high, constant P

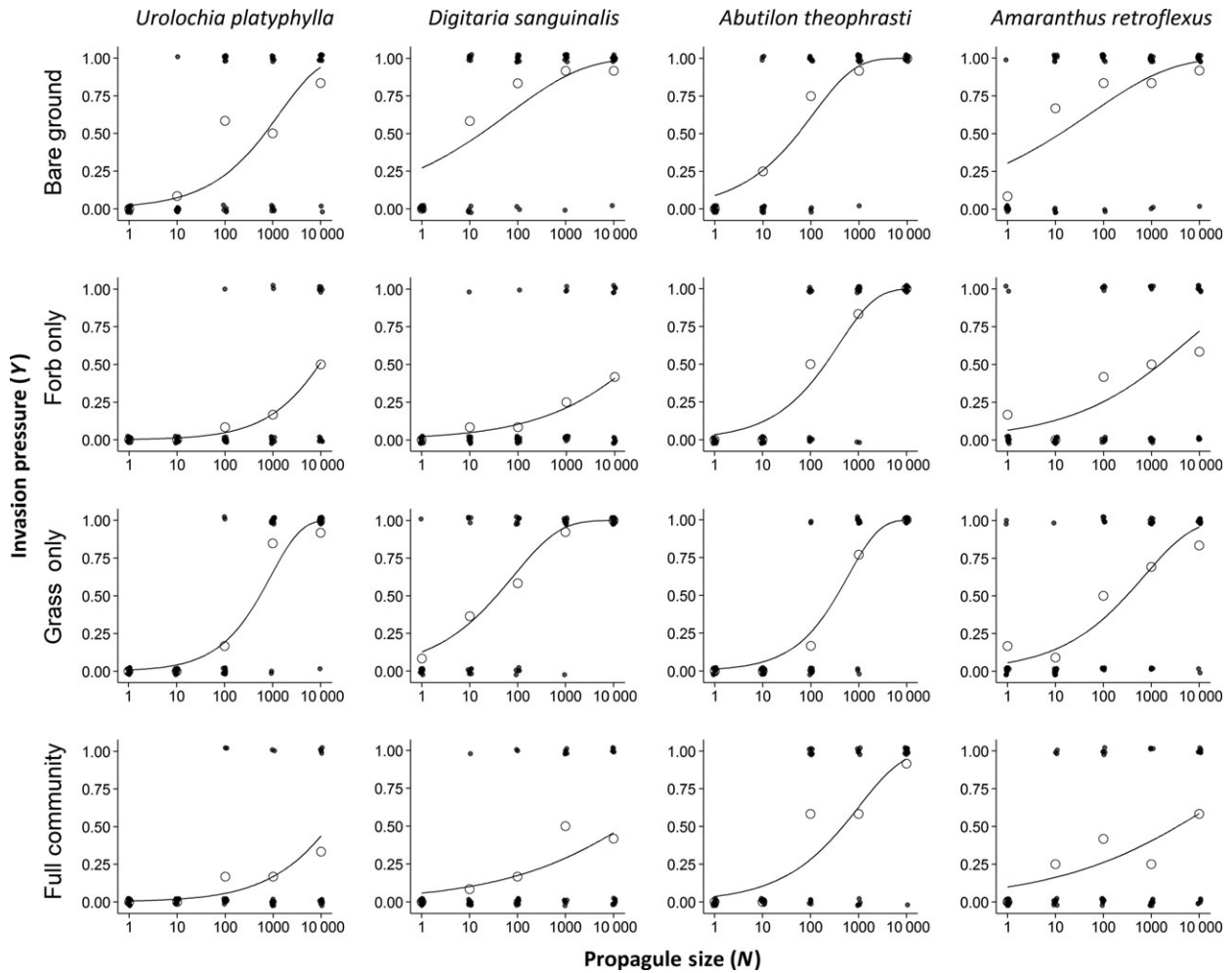


Fig. 1 Establishment of all four species (columns) in all four communities (rows) across the range of propagule sizes. Line depicts the GLMM predictions. Closed circles are the actual establishment data, and open circles show treatment averages.

Table 3 Predicted propagule size to achieve 10, 50, 95, and 99% probability of invasion success based on GLMM estimates and estimates of the establishment probability for a single seed for each species (P') and the density-dependent parameter (D) in each community

Species	Receiving community	Guild	Seed size	Invasion pressure				P'	D
				10%	50%	95%	99%		
<i>Urochloa platyphylla</i>	Bare ground	Grass	Large	18	679	11 370	26 023	0.023	-0.481
	Forb only	Grass	Large	366	9251	113 796	237 860	0.003	-0.417
	Grass only	Grass	Large	36	541	4446	8255	0.009	-0.305
	Full community	Grass	Large	321	14 460	278 770	664 915	0.006	-0.506
<i>Digitaria sanguinalis</i>	Bare ground	Grass	Small	0	17	3405	16 143	0.317	-0.724
	Forb only	Grass	Small	88	22 271	1 645 247	5 822 889	0.023	-0.660
	Grass only	Grass	Small	1	36	923	2 391	0.137	-0.548
	Full community	Grass	Small	9	16 516	5 545 748	30 622 454	0.060	-0.749
<i>Abutilon theophrasti</i>	Bare ground	Forb	Large	1	54	1006	2381	0.095	-0.501
	Forb only	Forb	Large	7	203	2733	5865	0.035	-0.437
	Grass only	Forb	Large	22	352	3080	5824	0.013	-0.325
	Full community	Forb	Large	9	472	10 308	25 508	0.037	-0.526
<i>Amaranthus retroflexus</i>	Bare ground	Forb	Small	0	13	3815	20 428	0.362	-0.744
	Forb only	Forb	Small	4	1476	142 841	547 248	0.067	-0.680
	Grass only	Forb	Small	4	304	9024	24 425	0.059	-0.568
	Full community	Forb	Small	1	3524	1 959 022	12 544 500	0.105	-0.769

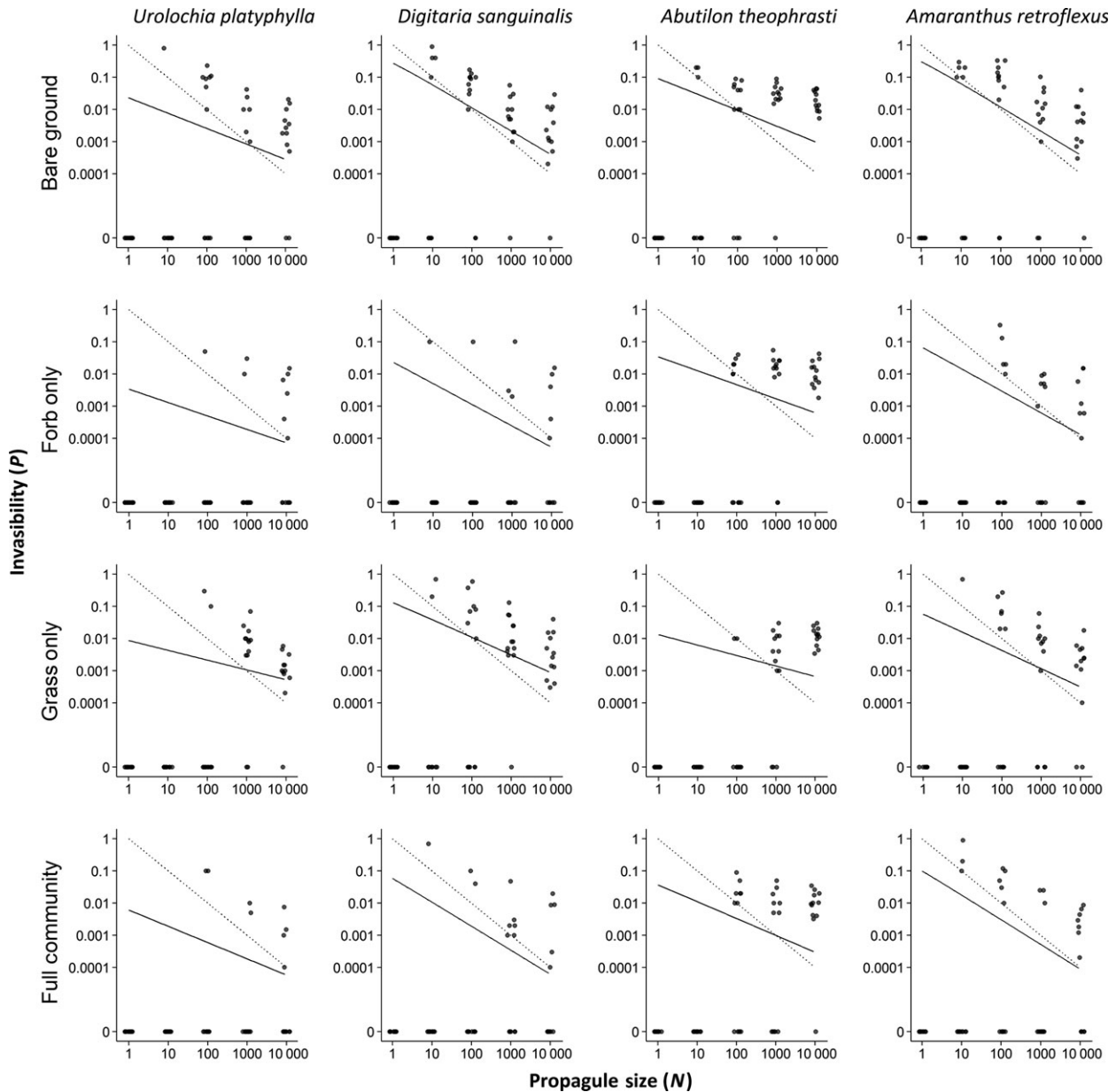


Fig. 2 Invasibility, P , of all four species (columns) in all four communities (rows) across the range of propagule sizes estimated from GLMMs (see Fig. 1). Points are observed per-capita emergence probabilities. The predicted value of P (solid line) is estimated from Eqn (2), using P' and D estimated by GLMM. A negative slope for this line means that germination is inhibited at increasing density. Note that this line often falls below the plotted cloud of points. This is because P is impossible to measure directly when it falls below $1/N$ (indicated by the dotted line). Any point falling below the dotted line will instead 'snap' to the x -axis. Thus, the solid line shown in the figure lays between observed values of P (above the dotted line) and estimated, non-zero values of P too small to be observed directly (below the dotted line). Observable values of P appear to show the predicted power relationship with N .

gives very high invasion pressure (probability of at least one individual establishing) with low propagule sizes, while a low, constant P results in a very low invasion pressure up to 1000–10 000 seeds (Fig. 3). Both scenarios with constant P produced an 'invasion cliff' (sensu Davis, 2009), an amount of log-scaled propagule input beyond which invasion pressure dramatically increased. In contrast, when P was allowed

to vary with N , invasion pressure grew more gradually as N increased. These results show that negative density dependence homogenises invasion pressure over a large range of propagule inputs.

We further explored the consequences of density-dependent establishment by modelling scenarios in which we held P' constant and varied D (Fig. 4). We varied D as 0 (assumes no relationship), -0.25 , -0.5 ,

-0.75 , and -1 . Under these scenarios, the constant P ($D = 0$) showed the classic ‘invasion cliff’ for invasion pressure, and when $D = -1$ P was constant across all propagule sizes (dotted line in Fig. 4). For slopes of -0.25 , -0.5 , and -0.75 , the invasion pressure was slightly higher than when the slope was 0 at low N , but then had a much lower invasion pressure at higher N .

Discussion

Propagule pressure, or the number and frequency of arriving individuals, plays a central role in plant invasions (Lockwood *et al.*, 2005; Simberloff, 2009). However, the actual role of propagule pressure in inva-

sions is determined by both the traits of the arriving species and the biotic and abiotic factors of the receiving habitat (Catford *et al.*, 2009). Davis (2009) explored this relationship by defining a simple model in which the probability of invasion success depends on both the propagule size and invasibility in equal measure. This model predicts that increases in propagule size lead to exponential increases in invasion probability, producing an ‘invasion cliff,’ a point beyond which log-scale increases in propagule size produce a sudden, dramatic increase in the probability of a successful invasion beyond a critical propagule size. However, this model assumes that *per-capita* establishment probability is constant for all propagule sizes (number of propagules in an introduction event). We have

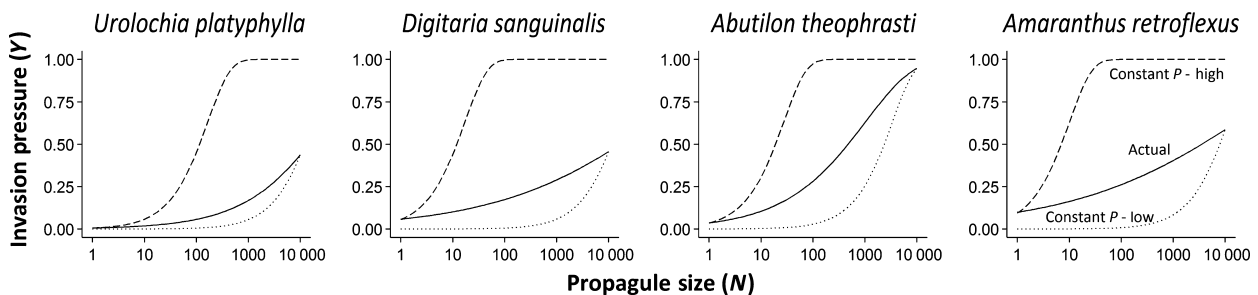


Fig. 3 Invasion pressure under three scenarios of invasibility (P), which is an integration of traits of the invading species and the receiving community. P is generally considered to be constant, and here we show the resulting invasion probabilities with P as the high (dashed line) or low (dotted line) from Fig. 2, while the solid line shows P as it varies (decreases linearly with log–log–propagule size).

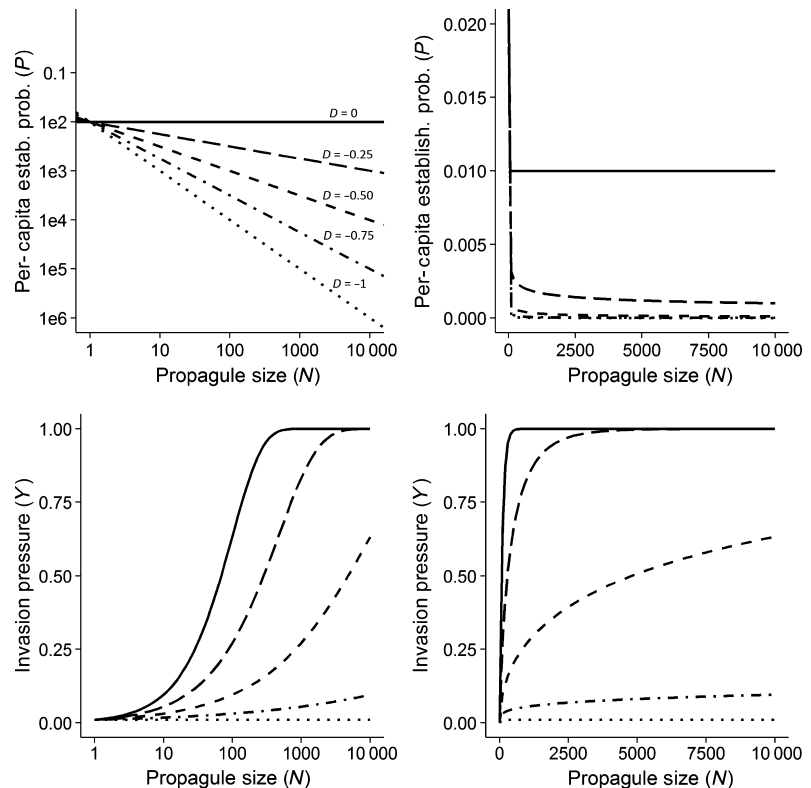


Fig. 4 Effects of variation in D on invasibility (P) (top row) and invasion pressure (Y) (bottom row) across five orders of magnitude in propagule size (N) in log (left panels) and linear (right panels) scales when the slope and intercept of P by N vary. In all cases, P was held to be 0.001 when $N = 100$ by also varying P' . For either graph, the black line is where $D = 0$ (Davis, 2009). Lines show different values of D : -0.25 , -0.5 , -0.75 , and -1 .

developed a generalisation of Davis's model that allows *per-capita* establishment to vary with propagule size; that is, we account for negative density dependence, which is a common population process (Westoby, 1984). Our results suggest that negative density dependence results in a 'smoothing out' of the invasion cliff. This makes the invasion pressure more uniform over a wider range of propagule sizes. It also means that much higher propagule sizes might be needed to promote invasion of more resistant communities.

This is in direct contrast with Davis (2009) description of the invasion cliff, in that an increase in the number of arriving propagules can easily overcome invasion-resistant communities. In other words, the original invasion cliff predicts that a 10-fold decrease in invasibility can be overcome with an equivalent 10-fold increase in propagule size. Suitable habitats (i.e., those that present non-limiting biotic and abiotic conditions to a particular species) that have relatively high invasion resistance could therefore be successfully invaded with a proportional increase in propagule pressure. However, our results suggest that, due to negative density dependence, orders of magnitude larger increases in propagule size are needed to overcome a given decrease in invasibility. In other words, the invading species achieves marginal returns on the investment of large seed numbers (large propagule size) in a given area, especially when density-dependent inhibition is strong. For some of our species, *per-capita* establishment probability dropped by several orders of magnitude over the sampled range of propagule pressure. Increases in propagule pressure were therefore associated with severely diminishing returns. Of course, our findings are limited to the relatively narrow range of species, functional traits, and communities we examined.

As a result of negative density-dependent establishment, very high propagule sizes may be required to ensure establishment, although in our study this was strongly influenced by functional traits. Plant functional traits are known to have strong effects on invasion success (Drenovsky *et al.*, 2012) and are widely studied to explain invasiveness (van Kleunen *et al.*, 2010). Functional traits that promote invasiveness also vary with the stage of invasion (Pyšek & Richardson, 2007), as the exotic species continually encounters new barriers to success at each stage (Theoharides & Duker, 2007). For example, traits related to dispersal and establishment will have the greatest impact during the early stages of invasion, while in later stages traits related to resource capture and fitness will promote invasiveness. For example, the very large-seeded *A. theophrasti* required the smallest propagule size for all communities to ensure successful invasion, with an

estimated 32 000–408 000 seeds m^{-2} (>99% invasion probability; Table 2). Mature *A. theophrasti* produce 700–17 000 seeds per plant (Warwick & Black, 1988), most of which likely disperse very near the mother plant due to a lack of obvious dispersal adaptations. This high seed density presents a trade-off to the invader, as our results suggest that *per-capita* establishment decreases exponentially with increasing seed density (Figs 3 and 4).

Our system of early-successional post-agricultural communities was primarily composed of fast-growing annuals, such as *Setaria* spp., *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl., *Acalypha virginica* L., *Conyza Canadensis* (L.) Cronquist, and *Lactuca seriola* L.. The invaders we introduced, *A. theophrasti*, *A. retroflexus*, *D. sanguinalis*, and *U. platyphylla*, commonly co-occur with this suite of species, often with patchy distributions that result from the interaction of seed dispersal, environmental variation, and management practices (Cardina *et al.*, 1997). None of the invaders in this study have any obvious dispersal adaptations and are thus more likely to be dispersed close to the mother plant in high densities. We only tested two species within each guild and seed mass, limiting generalisations, but we demonstrate that seed mass has played a strong role in invasion success for the species in this study.

The functional composition of the receiving community strongly affected the establishment success of the invaders in our study. We hypothesised that receiving communities that shared functional groups with the invader would present higher invasion resistance (grass-only communities would more strongly resist grass invaders). Gooden and French (2014) found that the invasion of a stoloniferous grass had the strongest impact on functionally similar native species, likely due to niche overlap, so-called limiting similarity hypothesis (MacArthur & Levins, 1967). However, evidence for limiting similarity in general is equivocal (Emery, 2007) and may be explained by narrow interpretations of functional groups or niches, phylogenetic distance, or introduction effort (Strauss *et al.*, 2006; Diez *et al.*, 2009). Our data also did not support the limiting similarity hypothesis. In fact, contrary to our predictions, grasses had the highest invasion pressure in grass-only communities, even higher than when there was no competition. Similarly, the *per-capita* establishment probability (P) was highest across the range of propagule sizes for grasses in grass-only communities. The full community (resident grasses and forbs) had the highest invasion resistance across all three invaders, with the forb-only community having roughly similar invasion resistance. This pattern was repeated in forbs, suggesting that in our system, knowledge of the resident plant

community itself carried more information than knowledge of its functional similarity to the invading species.

The functional traits of the invader and the community of the receiving location influence invasion success, but to our knowledge, no other studies have explicitly examined this relationship across a range of propagule sizes. Here we showed that invasion pressure, or the probability of at least one propagule establishing, varies among species and plant communities. Further, we found that density dependence was intense and varied among functional types, and probably played a major role in the relationship between propagule pressure and invasibility of old-field plant communities. Our results suggest that negative density dependence causes severe diminishing returns with increased propagule density, and increased propagule pressure may not readily overcome communities with low invasibility (or high resistance). As a result, site characteristics may play a much more important role in limiting invasion than previously supposed. More research is needed to understand how density-dependent inhibition of invasive plants influences the role of propagule pressure in determining the final outcome of invasion including testing additional species and functional traits.

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