

LETTER

Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment

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Abstract

Much uncertainty remains about traits linked with successful invasion – the establishment and spread of non-resident species into existing communities. Using a 20-year experiment, where 50 non-resident (but mostly native) grassland plant species were sown into savannah plots, we ask how traits linked with invasion depend on invasion stage (establishment, spread), indicator of invasion success (occupancy, relative abundance), time, environmental conditions, propagule rain, and traits of invaders and invaded communities. Trait data for 164 taxa showed that invader occupancy was primarily associated with traits of invaders, traits of recipient communities, and invader-community interactions. Invader abundance was more strongly associated with community traits (e.g. proportion legume) and trait differences between invaders and the most similar resident species. Annuals and invaders with high-specific leaf area were only successful early in stand development, whereas invaders with conservative carbon capture strategies persisted long-term. Our results indicate that invasion is context-dependent and long-term experiments are required to comprehensively understand invasions.

Keywords

Cedar Creek Ecosystem Science Reserve, ecosystem invasibility, functional traits, indicators of invasion, invasion stages, long-term grassland experiment, seed addition experiment, species invasiveness.

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INTRODUCTION

There has been a considerable research effort to identify the characteristics of successful invaders – non-resident species that can establish, become abundant and spread in communities into which they are introduced. Much uncertainty remains about traits linked with invasion. Seed mass, for example has been found to be positively, negatively and not linked at all with plant invasion (Pyšek & Richardson 2007; Catford *et al.* 2016). Acknowledging that different traits are linked with different processes of invasion (Dawson *et al.* 2009; Blackburn *et al.* 2011), recent work has highlighted the importance of considering both the stage of invasion (e.g. colonisation, survival, naturalisation, dominance; Dawson *et al.* 2009; Moravcová *et al.* 2015; Divíšek *et al.* 2018) and the type of invasion (e.g. wide geographic range vs high local abundance; Catford

et al. 2016). These findings have led to widespread acknowledgement that the broader context of invasion – for example propagule pressure, time since invasion, resource availability, environmental conditions, biotic interactions and characteristics of recipient communities (Kempel *et al.* 2013; Carboni *et al.* 2016; Conti *et al.* 2018) – likely influences the traits that are associated with successful invaders.

Such context dependence of relationships between traits and invasion success should not come as a surprise: diversity and multi-species coexistence are commonly thought to rely on interspecific tradeoffs where no one life-history strategy is optimal under all circumstances, allowing many species to coexist (Tilman 1990; Chesson 2000). A wide diversity of life-history strategies and trait syndromes should therefore be viable across sites and systems (Tilman 2011; Díaz *et al.* 2016). This diversity does not mean that attempting to predict

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invader occupancy and abundance is futile; rather, accurate prediction requires that the context of invasion be adequately considered.

We used a 20-year seed addition experiment to ask:

- (1) How are seven traits – lifespan, growth form, N-fixing ability, specific leaf area (SLA), leaf dry matter content (LMDC), plant height, seed mass – associated with invasion of non-resident species?
- (2) Do trait-based relationships vary with time, invasion stage (establishment in seeded areas, spread to unseeded areas) and indicator of invasion success (invader occupancy, invader relative abundance when present)?
- (3) Do traits of invaders, traits of recipient communities (means weighted by abundance), or invader-community trait-based interactions best explain the occupancy and abundance of invaders in seeded and unseeded areas?

Seeds of 50 grassland plant species, hereafter ‘invaders’, were sown into grassland openings in an established temperate oak savannah at Cedar Creek Ecosystem Science Reserve in Minnesota, USA (Tilman 1997). The ~2 ha savannah has been maintained through controlled spring burns in roughly every 2 years out of three for the last 50 years, has been free of livestock for > 70 years, and has never been ploughed or cultivated. The majority of our invaders were rare or absent in plots to which they were added. Only 4 of the 50 invaders are non-native to Minnesota, reducing the relevance of issues around the transfer of species across biogeographical boundaries (e.g. enemy release; Fridley & Sax 2014; Buckley & Catford 2016). Although most invasion studies focus on exotic species, native species invasions can provide insights into the process of invasion and importance of context (e.g. Tilman 1997; Davis & Pelsor 2001; Mwangi *et al.* 2007). We used trait data, collected locally, to characterize 164 resident and invader taxa that were observed in the 20-year experiment. The seven study traits were selected based on hypothesised relationships with invasion success (see Appendix S1 for rationale).

METHODS

Study design

Cedar Creek (45.4° N, 93.2° W) has nitrogen-limited sandy soils, annual precipitation of ~770 mm, mean summer temperatures of 27 °C, and winter lows of –14 °C. In August 1991, 30 2 m × 2 m permanently marked plots were haphazardly positioned throughout the experimental savannah (Fig. S1; 45.397° N, 93.181° W; Tilman 1997). Each plot was divided into four 1 m × 1 m subplots, and percent cover of all vascular plant species, bare mineral soil and litter were estimated (see Appendix S3 for additional details about all methods).

In June 1992, 10 seed treatments were randomly assigned to two subplots per plot (hereafter ‘seeded subplots’, cf. ‘unseeded subplots’, Fig. S1). These involved the addition of no species (a control), 5, 10, 15, 20, 25, 30, 35, 40 and 54 species (Fig. S1). There were six replicates per treatment, with combinations of species in each replicate randomly

drawn from a pool of 54 total species. 4.5 g m⁻² seeds of each species were added. Seeds were gathered on site or obtained from a local company (Prairie Restorations, Minnesota).

After 1991, subplots were surveyed eight times using the same method as in 1991. 164 plant taxa were recorded across all subplots and years, of which 85 were observed in 1991, prior to seeding (Table S1, Fig. S2). Fifty-four non-sown taxa colonised the subplots naturally after 1991, but high turnover meant that some of these gains were offset by losses (total plant richness varied from 84 species in 1992 to 113 species in 2012). Our analytical approach accounted for the changing recipient community by updating the community each time-step, such that community changes would not have affected our findings.

Twenty-seven of the sown species were present in at least one plot in 1991. To account for this, sown species were considered *target invaders* only if they were absent from a given 2 m × 2 m plot in 1991, before seed addition. We define the *recipient community* as all species present in a given subplot at a given point in time (whether sown or not), excluding the target invader. Two sown invaders that were never observed (*Symphytotrichum novae-angliae* and *Mimulus ringens*) were excluded from analysis. We treated the two sown woody species (*Celastrus scandens* and *Rosa arkansana*) as members of recipient communities because our focus was on invasion of herbaceous species. Of the 50 resulting target invaders, 46 are native to MN, 43 are perennial, 12 are grasses (Poaceae), 10 are leguminous forbs (Fabaceae) and 28 are non-leguminous forbs (Table S1).

Four soil cores (20 cm deep, 2.5 cm diameter) were collected in each plot in 1991, extracted with 0.01 M KCl, and analysed to give extractable soil nitrogen (NO₃) concentration and soil moisture (Tilman 1997). Although only for a single year, these variables were used to indicate local environmental conditions: they corresponded with site topography, which ranged from drier, elevated, nutrient-poor soils, to low-lying, occasionally saturated soils that were comparatively nitrogen rich (correlation between elevation at 5 m × 5 m resolution and: soil moisture, $r = -0.570$; soil NO₃, $r = 0.462$).

Plant traits

We classified all taxa based on lifespan (annual and biennial OR perennial), growth form (grass OR forb) and ability to fix nitrogen (legume OR non-legume) (Tilman 1997; USDA-NRCS 2018; Table S1).

In the summers of 2014 and 2015, we measured maximum vegetative height, LDMC and SLA of 143 taxa growing naturally at Cedar Creek following Pérez-Harguindeguy *et al.* (2013). Dried seed masses were determined from plants at Cedar Creek or from local suppliers (Prairie Moon, Prairie Restorations). These measurements provided numerical trait data for 96.3% of the vegetation cover in all subplots across all years. Of 570 species-trait measurements used in the study, 531 were measured on plants < 1 km of the study site; 30 used means of congeneric or confamilial species at Cedar Creek (Table S2); and 9 were from Kew Seed Information Database (Liu *et al.* 2008).

We examined five forms of each individual numerical trait (Fig. 1), which we hypothesised would relate to occupancy and abundance in different ways (Appendix S1):

- (i) *Invader* mean trait value indicates the intrinsic invasiveness of invaders (van Kleunen *et al.* 2010; Richardson & Pyšek 2012).
- (ii) *Community-weighted mean* (CWM) trait value, calculated as mean trait value weighted by proportional cover, indicates recipient community's intrinsic invasibility (Richardson & Pyšek 2012).
- (iii) *Invader-community hierarchical distance* ($\overline{Invader - Community}$) indicates relative difference between invader and CWM traits. Depending on context, higher (e.g. height) or lower (e.g. SLA in resource-limited plots) hierarchical distance can indicate when invaders have higher fitness than recipient communities (Lai *et al.* 2015).
- (iv) *Invader-community dissimilarity*, or absolute trait distance ($|\overline{Invader} - \overline{Community}|$), indicates net differences between invader and CWM traits (similar to Lai *et al.* 2015). This may relate to the extent of environmental sorting (trait underdispersion) or niche differentiation (trait overdispersion).
- (v) *Invader-community gap size*, calculated as the difference between trait values of resident species that fall immediately above and below invaders' trait values ($\bar{a} < i < \bar{b}$; gap size = $\bar{b} - \bar{a}$; Fig. 1), indicates potential degree of niche differentiation between invaders and their nearest 'functional neighbours' in recipient communities (similar to Gallien *et al.* 2014).

Statistical analyses

Four response variables of invasion

We used hierarchical linear regression models to identify variables associated with invasion of non-resident species (Jamil *et al.* 2012; Pollock *et al.* 2012). We examined two indicators of invasion success (occupancy and abundance) at both of two stages of invasion (establishment and spread), giving four response variables in total. All analyses relate to standing live vegetation.

Occupancy was the presence or absence of a target invader in seeded subplots (for establishment) or unseeded subplots (for spread).

Relative abundance was the proportion of total vascular plant cover in seeded subplots (for establishment) or unseeded subplots (for spread) made up of the target taxon when it was present (Catford *et al.* 2012).

Establishment (sensu Blackburn *et al.* 2011) encompasses recruitment and/or survival and/or reproduction in the site of introduction. Establishment was defined as a target invader's occupancy or abundance when present in the subplots into which they were sown, calculated for each survey year (Fig. S1b). Establishment therefore reflects both successful invasion, and the dynamics of establishment and persistence, because an invader could be present, absent and present again in subsequent years.

Spread (sensu Blackburn *et al.* 2011) encompasses dispersal and establishment beyond the site of introduction – albeit only over a short distance in our study. Spread was defined as a target invader's occupancy or abundance when present in unseeded

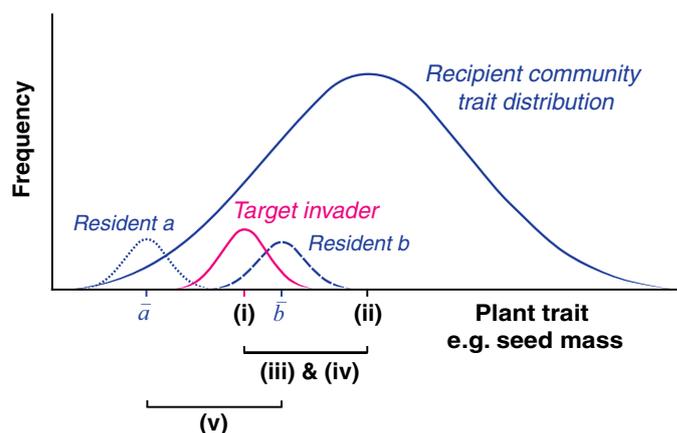


Figure 1 Sketch showing the five trait forms linked with our hypotheses of invasion success that relate to invader traits, community traits, and invader-community trait-based interactions (see Appendix S1 for rationale of predictions). The solid blue line shows the hypothetical distribution of trait values for the recipient community, the dashed blue lines indicate trait values for two species in the recipient community (Residents a & b), and the pink line shows the trait distribution of a target invader. (i) *Invader trait* indicates the 'intrinsic invasiveness' of the target invader, represented by mean trait value across individuals of the target invader; (ii) *Community-weighted mean* (CWM) trait value indicates recipient community's 'intrinsic invasibility', calculated as mean trait value weighted by proportional cover; (iii) *Invader-community hierarchical distance* indicates whether invaders had a higher or lower trait value than the CWM of recipient communities, and the magnitude of this difference ($iii = i - ii$); (iv) *Invader-community dissimilarity* (absolute trait distance) indicates how different the invader is to the community regardless of the direction of that difference ($iv = |i - ii|$); (v) *Invader-community trait gap size* indicates the degree of niche differentiation between the invader and its nearest 'functional neighbours', calculated as the difference between the trait values of the resident species that fall immediately above and below the invader's trait value in the recipient community ($v = \bar{b} - \bar{a}$).

subplots that were adjoining seeded subplots in which invaders had established (Fig. S1b). As such, spread includes both vegetative and seed-mediated expansion of target invaders. Because the spatial arrangement of the subplots within plots meant invaders in unseeded subplots could have arrived from either of the seeded subplots, spread was analysed at the plot level (30 plots), combining data from both unseeded subplots (Fig. S1).

Regression model structure

In all models: Species traits and year were included as fixed effects (Table 1, Appendix S2). For each numerical trait (plant height, LDMC, SLA, seed mass), we used each of the five trait forms as regressors (labelled i to v in *Plant traits*, above, Fig. 1). For each categorical trait (lifespan, growth form, legume), we ran models that included (i) invader trait category only, (ii) proportional cover of that trait category in recipient community only, and (iii) interactions between invader and proportional cover in community. We included target invaders and plot (for spread) or subplot nested within plot (for establishment) as random intercept terms to account for similar responses within invader species and for repeated measurements respectively. By including year as a fixed effect, we explicitly modelled temporal trends in trait interactions. The random intercepts accounted for repeated measurements within plots and subplots (Pinheiro & Bates 2000).

In establishment models for both occupancy and abundance: we included the total number of other invader species sown into each subplot to account for potential interactions among invaders and their seed rain. We represented environmental conditions with variables indicating soil moisture (range = 2.49–16.46%) and soil nitrate concentration (range = 0.013–1.85 mg kg⁻¹), both of which were measured in 1991 only. We allowed the slope of the NO₃ term to vary (as a random effect) by species, as this is a primary limiting resource at our site, and species-level responses to NO₃ are known to vary greatly (Tilman 1997). We did not fit fixed effect estimates by species because we lacked sufficient power.

In spread models for both occupancy and abundance: we used cumulative abundance of target invaders in seeded subplots from each survey year and all previous surveys to indicate potential cumulative seed rain into unseeded subplots. Preliminary analyses indicated that environmental variables were not significantly related to spread, so we did not consider them further.

Probability of occupancy was modelled using binomial generalized linear mixed models in the lme4 package (Bates *et al.* 2013) in R version 3.5 (R Core Team 2014). Abundance data were zero-inflated, so we modelled *abundance conditional on presence* (i.e. removed zeros) and used mixed-effects beta regression in the glmmADMB R package (Fournier *et al.* 2012; Skaug *et al.* 2013). All models used a logit link function. Apart from year, which was coded as an integer varying from 0 (1992) to 20 (2012), all non-binary numeric variables were centred and scaled (Appendix S6). For details on models and convergence criteria, see Appendices S2, S3, S4 and S6.

Model selection

To identify the ‘best’ regression forms, we conducted model selection in two steps. In Step 1, we compiled a series of models that varied in structure and complexity (Appendix S2). We did not mix trait forms in Step 1, so we had five subsets of models – one for each trait form. We used the structure of the top-ranked model for each response variable from Step 1 as our template for models analysed in Step 2. Into that

template, we sequentially substituted different trait forms that had important effects in Step 1. We considered trait forms important if they were significantly related ($P < 0.05$) to response variables in the top-ranked model from each of the five model subsets analysed in Step 1. The models in Step 2 could potentially include different forms for different traits (e.g. SLA hierarchical distance and CWM seed mass), but only one form of each trait was used in each model (e.g. CWM SLA was never used with invader SLA); this was because different trait forms were highly correlated, and so we could identify trait forms that best explained invasion-thereby addressing Question 3.

We ranked all models using Bayesian Information Criterion (BIC, Jones 2011). We considered all models that differed in BIC from the best-supported model by ≤ 5 to have support from the data (Hegyi & Garamszegi 2011). We present results of the best-supported models in the main paper and all models with $\Delta\text{BIC} \leq 5$ in Fig. S3. We considered effects of explanatory variables to be significant if 95% confidence intervals did not cross zero in at least one of the models with $\Delta\text{BIC} \leq 5$. We calculated marginal and conditional R^2 values for the occupancy models to indicate variance explained, respectively, by fixed and random effects, and by fixed effects only (Nakagawa & Schielzeth 2013). We could not calculate R^2 values for the abundance models because there is currently no available method for mixed-effect beta regression (Nakagawa *et al.* 2017; Nakagawa, pers. comm, Nov. 2017).

RESULTS

General trends

Relative abundance of invaders increased with time in seeded subplots and in unseeded subplots (Figs 2m and 3h). Invaders that established and accumulated high abundance in seeded subplots over the duration of the experiment were highly likely to spread to, and reach high abundance in, adjacent unseeded subplots (Fig. 3a,i).

Table 1 Main explanatory variables considered (= ‘yes’) in occupancy and abundance models for invader establishment in seeded subplots and invader spread into unseeded subplots

Variable	Description	Variable type	Establishment	Spread
Year	Survey year	Temporal	Yes	Yes
No_seeded	Number target invader species added to given subplot	Propagule pressure	Yes	No
Seeded subplot abundance	Seeded subplot cumulative abundance	Propagule pressure	No	Yes
Moisture	Soil moisture in 1991	Environmental	Yes	No
Soil NO ₃	Soil NO ₃ concentration in 1991	Environmental	Yes	No
SLA	Absolute or relative specific leaf area of invader and/or community	Numerical trait (5 forms)	Yes	Yes
Height	Absolute or relative height of invader and/or community	Numerical trait (5 forms)	Yes	Yes
Seed	Absolute or relative seed mass of invader and/or community	Numerical trait (5 forms)	Yes	Yes
LDMC	Absolute or relative leaf dry matter content of invader and/or community	Numerical trait (5 forms)	Yes	Yes
Prop_peren	Proportion of community cover that is perennial	Categorical trait	Yes	Yes
Prop_grass	Proportion of community cover that is grass	Categorical trait	Yes	Yes*
Prop_legume	Proportion of community cover that is legume	Categorical trait	Yes	Yes
Lifespan	Lifespan of invader (annual & biennial OR perennial)	Categorical trait	Yes	Yes
Grass	Growth form of invader (grass OR forb)	Categorical trait	Yes	Yes*
Legume	N-fixing ability of invader (legume OR non-legume)	Categorical trait	Yes	Yes

These variables were available for selection during the model selection process; *Variable included in spread-occupancy models but not spread-abundance models. A full list of specific variables is provided in Appendix S2.

The number of sown invaders was not related to establishment of target invaders, suggesting that the presence of other invaders in seeded subplots did not strongly affect invasion of individual species in our experiment.

Question 1: Traits linked with invasion success

Invader N-fixing ability, life span and growth form were linked with invader occupancy but not abundance for both establishment (seeded subplots) and spread (unseeded subplots; Table 2; Fig. 4). Legumes had higher occupancy than non-legumes when directly sown (Fig. 2l). By the end of the experiment, perennial and grass invaders had higher occupancy than annuals and forbs in both seeded and unseeded subplots (Figs 2j,k and 3c,g).

Recipient communities with higher perennial cover had higher invader occupancy and abundance in seeded subplots (Fig. 2d,o), but the opposite was true for invader abundance in unseeded subplots (Fig. 3l). Invader abundance was higher in seeded subplots with low proportional legume cover (Fig. 2p), but – in the long-term – the opposite was true in unseeded subplots (Fig. 3m).

Seed mass and LDMC had the most consistent long-term invasion trends, relating to three of our four response variables (Table 2). Apart from the first few years of invasion, invader occupancy and – in seeded subplots – invader abundance was highest in communities with heavier seeds (Figs 2h, r and 3e) and higher LDMC (Figs 2i,s and 3f), whether in absolute terms (i.e. based on CWM) or relative to invaders (i.e. based on hierarchical trait distances). SLA and plant height were associated with invasion, but trends varied over time and depending on invasion stage and indicator (discussed below).

Question 2: Trait-based relationships varied with time, invasion stage and indicator of invasion success

Factors related to invasion were not uniform across invasion stages or indicators of invasion success, and were not uniform over time (Figs 2–4, Table 2, Appendix S3).

Time: Relationships between invader occupancy in seeded subplots and invader lifespan, invader growth form and community LDMC varied over time (Fig. 2i–k). In unseeded subplots, invaders with higher SLA than recipient communities initially had higher occupancy, and invader abundance was initially higher where communities had higher SLA CWM; these trends reversed with time (Fig. 3d,j; Fig. S2).

Stage: Invaders with dissimilar heights to recipient communities (Fig. 2c) or their nearest functional neighbours (Fig. 2q) were more likely to occupy and reach high abundance in seeded subplots, respectively, but the opposite was true in unseeded subplots (except for short-term abundance; Fig. 3b,k). Invaders were more abundant in seeded subplots that had low legume cover (Fig. 2p), but – from 10 years onwards – the opposite trend was true in unseeded subplots (Fig. 3m). Invader occupancy and abundance in seeded subplots were positively related to community perennial cover (Fig. 2d,o) – in contrast to long-term abundance trends in unseeded subplots (Fig. 3l). Invader occupancy was higher

when invaders had lower SLA values than recipient communities in seeded (Fig. 2b) and unseeded (long-term only, Fig. 3d) subplots, but invader abundance was higher in unseeded subplots with low SLA communities (long-term only, Fig. 3j).

Indicator: Invader occupancy was lower but abundance higher in seeded subplots with higher initial soil NO₃ (Fig. 2a, n).

Question 3: Relative importance of invader traits, community traits, and invader-community trait-based interactions

Based on our best-supported models, invader occupancy was related to four of the five trait forms (all but gap size, Fig. 1) – albeit in different ways and via different numerical traits (Figs 2–4, Appendix S4), indicating that invader traits, community traits and invader-community interactions all influence invader occupancy. In contrast, invader abundance was related to community traits (CWM) and gap size; intrinsic invader traits were unrelated to invader abundance in any of best-supported (or competing) models (Figs 2 and 3; Fig. S3, Appendix S4).

Model performance

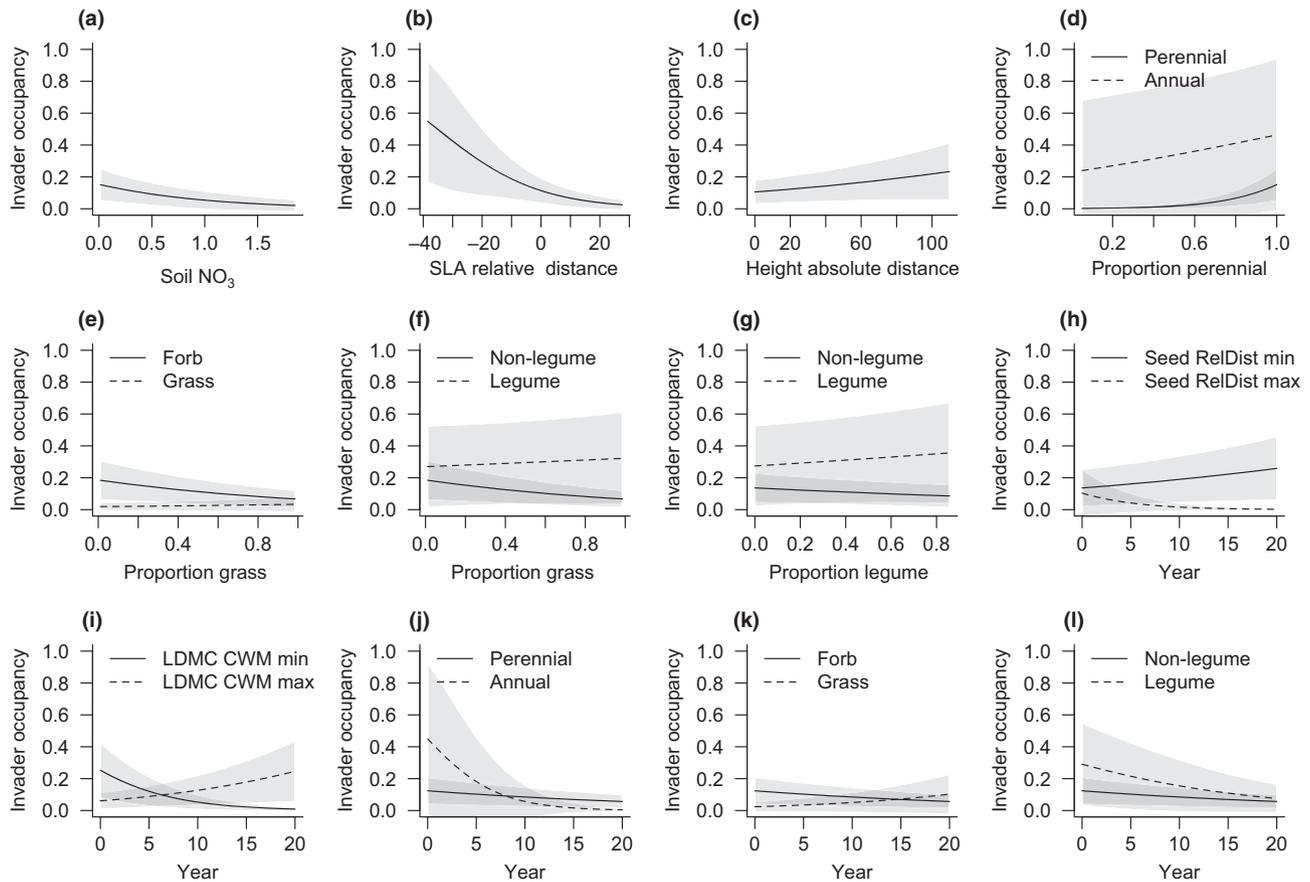
The best-supported models for occupancy in seeded and unseeded subplots accounted for about 63% and 59% of observed variance, respectively (conditional R^2), and their fixed effects accounted for 15% and 44% (marginal R^2 , Appendix S3). Results of the best model and competing models for each response variable had consistent ecological interpretations (Fig. S3, Appendix S4); the only exception was LDMC in the establishment-abundance model, suggesting that LDMC is not strongly linked with invader abundance in seeded subplots (Fig. S3b).

DISCUSSION

Our 20-year experiment showed that factors associated with invasion of non-resident species are not uniform across time, stages or indicators of invasion (Table 2, Fig. 4). Despite the variation in observed relationships, our study accords with existing theories that propagule pressure, environmental conditions, invader and community traits and their interactions, time, and indicator and stage of invasion all collectively affect invasion outcomes (Catford *et al.* 2009; Blackburn *et al.* 2011; Richardson & Pyšek 2012). All seven traits that we examined were related to at least one indicator or stage of invasion, but the strength, direction and consistency of their relationships varied. Invader occupancy was related to four trait forms, whereas invader abundance was mostly associated with CWM plus invader differentiation from functionally similar residents. We discuss the main findings to our three research questions after briefly discussing general trends.

Invaders' cumulative abundance in seeded subplots was positively associated with their occupancy and relative abundance in adjacent unseeded subplots. This was presumably because of higher propagule rain (or clonal spread) and higher

Establishment stage: invader occupancy in seeded subplots



Establishment stage: invader abundance in seeded subplots

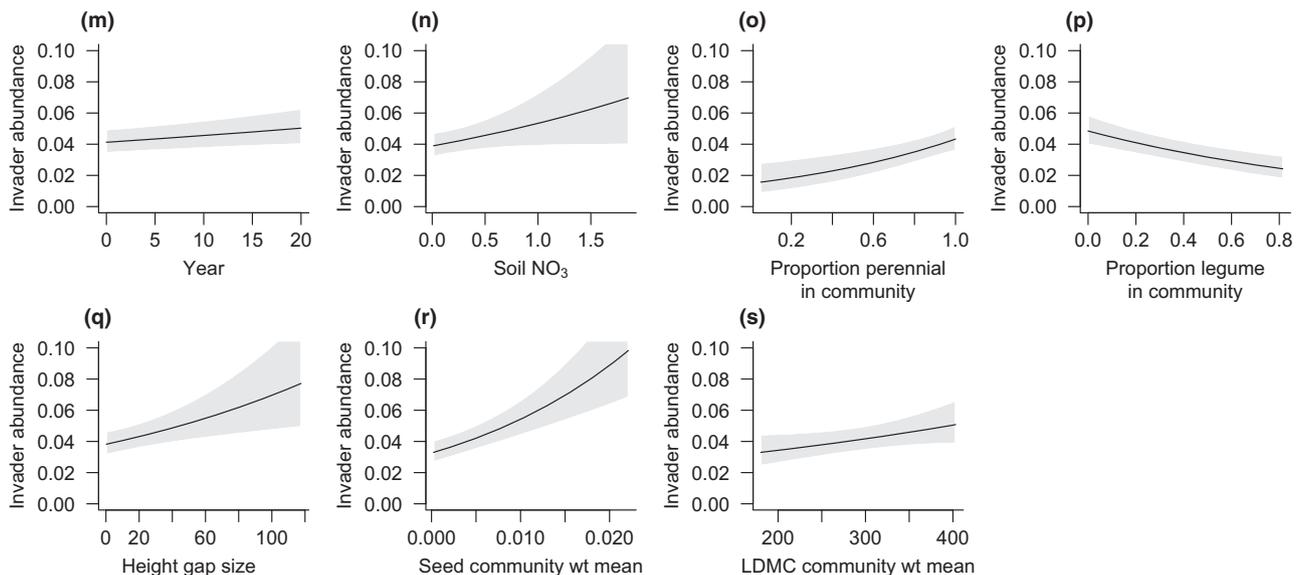
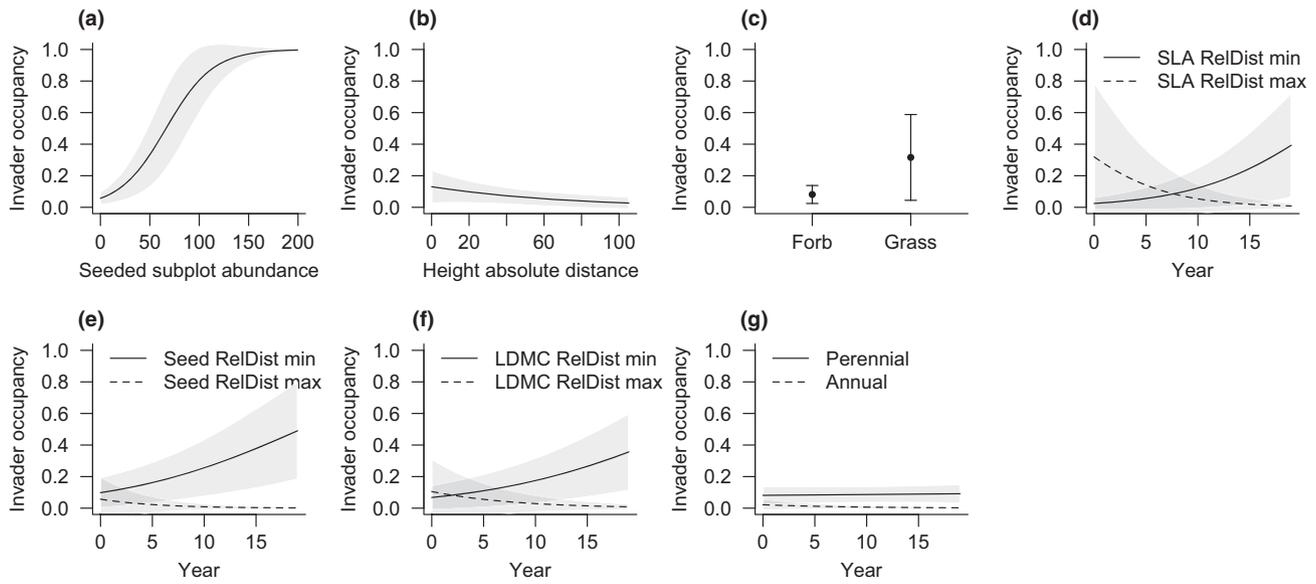


Figure 2 The establishment stage of invasion, modelled as occupancy and abundance of 50 target invaders, sown into seeded subplots. Panels show results for the best supported model for: (a–l) invader probability of occupancy (top panels); and (m–s) invader proportional abundance, conditional on presence (bottom panels); variables that were significantly related to invader occupancy and abundance are displayed. Each observation in the data represented the response of an individual invader in a given year, in a given subplot, and observations were grouped by species with a random effect. Effects of explanatory variables are shown holding all other explanatory variables in each of the two models constant, such that each response can be interpreted independently of other variables in that model. When a numeric variable interacted with another numeric variable, the response was displayed for the minimum (min) and maximum (max) values in the data. Relative distance (or RelDist) refers to hierarchical trait distance; absolute distance refers to invader–community dissimilarity (Fig 1).

Spread stage: invader occupancy in unseeded subplots



Spread stage: invader abundance in unseeded subplots

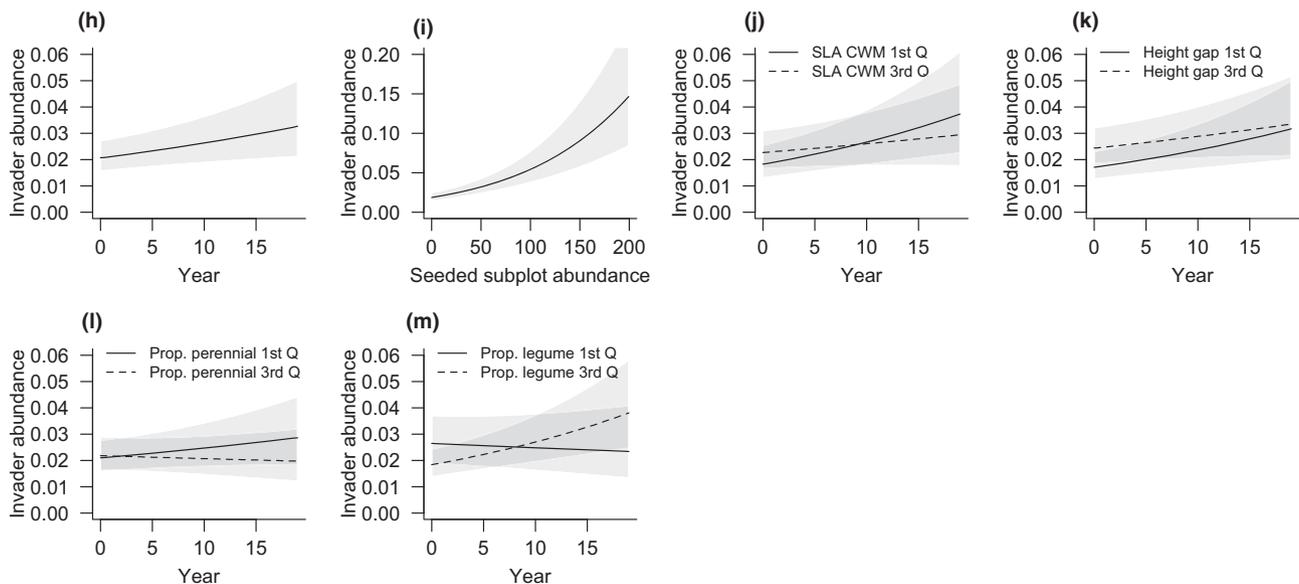


Figure 3 The spread stage of invasion, modelled as occupancy and abundance of 50 target invaders, which spread to unseeded subplots. Panels show results for the best supported model for: (a–g) invader probability of occupancy (top panels); and (h–m) invader proportional abundance, conditional on presence (bottom panels); variables that were significantly related to invader occupancy and abundance are displayed. Each observation in the data represented the response of an individual invader in a given year, in a given plot, and observations were grouped by species with a random effect. Effects of explanatory variables are shown holding all other explanatory variables in each of the two models constant, such that each response can be interpreted independently of other variables in that model. When a numeric variable interacted with another numeric variable, the response was displayed for: (d–f) the minimum and maximum values in the data (min, max); and (j–m) the first and third quartile in the data (1st Q, 3rd Q). The values at which to plot interactions were chosen based on the distribution of the data. The y -axis is displayed with a different range on panel (i). Relative distance (or RelDist) refers to hierarchical trait distance; absolute distance refers to invader–community dissimilarity (Fig 1).

suitability of the local ecological conditions for population growth. Given that abundances of invader species increased over 20 years in both seeded and unseeded areas, it not only seems likely that some invaders have formed self-sustaining populations in vicinities where sown, but also that their local population sizes will continue to increase – at least until density-dependent effects become stronger.

Question 1: Traits associated with invasion

Legumes had higher occupancy than non-legumes where directly sown (Fig. 2l), as expected (Appendix S1), but N-fixing ability of invaders was unrelated to their abundance or spread. This was a surprising result given the study system is nitrogen-limited (Tilman 1997), but previous work has shown

Table 2 Observed conditions under which the occupancy and abundance of target invaders in seeded and unseeded subplots are *highest* in the short-term (< 5 years) and long-term (> 10 years)

Invasion stage	Establishment in seeded subplots highest when...				Spread to unseeded subplots highest when...			
	Occupancy		Abundance		Occupancy		Abundance	
Invasion indicator	Short	Long	Short	Long	Short	Long	Short	Long
Short- or long-term trends	Short	Long	Short	Long	Short	Long	Short	Long
Soil NO ₃ in plot in 1991	Low	Low	High	High	NA	NA	NA	NA
Invader growth form	Forb	Grass	–	–	Grass	Grass	–	–
Invader lifespan	Annual	Perennial	–	–	Perennial	Perennial	–	–
Proportion perennial in community	High	High	High	High	–	–	–	Low
Invader N-fixing ability	Legume	Legume	–	–	–	–	–	–
Proportion legume in community	–	–	Low	Low	–	–	Low	High
Functional group similarity [^]	I = C	I = C	–	–	–	–	NA	NA
Plant height	I ≠ C	I ≠ C	I ≠ neighbours	I ≠ neighbours	I = C	I = C	I ≠ neighbours	I = neighbours
LDMC	C = low	C = high	C = high	C = high	–	C > I	–	–
SLA	C > I	C > I	–	–	I > C	C > I	C = high	C = low
Seed mass	–	C > I	C = high	C = high	–	C > I	–	–
Invader abundance in seeded subplots	NA	NA	NA	NA	High	High	High	High
Trends through time	Conditional		Increased with time		Conditional		Increased with time	

For example, occupancy in seeded subplots was highest when soil NO₃ was low in both the short- and long-term, and when invaders were forbs (short-term) or grasses (long-term). I indicates non-resident (target) invader; C indicates recipient community; I = C indicates that successful invaders are similar to community for that given trait (trait underdispersion), whereas I ≠ C indicates that successful invaders are dissimilar to community for that trait (trait overdispersion), i.e. absolute distance; I > C and I < C indicate cases where successful invader has higher and lower trait values than the recipient community respectively, i.e. hierarchical or relative distance; neighbours refers to invader's two nearest functional neighbours in the recipient community, i.e. trait gap size (Fig. 1). Hyphens indicate no statistically significant relationship; NA indicates that the relationship was not formally tested. Functional group similarity refers to interactions between invaders and the recipient communities based on species' growth form, lifespan and N-fixing ability.

that deer herbivory can severely constrain the abundance of legumes in the study savannah (Knops *et al.* 2000). Invaders that spread into unseeded subplots were more abundant in the long-term when recipient communities had high proportional cover of legumes and low perennial cover, likely because of greater N availability in these communities – consistent with findings elsewhere (Mwangi *et al.* 2007). Importantly, relationships between invasion and community legume and perennial cover varied, perhaps reflecting temporal variation in the extent of light, N and moisture limitation (Mwangi *et al.* 2007; Willis *et al.* 2010).

We were surprised that grass-, perennial- or legume-dominated communities did not have lower abundances of invading grasses, perennials or legumes respectively. Studies at Cedar Creek (Symstad 2000; Fargione *et al.* 2003) and elsewhere (Emery 2007; Mwangi *et al.* 2007) have found that invader abundance was greatest when invaders were functionally distinct from invaded communities. Biotic resistance from limiting similarity is not universal though (Price & Pärtel 2013). For example, competition experiments revealed that *Phragmites australis* invasion was more strongly inhibited by annual species rather than by species similar to *P. australis* (Byun *et al.* 2013). Our findings may differ from other studies at Cedar Creek because our study used more detailed trait-based information and did not rely so heavily on functional group classifications, and because it occurred in a more heterogeneous environment where effects of environmental sorting would be stronger (Kraft *et al.* 2015).

Higher long-term occupancy of invaders that were grasses, perennials or had lower SLA than recipient communities (Figs 2k,j,b and 3c,d,g) may reflect the longer lifespans of plants with these characteristics (Wright *et al.* 2004;

Lauenroth & Adler 2008), and the greater ability of grasses (cf forbs, though there are exceptions) to spread clonally (Lauenroth & Adler 2008). Despite the apparent logic of these results, the lifespan and SLA results nevertheless seem to contradict common findings where annual species and those with fast leaf economics (indicated by high SLA) are typically more successful as invaders (van Kleunen *et al.* 2010). We provide two explanations for this. First, most seed addition experiments are of much shorter durations than ours. Had we run the experiment for five and not 20 years, and had we only examined species occupancy, we too would have concluded that annuals and invaders with higher relative SLA posed a higher invasion risk than perennials or low SLA species. However, our full set of results show that such conclusions are true only under certain conditions. Second, in observational studies of invasions, which largely focus on exotic species, invading species are typically found in modified ecosystems (Catford *et al.* 2011; Moles *et al.* 2012) or disturbed sites characterized by high resource availability; under these conditions, the importance of resource conservation and longevity are secondary to high growth rates and short generation times (Kuster *et al.* 2008; Moravcová *et al.* 2015). In our study savannah, resource availability was low and disturbance matched historical forms and levels. It is thus fitting that longer lived invaders and those with more conservative carbon capture strategies persisted longer in the experimental plots. The potential benefits of being exotic (Buckley & Catford 2016; Catford *et al.* 2018) may also explain why our results – based on invasion of mostly native, non-resident species – differ from observational studies of exotic invasions.

Long-term invader occupancy and, in seeded subplots, abundance were greater in communities that had seed masses and

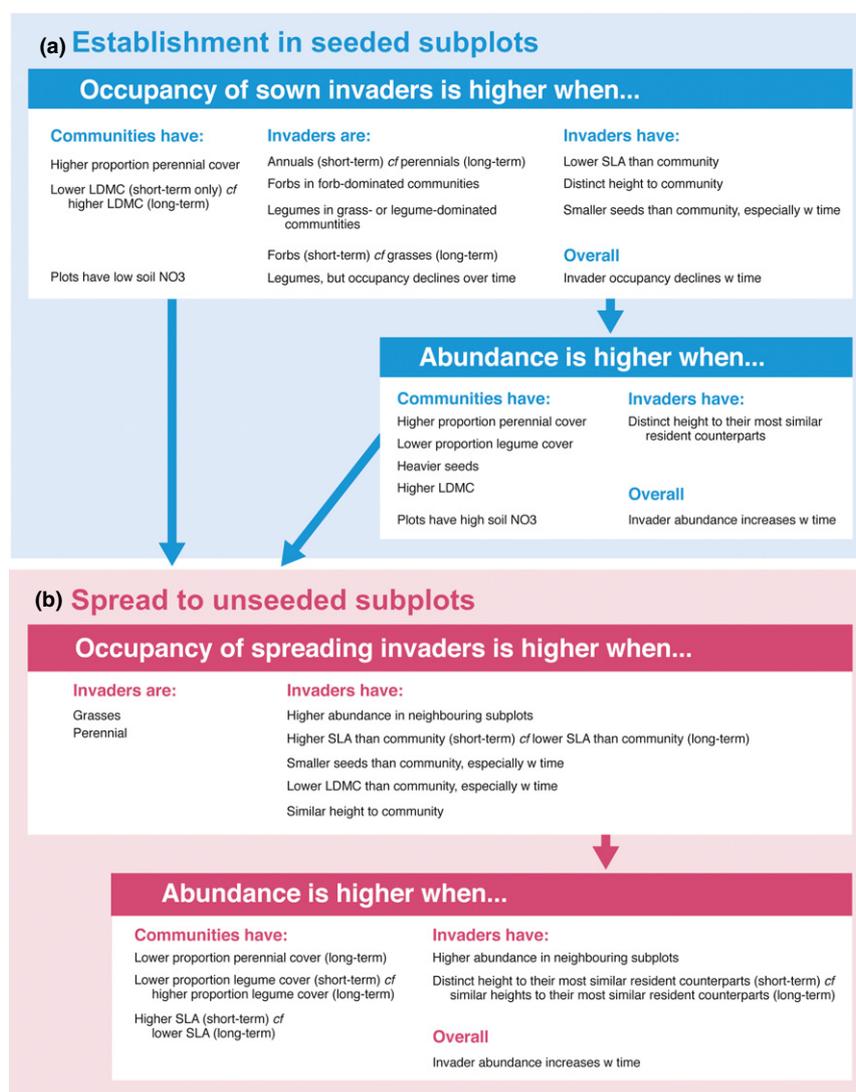


Figure 4 Summary of overall results showing conditions and traits associated with (a) occupancy and abundance of sown, target invaders that established in seeded subplots, and (b) occupancy and abundance of established invaders that spread from seeded subplots to adjacent unseeded subplots. Short-term refers to trends within the first 5 years of the experiment; long-term refers to trends in the last 10 years of the experiment; w is an abbreviation for “with”.

LDMCs that were high or higher than invaders (Figs 2h,i,r,s and 3e,f). If we ignore invader abundance in unseeded subplots, which was unrelated to seed mass and LDMC, these results suggest that communities dominated by species with heavier seeds and longer lived, tougher leaves are more invisable in the long-term than communities with lighter seeds and low LDMC.

Reflecting the well-established trade-off between seed mass and number (Moles 2018), communities dominated by species with fewer, heavier seeds may be more seed-limited than lighter seeded communities (Tilman 1997; Turnbull *et al.* 2000). As such, heavier seeded communities may thus have greater numbers of unoccupied safe sites, increasing the relative recruitment success of invaders in these communities (Duncan *et al.* 2009; Wandrag *et al.* in press). Because a set mass (rather than number) of seeds was added to seeded subplots, the seed mass-number trade-off remained intact in our experiment, such that light-seeded invaders would have had more seeds than heavier seeded species, and thus more

opportunities to recruit (Duncan *et al.* 2009; Wandrag *et al.* in press). The relative advantage of lighter, more numerous seeds was apparent for occupancy (where hierarchical distance was significant), but not abundance, the latter of which was mostly strongly related to seed mass CWM. That invader abundance was only linked with seed mass in seeded (cf unseeded) subplots may stem from the high rate of seed addition to seeded subplots (4.5 g m^{-2} per species): this high seeding rate may have enabled invaders to occupy most, if not all, available safe sites, whereas the unseeded subplots were presumably still seed-limited (Wandrag *et al.* in press).

We hypothesised that invaders with slower leaf economics than recipient communities (higher LDMC, lower SLA) would be more competitive and thus more abundant than their opposite counterparts in the long-term – reflecting resource economics (Reich 2014), and consistent with long-standing ideas of *K*-selected species replacing *r*-selected ones (Pianka 1970). Trends related to SLA were consistent with our hypotheses, but

trends related to LDMC were not (Appendix S1). The entire study savannah is burnt every 2 in 3 years such that the occurrence of fire does not explain invasion trends. However, communities with higher LDMC may be more flammable (Pérez-Harguindeguy *et al.* 2013) and thus experience hotter, more damaging fires, potentially making them more vulnerable to invasion by increasing resource availability and opportunities for colonisation (Davis & Pelsor 2001).

When seeded, invaders were most successful when their heights were distinct from the CWM and their nearest neighbours in recipient communities (Fig. 2c,q). These trends suggest that height differentiation from residents facilitates invader establishment (Fig. 1, Herben & Goldberg 2014), but the cause is unclear; competition for light alone would presumably favour invasion by species that are taller than (indicated by hierarchical distance), rather than distinct from, the recipient community (Willis *et al.* 2010). The opposite trends were observed in unseeded subplots in the long-term (Fig. 3b,k) – possibly reflecting the greater importance of environmental sorting or other selective pressures (which would select functionally similar cf. novel invaders; Kraft *et al.* 2015; Divíšek *et al.* 2018) for invader spread. Trait data for 53 species in the study savannah indicate that there is no correlation between clonality and relative plant height ($r = 0.11$, Cleland *et al.* 2008), so clonal spread does not explain these height-based trends.

Question 2: Trait-based relationships vary with time, stage and indicator of invasion

Our 20-year experiment showed that factors associated with invasion success are not uniform across time, stages, or indicators of invasion (Table 2, Fig. 4). Conditions that were favourable for some stages and indicators of invasion, and at some times, were disadvantageous or had negligible effects at others. These results highlight that how, where and when invasion is measured can affect ecological inferences. Our findings indicate that invasion events observed during the first few years after seed addition only tell part of the invasion story; comprehensive understanding of invasion requires long-term studies in natural, intact ecosystems.

Recent studies have shown that traits linked with invasion depend on invasion stage (Dawson *et al.* 2009; Moravcová *et al.* 2015; Conti *et al.* 2018; Divíšek *et al.* 2018), recipient community characteristics (Lai *et al.* 2015; Carboni *et al.* 2016; Conti *et al.* 2018), and the way invasion is measured (Carboni *et al.* 2016). However, we believe that our study is among the first to reveal that invasion trait-based trends also vary with time (see Kempel *et al.* 2013): even when examining a single indicator of invasion, traits of invaders or characteristics of recipient communities positively associated with early invasion could be negatively associated with later invasion.

Question 3: Relative importance of invader traits, community traits and invader-community trait-based interactions differ for invader occupancy and abundance

Invader occupancy was associated with all five trait forms we examined except gap size – more or less in line with our expectations (Appendix S1). In contrast, invader abundance was most

strongly linked with recipient community traits (CWM) and differentiation from invaders' nearest functional neighbours (gap size; Table 2, Fig. 4). Unlike occupancy, species that reach high relative abundance must be able to acquire a high share of available resources. Species can do this by outcompeting other species for limited resources (Tilman 1982), occupying distinct niches (Chesson 2000), or becoming abundant in sites with high levels of resource availability (Davis *et al.* 2000). It is therefore logical that community and invader-community interactions – both linked with biotic resistance (Conti *et al.* 2018) – strongly influence invader abundance, whereas intrinsic invader traits are of less importance.

By examining occupancy and relative abundance of 50 non-resident plant species in seeded and unseeded areas over 20 years, and characterising 164 taxa with seven traits, our study highlights the complexity and context dependence of biological invasions. Invasion success varied with time, invasion stage and indicator of success, and was influenced by traits of invaders, traits of recipient communities, and trait-based interactions between the two.

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AUTHOR CONTRIBUTIONS

JAC conceived the idea for the paper; DT established the experiment; ATC, JAC, MK, DT & PW surveyed the experiment; JAC, PW, JC-B & PR collected trait data; JAC & ALS designed the analytical approach; ALS undertook the modelling; JAC wrote the first draft of the paper with contributions from ALS; all authors helped write and edit subsequent drafts.

DATA AVAILABILITY

All of our analyses can be replicated using these data. Data available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.7709990>. All explanations for the data are provided in the MS and associated SI.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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