1   **Traits linked with species invasiveness and community invasibility vary with**

2   **time, stage and indicator of invasion in a long-term grassland experiment**

3

4   Jane A. Catford[1,2,3,4], Annabel L. Smith[5], Peter D. Wragg[6,7], Adam T. Clark[6,8,9],

5   Margaret Kosmala[6], Jeannine Cavender-Bares[6], Peter B. Reich[7,10] & David Tilman[6,11]

6

7   **Author addresses**

8   [1]Department of Geography, King's College London, Strand, London WC2R 2LS, UK

9   [2]School of BioSciences, The University of Melbourne, Vic 3010, Australia

10 [3]Fenner School of Environment & Society, Australian National University, Canberra,

11 ACT 2601, Australia

12 [4]Biological Sciences, University of Southampton, Southampton, SO17 1BJ, UK

13 [5]School of Natural Sciences, Zoology, Trinity College Dublin, The University of

14 Dublin, Dublin 2, Ireland

15 [6]Department of Ecology, Evolution & Behavior, University of Minnesota, St Paul,

16 MN 55108, USA

17 [7] Department of Forest Resources, University of Minnesota, St. Paul, MN 55108

18 USA.

19 [8] Department of Physiological Diversity, Helmholtz Center for Environmental

20 Research (UFZ), Permoserstrasse 15, Leipzig 04318, Germany

21 [9] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,

22 Synthesis Centre for Biodiversity Sciences (sDiv), Deutscher Platz 5e, 04103 Leipzig,

23 Germany

24   [10] Hawkesbury Institute for the Environment, Western Sydney University, Penrith,

25   NSW 2753, Australia.

26   [11] Bren School of Environmental Science and Management, University of California,

27   Santa Barbara, 2400 Bren Hall, Santa Barbara, CA 93106, USA

28   **Corresponding author:** Jane A. Catford, Department of Geography, King's College

29   London, Bush House NE, 30 Aldwych, London, WC2B 4BG, UK.

30   jane.catford@kcl.ac.uk

31

37

42

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.

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 – e.g. 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 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 two 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

118 experiment. The seven study traits were selected based on hypothesised relationships

119 with invasion success (see Appendix S1 for rationale).

120 **Methods**

121 *Study design*

122 Cedar Creek (45.4°N, 93.2°W) has nitrogen-limited sandy soils, annual precipitation

123 of ~770 mm, mean summer temperatures of 27°C, and winter lows of -14°C. In

124 August 1991, 30 2 m x 2 m permanently marked plots were haphazardly positioned

125 throughout the experimental savannah (Fig. S1; 45.397° N, 93.181° W; Tilman 1997).

126 Each plot was divided into four 1 m x 1 m subplots, and percent cover of all vascular

127 plant species, bare mineral soil, and litter were estimated (see Appendix S3 for

128 additional details about all methods).

129 In June 1992, ten seed treatments were randomly assigned to two subplots per plot

130 (hereafter "seeded subplots", cf. "unseeded subplots", Fig. S1). These involved the

131 addition of no species (a control), 5, 10, 15, 20, 25, 30, 35, 40, and 54 species (Fig.

132 S1). There were six replicates per treatment, with combinations of species in each

133 replicate randomly drawn from a pool of 54 total species. 4.5 g/m^2 seeds of each

134 species were used. Seeds were gathered on site or obtained from a local company

135 (Prairie Restorations, Minnesota).

136 After 1991, subplots were surveyed eight times using the same method as in 1991.

137 164 plant taxa were recorded across all subplots and years, of which 85 were observed

138 in 1991, prior to seeding (Table S1, Fig. S2). 54 non-sown taxa colonised the subplots

139 naturally after 1991, but high turnover meant that some of these gains were offset by

140 losses (total plant richness varied from 84 species in 1992 to 113 species in 2012).

141 Our analytical approach accounted for the changing recipient community by updating

142 the community each timestep, such that community changes would not have affected

143 our findings.

144 Twenty-seven of the sown species were present in at least one plot in 1991. To

145 account for this, sown species were considered **target invaders** only if they were

146 absent from a given 2 m x 2 m plot in 1991, before seed addition. We define the

147 **recipient community** as all species present in a given subplot at a given point in time

148 (whether sown or not), excluding the target invader. Two sown invaders that were

149 never observed (*Symphyotrichum novae-angliae* and *Mimulus ringens*) were excluded

150 from analysis. We treated the two sown woody species (*Celastrus scandens* and *Rosa*

151 *arkansana*) as members of recipient communities because our focus was on invasion

152 of herbaceous species. Of the 50 resulting target invaders, 46 are native to MN, 43 are

153 perennial, 12 are grasses (Poaceae), 10 are leguminous forbs (Fabaceae) and 28 are

154 non-leguminous forbs (Table S1).

155 Four soil cores (20 cm deep, 2.5 cm diameter) were collected in each plot in 1991,

156 extracted with 0.01 M KCl, and analyzed to give extractable soil nitrogen (NO_3)

157 concentration and soil moisture (Tilman 1997). Though only for a single year, these

158 variables were used to indicate local environmental conditions: they corresponded

159 with site topography, which ranged from drier, elevated, nutrient-poor soils, to low-

160 lying, occasionally saturated soils that were comparatively nitrogen rich (correlation

161 between elevation at 5 m x 5 m resolution and: soil moisture, r = -0.570; soil NO_3, r =

162 0.462).

163 *Plant traits*

164   We classified all taxa based on lifespan (annual and biennial OR perennial), growth

165   form (grass OR forb) and ability to fix nitrogen (legume OR non-legume) (Tilman

166   1997; USDA-NRCS 2018; Table S1).

167   In the summers of 2014 and 2015, we measured maximum vegetative height, leaf dry

168   matter content (LDMC) and specific leaf area (SLA) of 143 taxa growing naturally at

169   Cedar Creek following Pérez-Harguindeguy *et al.* (2013). Dried seed masses were

170   determined from plants at Cedar Creek or from local suppliers (Prairie Moon, Prairie

171   Restorations). These measurements provided numerical trait data for 96.3% of the

172   vegetation cover in all subplots across all years. Of 570 species-trait measurements

173   used in the study, 531 were measured on plants <1 km of the study site; 30 used

174   means of congeneric or confamilial species at Cedar Creek (Table S2); and 9 were

175   from Kew Seed Information Database (Liu *et al.* 2008).

176   We examined five forms of each individual numerical trait (Fig. 1), which we

177   hypothesised would relate to occupancy and abundance in different ways (Appendix

178   S1):

179   i.   *Invader* mean trait value indicates the intrinsic invasiveness of invaders (van

180   Kleunen *et al.* 2010; Richardson & Pyšek 2012).

181   ii.   *Community-weighted mean* (CWM) trait value, calculated as mean trait value

182   weighted by proportional cover, indicates recipient community's intrinsic

183   invasibility (Richardson & Pyšek 2012).

184   iii. *Invader-community hierarchical distance* ($\overline{Invader} - \overline{Community}$) indicates

185   differences between invader and CWM traits. Depending on context, higher

186   (e.g. height) or lower (e.g. SLA in resource-limited plots) hierarchical distance

187   can indicate when invaders have higher fitness than recipient communities

188   (Lai *et al.* 2015).

189   iv.   *Invader-community dissimilarity,* or absolute trait distance ($|\overline{Invader} -$

190        $\overline{Community}|$), indicates net differences between invader and CWM traits

191   (similar to Lai *et al.* 2015). This may relate to the extent of environmental

192   sorting (trait underdispersion) or niche differentiation (trait overdispersion).

193   v.   *Invader-community gap size*, calculated as the difference between trait values

194   of resident species that fall immediately above and below invaders' trait

195   values ($\bar{a} < i < \bar{b}$; gap size $= \bar{b} - \bar{a}$; Fig. 1), indicates potential degree of niche

196   differentiation between invaders and their nearest "functional neighbours" in

197   recipient communities (similar to Gallien *et al.* 2014).

198   ***Statistical analyses***

199   *Four response variables of invasion*

200   We used hierarchical linear regression models to identify variables associated with

201   invasion of non-resident species (Jamil *et al.* 2012; Pollock *et al.* 2012). We examined

202   two indicators of invasion success (occupancy and abundance) at both of two stages

203   of invasion (establishment and spread), giving four response variables in total. All

204   analyses relate to standing live vegetation.

205   *Occupancy* was the presence or absence of a target invader in seeded subplots (for

206   establishment) or unseeded subplots (for spread).

207   *Relative abundance* was the proportion of total vascular plant cover in seeded

208   subplots (for establishment) or unseeded subplots (for spread) made up of the target

209   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 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

235　　including year as a fixed effect, we explicitly modelled temporal trends in trait

236　　interactions. The random intercepts accounted for repeated measurements within plots

237　　and subplots (Pinheiro & Bates 2000).

238　　*In establishment models for both occupancy and abundance:* we included the total

239　　number of other invader species sown into each subplot to account for potential

240　　interactions among invaders and their seed rain. We represented environmental

241　　conditions with variables indicating soil moisture (range = 2.49–16.46%) and soil

242　　nitrate concentration (range = 0.013–1.85 mg kg^{-1}), both of which were measured in

243　　1991 only. We allowed the slope of the NO3 term to vary (as a random effect) by

244　　species, as this is a primary limiting resource at our site, and species-level responses

245　　to NO3 are known to vary greatly (Tilman 1997). We did not fit fixed effect estimates

246　　by species because we lacked sufficient power.

247　　*In spread models for both occupancy and abundance:* we used cumulative abundance

248　　of target invaders in seeded subplots from each survey year and all previous surveys

249　　to indicate potential cumulative seed rain into unseeded subplots. Preliminary

250　　analyses indicated that environmental variables were not significantly related to

251　　spread, so we did not consider them further.

252　　*Probability of occupancy* was modelled using binomial generalized linear mixed

253　　models in the lme4 package (Bates *et al.* 2013) in R version 3.5 (R Core Team 2014).

254　　Abundance data were zero-inflated, so we modelled *abundance conditional on*

255　　*presence* (i.e. removed zeros) and used mixed-effects beta regression in the

256　　glmmADMB R package (Fournier *et al.* 2012; Skaug *et al.* 2013). All models used a

257　　logit link function. Apart from year, which was coded as an integer varying from 0

258　　(1992) to 20 (2012), all non-binary numeric variables were centered and scaled

259   (Appendix S6). For details on models and convergence criteria, see Appendices S2,

260   S3, S4 and S6.

261   *Model selection*

262   To identify the "best" regression forms, we conducted model selection in two steps. In

263   Step 1, we compiled a series of models that varied in structure and complexity

264   (Appendix S2). We did not mix trait forms in Step 1, so we had five subsets of models

265   – one for each trait form. We used the structure of the top-ranked model for each

266   response variable from Step 1 as our template for models analysed in Step 2. Into that

267   template, we sequentially substituted different trait forms that had important effects in

268   Step 1. We considered trait forms important if they were significantly related

269   ($P<0.05$) to response variables in the top-ranked model from each of the five model

270   subsets analysed in Step 1. The models in Step 2 could potentially include different

271   forms for different traits (e.g. SLA hierarchical distance and CWM seed mass), but

272   only one form of each trait was used in each model (e.g. CWM SLA was never used

273   with invader SLA); this was because different trait forms were highly correlated and

274   so we could identify trait forms that best explained invasion, thereby addressing

275   Question 3.

276   We ranked all models using Bayesian Information Criterion (BIC, Jones 2011). We

277   considered all models that differed in BIC from the best-supported model by ≤ 5 to

278   have support from the data (Hegyi & Garamszegi 2011). We present results of the

279   best-supported models in the main paper and all models with $\Delta BIC \leq 5$ in Fig. S3. We

280   considered effects of explanatory variables to be significant if 95% confidence

281   intervals did not cross zero in at least one of the models with $\Delta BIC \leq 5$. We calculated

282   marginal and conditional R^2 values for the occupancy models to indicate variance

283   explained respectively by fixed and random effects, and by fixed effects only

284 (Nakagawa & Schielzeth 2013). We could not calculate R^2 values for the abundance

285 models because there is currently no available method for mixed-effect beta

286 regression (Nakagawa, pers. comm, Nov 2017; Nakagawa & Schielzeth 2016).

287 **Results**

288 *General trends*

289 Relative abundance of invaders increased with time in seeded subplots and in

290 unseeded subplots (Figs 2m, 3h). Invaders that established and accumulated high

291 abundance in seeded subplots over the duration of the experiment were highly likely

292 to spread to, and reach high abundance in, adjacent unseeded subplots (Figs 3a, 3i).

293 The number of sown invaders was not related to establishment of target invaders,

294 suggesting that the presence of other invaders in seeded subplots did not strongly

295 affect invasion of individual species in our experiment.

296 *Question 1: Traits linked with invasion success*

297 Invader N-fixing ability, life span and growth form were linked with invader

298 occupancy but not abundance for both establishment (seeded subplots) and spread

299 (unseeded sublots; Table 2; Fig. 4). Legumes had higher occupancy than non-legumes

300 when directly sown (Fig. 2l). By the end of the experiment, perennial and grass

301 invaders had higher occupancy than annuals and forbs in both seeded and unseeded

302 subplots (Figs 2j, 2k, 3c, 3g).

303 Recipient communities with higher perennial cover had higher invader occupancy and

304 abundance in seeded subplots (Figs 2d & 2o), but the opposite was true for invader

305 abundance in unseeded subplots (Fig. 3l). Invader abundance was higher in seeded

subplots with low proportional legume cover (Fig. 2p), but – in 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, 2r, 3e) and higher LDMC (Figs 2i, 2s, 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, 3 & 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 (Figs 3d, 3j, 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; Figs 3b, 3k). 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 (Figs 2d, 2o) – 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 NO_3 (Figs 2a, 2n).

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, 3 & 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, 3 & 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

354 ecological interpretations (Fig. S3, Appendix S4); the only exception was LDMC in

355 the establishment-abundance model, suggesting that LDMC is not strongly linked

356 with invader abundance in seeded subplots (Fig. S3b).

357 **Discussion**

358 Our 20-year experiment showed that factors associated with invasion of non-resident

359 species are not uniform across time, stages, or indicators of invasion (Table 2, Fig. 4).

360 Despite the variation in observed relationships, our study accords with existing

361 theories that propagule pressure, environmental conditions, invader and community

362 traits and their interactions, time, and indicator and stage of invasion all collectively

363 affect invasion trends (Catford *et al.* 2009; Blackburn *et al.* 2011; Richardson &

364 Pyšek 2012). All seven traits that we examined were related to at least one indicator

365 or stage of invasion, but the strength, direction and consistency of their relationships

366 varied. Invader occupancy was related to four trait forms, while invader abundance

367 was mostly associated with CWM plus invader differentiation from functionally

368 similar residents. We discuss the main findings to our three research questions after

369 briefly discussing general trends.

370 Invaders' cumulative abundance in seeded subplots was positively associated with

371 their greater occupancy and relative abundance in adjacent unseeded subplots. This

372 was presumably because of higher propagule rain (or clonal spread) and higher

373 suitability of the local ecological conditions for population growth. Given that

374 abundances of invader species increased over 20 years in both seeded and unseeded

375 areas, it not only seems likely that some invaders have formed self-sustaining

376 populations in vicinities where sown, but also that their local population sizes will

377 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 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 heterogenous

402 environment where effects of environmental sorting would be stronger (Kraft *et al.*

403 2015).

404 Higher long-term occupancy of invaders that were grasses, perennials or had lower

405 SLA than recipient communities (Figs 2k,j,b, 3c,d,g) may reflect the longer lifespans

406 of plants with these characteristics (Wright *et al.* 2004; Lauenroth & Adler 2008), and

407 the greater ability of grasses (cf forbs, though there are exceptions) to spread clonally

408 (Lauenroth & Adler 2008). Despite the apparent logic of these results, the lifespan

409 and SLA results nevertheless seem to contradict common findings where annual

410 species and those with fast leaf economics (indicated by high SLA) are typically more

411 successful as invaders (van Kleunen *et al.* 2010). We provide two explanations for

412 this. First, most seed addition experiments are of much shorter durations. Had we run

413 the experiment for five and not 20 years, and had we only examined species

414 occupancy, we too would have concluded that annuals and invaders with higher

415 relative SLA posed a higher invasion risk than perennials or low SLA species.

416 However, our full set of results show that such conclusions are true only under certain

417 conditions. Second, in observational studies of invasions, which largely focus on

418 exotic species, invading species are typically found in modified ecosystems (Catford

419 *et al.* 2011; Moles *et al.* 2012) or disturbed sites characterized by high resource

420 availability; under these conditions, the importance of resource conservation and

421 longevity are secondary to high growth rates and short generation times (Kuster *et al.*

422 2008; Moravcová *et al.* 2015). In our study savannah, resource availability was low

423 and disturbance matched historical forms and levels. It is thus fitting that longer-lived

424 invaders and those with a more conservative carbon capture strategy persisted longer

425 in the experimental plots. The potential benefits of being non-native (Buckley &

426 Catford 2016; Catford *et al.* 2018) may also explain why our results – based on

427 invasion of mostly native, non-resident species – differ from observational studies of

428   exotic invasions.

429   Long-term invader occupancy and, in seeded subplots, abundance were greater in

430   communities that had seed masses and LDMCs that were high or higher than invaders

431   (Figs 2h-i, 2r-s, 3e-f). If we ignore invader abundance in unseeded subplots, which

432   was unrelated to seed mass and LDMC, these results suggest that communities

433   dominated by species with heavier seeds and longer-lived, tougher leaves are more

434   invasible in the long-term than communities with lighter seeds and low LDMC.

435   Reflecting the well-established tradeoff between seed mass and number (Moles 2018),

436   communities dominated by species with fewer, heavier seeds may be more seed-

437   limited than lighter-seeded communities (Tilman 1997; Turnbull *et al.* 2000). As

438   such, heavier-seeded communities may thus have greater numbers of unoccupied safe

439   sites, increasing the relative recruitment success of invaders in these communities

440   (Duncan *et al.* 2009; Wandrag *et al.* under revision). Because a set mass (rather than

441   number) of seeds was added to seeded subplots, the seed mass-number tradeoff

442   remained intact in our experiment, such that light-seeded invaders would have had

443   more seeds than heavier seeded species, and thus more opportunities to recruit

444   (Duncan *et al.* 2009; Wandrag *et al.* under revision). The relative advantage of lighter,

445   more numerous seeds was apparent for occupancy (where hierarchical distance was

446   significant), but not abundance, the latter of which was mostly strongly related to seed

447   mass CWM. That invader abundance was only linked with seed mass in seeded (cf

448   unseeded) subplots may stem from the high rate of seed addition to seeded subplots

449   (4.5 g/m^2 per species): the high seeding rate may have enabled invaders to occupy

450   most, if not all, available safe sites, whereas the unseeded subplots were presumably

451   still seed-limited (Wandrag *et al.* under revision).

452   We hypothesised that invaders with slower leaf economics than recipient communities

453   (higher LDMC, lower SLA) would be more competitive and thus more abundant than

454   their opposite counterparts in the long-term – reflecting resource economics (Reich

455   2014), and consistent with long-standing ideas of *K*-selected species replacing *r*-

456   selected ones (Pianka 1970). Trends related to SLA were consistent with our

457   hypotheses, but trends related to LDMC were not (Appendix S1). The entire study

458   savannah is burnt every two in three years such that the occurrence of fire does not

459   explain invasion trends. However, communities with higher LDMC may be more

460   flammable (Pérez-Harguindeguy *et al.* 2013) and thus experience hotter, more

461   damaging fires, potentially making them more vulnerable to invasion by increasing

462   resource availability and opportunities for colonisation (Davis & Pelsor 2001).

463   When seeded, invaders were most successful when their heights were distinct from

464   the CWM and their nearest neighbours in recipient communities (Figs 2c, 2q). These

465   trends suggest that height differentiation from residents facilitates invader

466   establishment (Fig. 1, Herben & Goldberg 2014), but the cause is unclear;

467   competition for light alone would presumably favour invasion by species that are

468   taller than (indicated by hierarchical distance), rather than distinct from, the recipient

469   community (Willis *et al.* 2010). The opposite trends were observed in unseeded

470   subplots (Figs 3b, 3k) – possibly reflecting the greater importance of environmental

471   sorting or other selective pressures (which would select functionally similar cf. novel

472   invaders; Kraft *et al.* 2015; Divíšek *et al.* 2018) for invader spread. Trait data for 53

473   species in the study savannah indicate that there is no correlation between clonality

474   and relative plant height (r = 0.11, Cleland *et al.* 2008), so clonal spread does not

475   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 different niches (Chesson 2000), or becoming abundant in sites with high levels of resource availability (Davis *et al.* 2000). It is therefore logical that community invasibility 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.

References

1.

Bates, D., Maechler, M. & Bolker, B. (2013). lme4: linear mixed-effects models using S4 classes. R package, version 0.999999-2. http://lme4.r-forge.r-project.org/.

2.

Blackburn, T.M., Pysek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarosík, V. *et al.* (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26, 333-339.

3.

Buckley, Y.M. & Catford, J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, 104, 4-17.

4.

Byun, C., de Blois, S. & Brisson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, 101, 128-139.

5.

Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C. *et al.* (2016). What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. *Ecology Letters*, 19, 219-229.

6.

Catford, J.A., Baumgartner, J.B., Vesk, P.A., White, M., Buckley, Y.M. & McCarthy, M.A. (2016). Disentangling the four demographic dimensions of species invasiveness. *Journal of Ecology*, 104, 1745-1758.

7.

Catford, J.A., Bode, M. & Tilman, D. (2018). Introduced species that overcome life history tradeoffs can cause native extinctions. *Nature Communications*, 9, 2131.

8.

553 Catford, J.A., Downes, B.J., Gippel, C.J. & Vesk, P.A. (2011). Flow regulation

554 reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal*

555 *of Applied Ecology*, 48, 432-442.

556 9.

557 Catford, J.A., Jansson, R. & Nilsson, C. (2009). Reducing redundancy in invasion

558 ecology by integrating hypotheses into a single theoretical framework. *Diversity &*

559 *Distributions*, 15, 22-40.

560 10.

561 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review*

562 *of Ecology and Systematics*, 31, 343-366.

563 11.

564 Cleland, E.E., Clark, C.M., Collins, S.L., Fargione, J.E., Gough, L., Gross, K.L. *et al.*

565 (2008). Species responses to nitrogen fertilization in herbaceous plant communities,

566 and associated species traits. 89, 1175-1175.

567 12.

568 Conti, L., Block, S., Parepa, M., Münkemüller, T., Thuiller, W., Acosta, A.T.R. *et al.*

569 (2018). Functional trait differences and trait plasticity mediate biotic resistance to

570 potential plant invaders. *Journal of Ecology*, 106, 1607-1620.

571 13.

572 Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant

573 communities: a general theory of invasibility. *Journal of Ecology*, 88, 528-534.

574 14.

575 Davis, M.A. & Pelsor, M. (2001). Experimental support for a resource-based

576 mechanistic model of invasibility. *Ecology Letters*, 4, 421-428.

577 15.

578 Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. (2009). Factors explaining alien plant

579 invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of*

580 *Ecology*, 97, 657-665.

581 16.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. *et al.*
(2016). The global spectrum of plant form and function. *Nature*, 529, 167-171.

17.

Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N.J., Lososová, Z., Pyšek, P. *et al.*
(2018). Similarity of introduced plant species to native ones facilitates naturalization,
but differences enhance invasion success. *Nature Communications*, 9, 4631.

18.

Duncan, R.P., Diez, J.M., Sullivan, J.J., Wangen, S. & Miller, A.L. (2009). Safe sites,
seed supply, and the recruitment function in plant populations. *Ecology*, 90, 2129-
2138.

19.

Emery, S.M. (2007). Limiting similarity between invaders and dominant species in
herbaceous plant communities? *Journal of Ecology*, 95, 1027-1035.

20.

Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion:
An experimental test of neutral versus niche processes. *Proceedings of the National
Academy of Sciences of the United States of America*, 100, 8916-8920.

21.

Fournier, D., Skaug, H., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. *et al.*
(2012). AD Model Builder: using automatic differentiation for statistical inference of
highly parameterized complex nonlinear models. *Optimization Methods and Software*,
27, 233-249.

22.

Fridley, J.D. & Sax, D.F. (2014). The imbalance of nature: revisiting a Darwinian
framework for invasion biology. *Global Ecology and Biogeography*, 23, 1157-1166.

23.

Gallien, L., Carboni, M. & Münkemüller, T. (2014). Identifying the signal of
environmental filtering and competition in invasion patterns – a contest of approaches
from community ecology. *Methods in Ecology and Evolution*, 5, 1002-1011.

24.

Hegyi, G. & Garamszegi, L. (2011). Using information theory as a substitute for stepwise regression in ecology and behavior. *Behavioral Ecology and Sociobiology*, 65, 69-76.

25.

Herben, T. & Goldberg, D.E. (2014). Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits. *Journal of Ecology*, 102, 156-166.

26.

Jamil, T., Ozinga, W.A., Kleyer, M. & ter Braak, C.J.F. (2012). Selecting traits that explain species–environment relationships: a generalized linear mixed model approach. *Journal of Vegetation Science*, n/a-n/a.

27.

Jones, R.H. (2011). Bayesian information criterion for longitudinal and clustered data. *Statistics in Medicine*, 30, 3050-3056.

28.

Kempel, A., Chrobock, T., Fischer, M., Rohr, R.P. & van Kleunen, M. (2013). Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *Proceedings of the National Academy of Sciences*, 110, 12727-12732.

29.

Knops, J.M.H., Ritchie, M.E. & Tilman, D. (2000). Selective herbivory on a nitrogen fixing legume (Lathyrus venosus) influences productivity and ecosystem nitrogen pools in an oak savanna. *Écoscience*, 7, 166-174.

30.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592-599.

31.

Kuster, E.C., Kühn, I., Bruelheide, H. & Klotz, S. (2008). Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, 96, 860-868.

642 31.

643 Lai, H.R., Mayfield, M.M., Gay-des-combes, J.M., Spiegelberger, T. & Dwyer, J.M.

644 (2015). Distinct invasion strategies operating within a natural annual plant system.

645 *Ecology Letters*, 18, 336-346.

646 32.

647 Lauenroth, W.K. & Adler, P.B. (2008). Demography of perennial grassland plants:

648 survival, life expectancy and life span. *Journal of Ecology*, 96, 1023-1032.

649 33.

650 Liu, K., Eastwood, R.J., Flynn, S., Turner, R.M. & Stuppy, W.H. (2008). Seed

651 Information Database. Royal Botanic Gardens, Kew.

652 34.

653 Moles, A.T. (2018). Being John Harper: Using evolutionary ideas to improve

654 understanding of global patterns in plant traits. *Journal of Ecology*, 106, 1-18.

655 35.

656 Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L. *et*

657 *al.* (2012). Invasions: the trail behind, the path ahead, and a test of a disturbing idea.

658 *Journal of Ecology*, 100, 116-127.

659 36.

660 Moravcová, L., Pyšek, P., Jarošík, V. & Pergl, J. (2015). Getting the right traits:

661 reproductive and dispersal characteristics predict the invasiveness of herbaceous plant

662 species. *PLoS ONE*, 10, e0123634.

663 37.

664 Mwangi, P., N., Schmitz, M., Scherber, C., Roscher, C., Schumacher, J., Scherer-

665 Lorenzen, M. *et al.* (2007). Niche pre-emption increases with species richness in

666 experimental plant communities. *Journal of Ecology*, 95, 65-78.

667 38.

668 Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2

669 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4,

670 133-142.

671 39.

Nakagawa, S. & Schielzeth, H. (2016). Coefficient of determination R2 and intra-class correlation coefficient ICC from generalized linear mixed-effects models revisited and expanded. *bioRxiv*.

40.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.* (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167-234.

41.

Pianka, E.R. (1970) On r- and K-selection. *The American Naturalist*, 104, 592-597.

42.

Pinheiro, J.C. & Bates, D.M. (2000). Nonlinear Mixed-effects Models: Basic Concepts and Motivating Examples. In: *Mixed-Effects Models in S and S-PLUS* (eds. Pinheiro, JC & Bates, DM). Springer New York New York, NY, pp. 273-304.

43.

Pollock, L.J., Morris, W.K. & Vesk, P.A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, 35, 716-725.

44.

Price, J.N. & Pärtel, M. (2013). Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos*, 122, 649-656.

45.

Pyšek, P. & Richardson, D.M. (2007). Traits associated with invasiveness in alien plants: Where do we stand? . In: *Biological invasions* (ed. Nentwig, W). Springer-Verlag Berlin & Heidelberg, pp. 97-126.

46.

R Core Team (2014). R: A language and environment for statistical computing. Available at: http://www.R-project.org/.

47.

Reich, P.B. (2014). The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102, 275-301.

48.

702 Richardson, D.M. & Pyšek, P. (2012). Naturalization of introduced plants: ecological

703 drivers of biogeographical patterns. *New Phytologist*, 196, 383-396.

704 49.

705 Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2013).

706 Generalized linear mixed models using AD Model Builder. p. R package.

707 50.

708 Symstad, A.J. (2000). A test of the effects of functional group richness and

709 composition on grassland invasibility. *Ecology*, 81, 99-109.

710 51.

711 Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton

712 University Press, Princeton, MA.

713 52.

714 Tilman, D. (1990). Constraints and tradeoffs: toward a predictive theory of

715 competition and succession. *Oikos*, 58, 3-15.

716 53.

717 Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland

718 biodiversity *Ecology*, 78, 81-92.

719 54.

720 Tilman, D. (2011). Diversification, biotic interchange, and the universal trade-off

721 hypothesis. *The American Naturalist*, 178, 355-371.

722 55.

723 Turnbull, L.A., Crawley, M.J. & Rees, M. (2000). Are plant populations seed-limited?

724 A review of seed sowing experiments. *Oikos*, 88, 225-238.

725 56.

726 USDA-NRCS (2018). The PLANTS Database. National Plant Data Team

727 Greensboro, NC 27401-4901 USA.

728 57.

729 van Kleunen, M., Weber, E. & Fischer, M. (2010). A meta-analysis of trait

730 differences between invasive and non-invasive plant species. *Ecology Letters*, 13,

731 235-245.

732 58.

733 Wandrag, E.M., Catford, J.A. & Duncan, R.P. (under revision). Quantifying niche

734 availability, niche overlap and competition for recruitment sites in plant populations

735 without explicit knowledge of niche axes. *Journal of Ecology*.

736 59.

737 Willis, C.G., Halina, M., Lehman, C., Reich, P.B., Keen, A., McCarthy, S. *et al.*

738 (2010). Phylogenetic community structure in Minnesota oak savanna is influenced by

739 spatial extent and environmental variation. *Ecography*, 33, 565-577.

740 60.

741 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.*

742 (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821-827.

743

Supporting Information

744   **Supporting Information**

745   **Appendix S1:** Hypotheses and rationale for selection of seven study traits and use of

746   multiple trait forms [SI text document].

747   **Appendix S2:** Structure of the candidate models for all four response variables

748   (invader occupancy and abundance in seeded and unseeded subplots) examined in

749   Step 1 and Step 2 of the model selection procedure, and description of all variables

750   [excel file].

751   **Appendix S3:** Additional details about statistical analyses [SI text document].

752   **Appendix S4:** Model selection results and top model coefficients for all four response

753   variables (invader occupancy and abundance in seeded and unseeded subplots) [excel

754   file].

755   **Appendix S5:** Pairwise correlations for all terms used in the models. [excel file].

756   **Appendix S6**: R code used in data processing and analysis:

757   https://github.com/annabellisa/Catford_E93 [github repository].

758   **Table S1:** Characteristics of all 164 taxa observed in the study, including functional

759   groups, frequency of occurrence and mean trait values. Descriptions of data are

760   provided within the file [excel file].

761   **Table S2:** Source of numerical trait data for the 164 taxa observed in this study [SI

762   text document].

763   **Figure S1:** Map of oak savannah study site showing location of experimental plots.

764   (a) Locations of the 30 2 m x 2 m experimental plots; (b) number of sown invaders

765   (see colour legend) added to seeded subplots (NW and SE corners of the plots) in

766   1992 and number of invaders still present in seeded subplots in 2012 (integers next to

767   subplots). The establishment models used data from 54 of the 120 subplots into which

768   seed were added. The spread models used combined data from the two unseeded

769   control subplots within each of the 30 plots (i.e. 2 unseeded subplots were summed

770   and analysed as a single data point, giving 30 plots) [SI text document].

771   **Figure S2** Number of taxa observed across the 20-year experiment [SI text

772   document].

773   **Figure S3** Coefficients for all models with a Δ BIC of <5 for a) establishment

774   probability, b) establishment abundance, c) spread probability and d) spread

775   abundance [SI text document].

776   **Figure S4** Mean standardised cover of functional groups over time. "Other grass"

777   includes grasses identified at the genus level that could not be classified as C3 or C4

778   [SI text document].

779

780

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

| 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

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). For example, occupancy in seeded subplots was highest when soil NO_3 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 > C and I < C indicate cases where successful invader has higher and lower trait values than the recipient community respectively; 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.

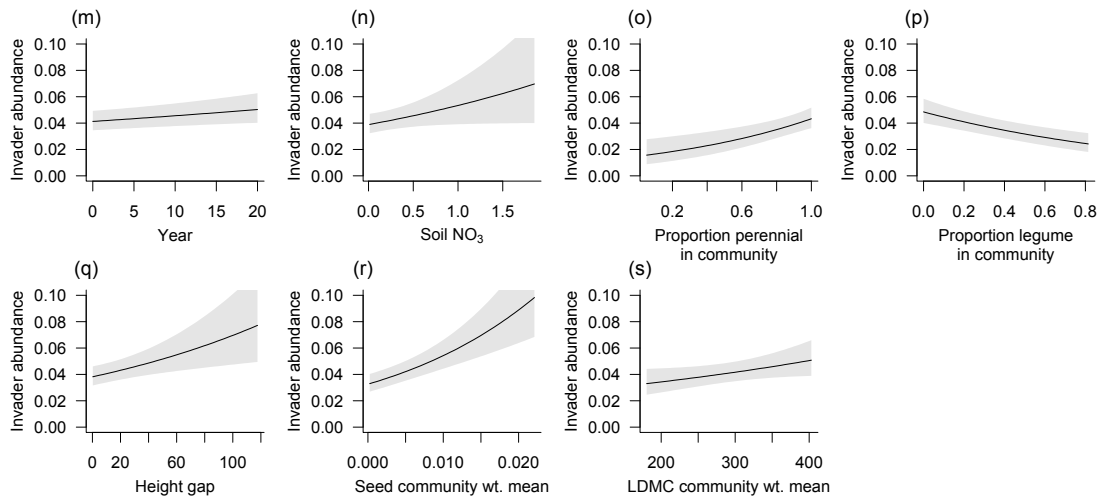| Invasion stage	Establishment in seeded subplots highest when…				Spread to unseeded subplots highest when…			
Invasion indicator	Occupancy		Abundance		Occupancy		Abundance	
Short- or long-term trends	Short	Long	Short	Long	Short	Long	Short	Long
Soil NO_3 in plot in 1991	Low	Low	High	High	NA	NA	NA	NA
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	
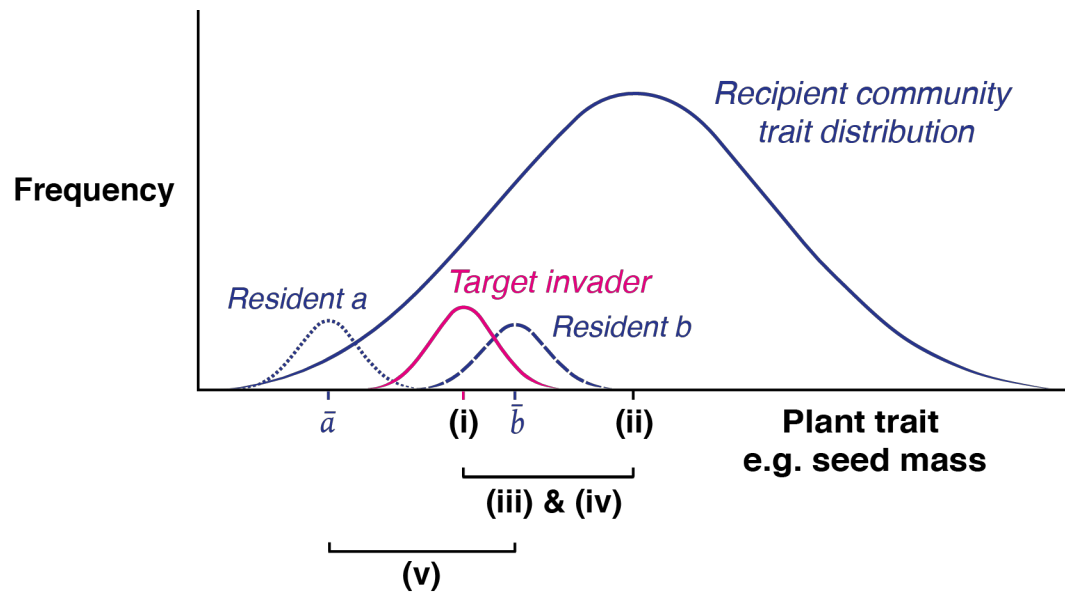
Figure 1 Sketch showing the five trait forms linked with our hypotheses of invasion success that relate to invader traits, community traits, and invader-community trait-based interactions (see Appendix S1 for rationale of predictions). The solid blue line shows the hypothetical distribution of trait 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 trait 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 ($v = \bar{b} - \bar{a}$).

ESTABLISHMENT STAGE: invader occupancy in seeded subplots
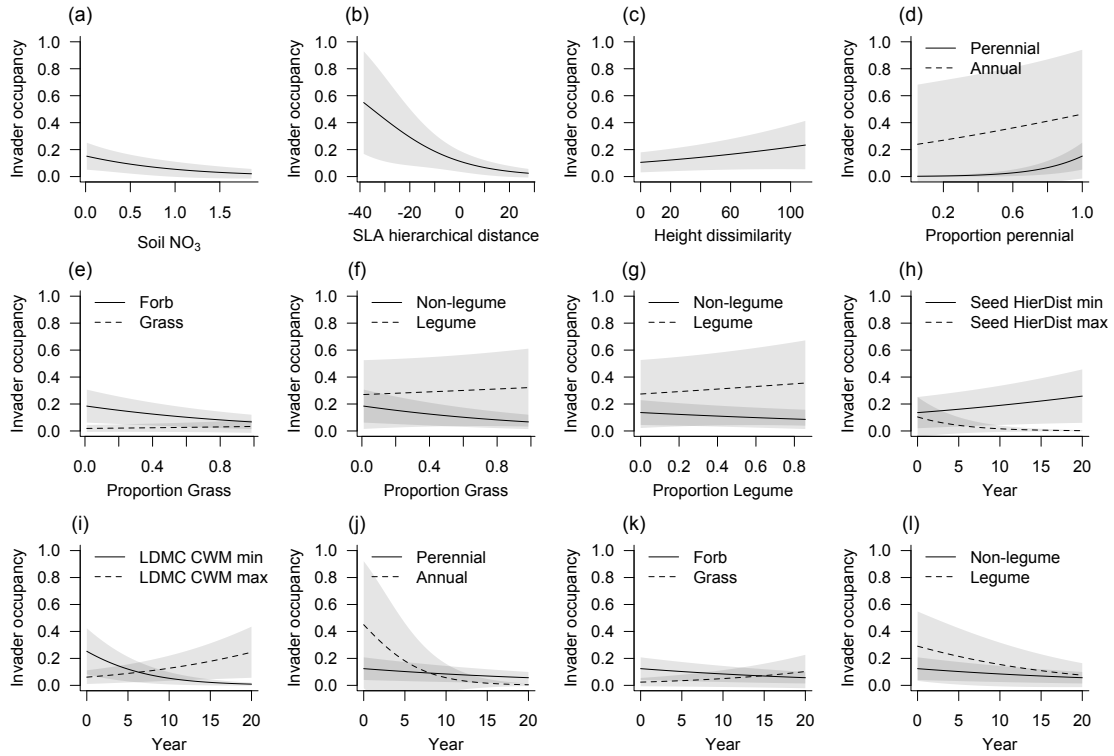
ESTABLISHMENT STAGE: invader abundance in seeded subplots

Figure 2 The establishment stage of invasion, modelled as occupancy and abundance of 50 target invaders, sown into seeded subplots. Plots show results for the best supported model for invader: *a-l*) probability of occupancy (top panels); and *m-s*) 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 and maximum values in the data.
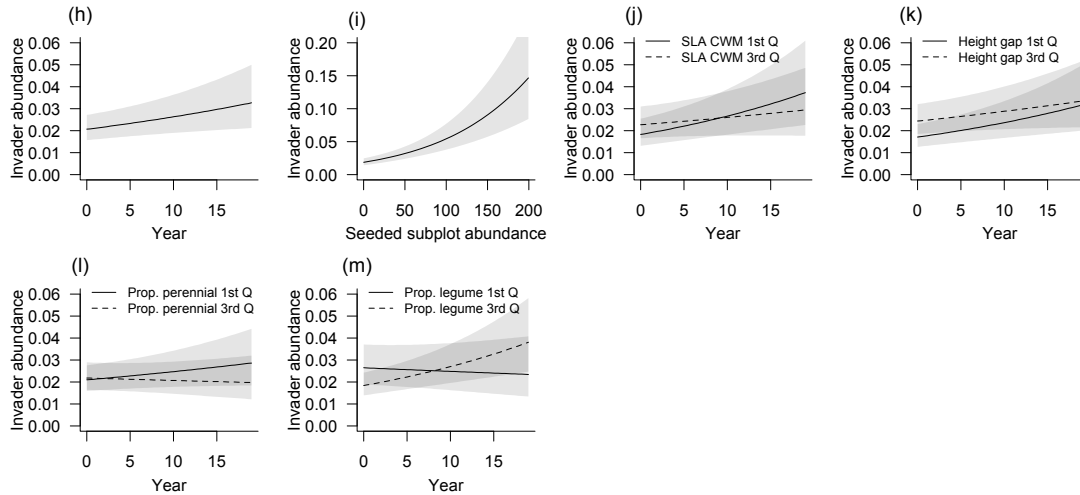
Figure 3 The spread stage of invasion, modelled as occupancy and abundance of 50 target invaders, which spread to unseeded subplots. Plots show results for the best supported model for invader: *a-g*) probability of occupancy (top panels); and *h-m*) proportional abundance, conditional on presence (bottom 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: *d-f*) the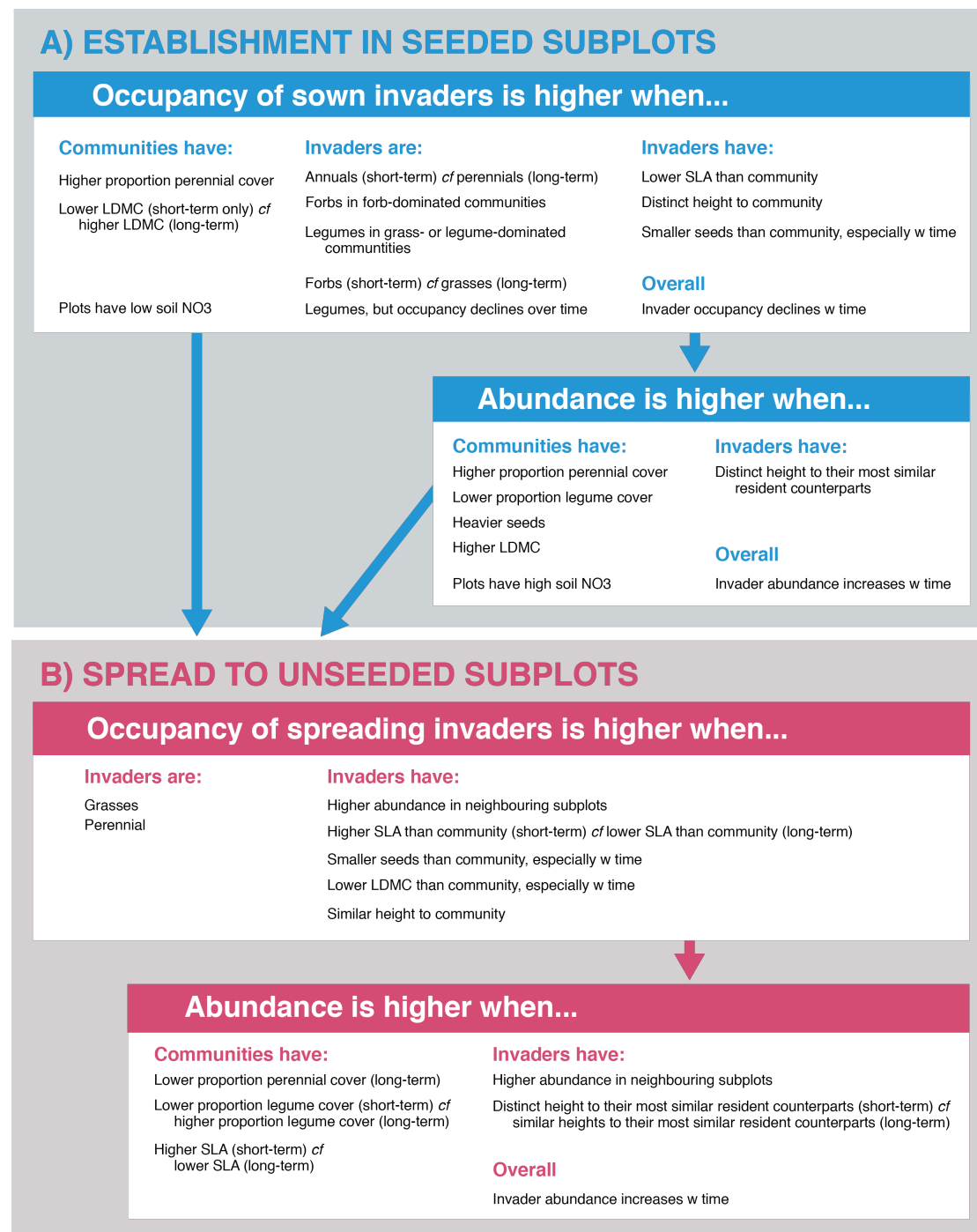 minimum and maximum values in the data; and *j-m*) the first and third quartile in the data. The values at which to plot interactions were chosen based on the distribution of the data. The y-axis is displayed with a different range on panel (*i*).

A) ESTABLISHMENT IN SEEDED SUBPLOTS

Occupancy of sown invaders is higher when...

Communities have:

Higher proportion perennial cover

Lower LDMC (short-term only) *cf* higher LDMC (long-term)

Plots have low soil NO3

Invaders are:

Annuals (short-term) *cf* perennials (long-term)

Forbs in forb-dominated communities

Legumes in grass- or legume-dominated communities

Forbs (short-term) *cf* grasses (long-term)

Legumes, but occupancy declines over time

Invaders have:

Lower SLA than community

Distinct height to community

Smaller seeds than community, especially w time

Overall

Invader occupancy declines w time

Abundance is higher when...

Communities have:

Higher proportion perennial cover

Lower proportion legume cover

Heavier seeds

Higher LDMC

Plots have high soil NO3

Invaders have:

Distinct height to their most similar resident counterparts

Overall

Invader abundance increases w time

B) SPREAD TO UNSEEDED SUBPLOTS

Occupancy of spreading invaders is higher when...

Invaders are:

Grasses
Perennial

Invaders have:

Higher abundance in neighbouring subplots

Higher SLA than community (short-term) *cf* lower SLA than community (long-term)

Smaller seeds than community, especially w time

Lower LDMC than community, especially w time

Similar height to community

Abundance is higher when...

Communities have:

Lower proportion perennial cover (long-term)

Lower proportion legume cover (short-term) *cf* higher proportion legume cover (long-term)

Higher SLA (short-term) *cf* lower SLA (long-term)

Invaders have:

Higher abundance in neighbouring subplots

Distinct height to their most similar resident counterparts (short-term) *cf* similar heights to their most similar resident counterparts (long-term)

Overall

Invader abundance increases w time

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.