Effects of species traits and abiotic factors during the stages of plant invasions

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Abstract

1
2 1. The success of species invasions depends on multiple factors act-
3 ing over the four invasion stages transport, colonisation, establish-
4 ment, and landscape spread. Each of these stages is influenced simul-
5 taneously by particular species traits and abiotic factors. While the
6 importance of many of these determinants has already been inves-
7 tigated in relative isolation, they are rarely studied in combination
8 and even then mostly ignore the final phase, i.e., landscape spread.
9 2. Here we address this shortcoming by exploring the effect of both
10 species traits and abiotic factors on the success of invasions using an
11 individual-based mechanistic model, and relate those factors to the
12 stages of invasion. This approach enables us to explicitly control abi-
13 otic factors (temperature as surrogate for productivity, disturbance

and propagule pressure) as well as to monitor whole-community trait distributions of environmental adaptation, mass and dispersal abilities. We simulated introductions of plant individuals to an oceanic island to assess which abiotic factors and species traits contribute to invasion success.

3. We found that the most influential factors were higher propagule pressure and a particular set of traits. This invasion trait syndrome was characterized by a relative similarity in functional traits of invasive species to natives, while invasives had on average higher environmental tolerances, higher body mass and increased dispersal abilities, i.e., were more generalist and dispersive.

4. Our results highlight the importance in management practice of reducing the import of alien species, especially from similar habitats.

Introduction

Species invasions are highly complex phenomena, influenced by several interacting factors, such as species traits, disturbance, or evolutionary history (Theoharides & Dukes, 2007). Gaining an understanding of these factors is necessary to understand the whole invasion process (Fleming & Dibble, 2015) and establish effective countermeasures (Mehta, Haight, Homans, Polasky, & Venette, 2007). Yet, the relative importance of various factors are difficult to derive from studies focussing only on single invasion events (Catford, Jansson, & Nilsson, 2009). Considering the impending global change scenarios and increased rate of biotic exchange, however, generalizable findings about biological invasions are still urgently needed (van Kleunen et al., 2015).

In the last decades, a number of single factors could be identified that contribute to the success of species invasions. A prominent role falls to the number of intro-

duced individuals, i.e., propagule pressure, as it ensures minimal viable population sizes (Lockwood, Cassey, & Blackburn, 2005). Other abiotic factors such as enhanced productivity and increased disturbance have also been suggested to facilitate invasions in some circumstances (Huston, 2004). Beyond these abiotic factors, species traits may also determine invasibility. Arguably the most obvious of these traits is sufficient pre-adaptation to the abiotic environmental conditions of the invaded habitats (Carboni et al., 2016). Furthermore, invasive species need to be able to compete with native species to establish (Hui et al., 2016). Lastly, increased dispersal abilities and broad environmental niche preferences, i.e. generalism, will enable alien species to spread (Rejmánek, 2000). All these invasion factors and stages vary in their level of expression, depending on the system and taxa.

Theoharides and Dukes (2007) put forward a helpful framework integrating many of these factors and stages. They divide the entire invasion process into four stages: transport, colonisation, establishment, and landscape spread. These stages represent a set of community assembly filters that must be overcome before an alien species may be considered “invasive”. The stages do not represent a strict chronology, but rather a set of interlocking and interdependent factors and processes. Hence, for a species to become invasive, it must (a) arrive in sufficient numbers, (b) be adapted enough to the environment to survive, (c) overcome the competition of native species and reproduce, and (d) disperse to establish new neighbouring populations (Theoharides & Dukes, 2007). The main filters involved in these stages are Allee effects, environmental filtering, biotic resistance, and dispersal ability, respectively. Each of these may be influenced by species traits as well as environmental conditions, as illustrated in fig. 1. Concurrent with this framework, it has been demonstrated that the combination of both abiotic factors and species traits has considerable effects on the success of

invasions (e.g. Küster, Durka, Kühn, & Klotz, 2010; Mata, Haddad, & Holyoak, 2013; Thuiller, Richardson, Rouget, Proches, & Wilson, 2006). However, many studies in the invasion literature still treat species traits and environmental conditions separately, and frequently only consider one factor at a time. To address this shortcoming, Catford et al. (2009) proposed an experimental design that varies propagule pressure, species composition, and abiotic conditions in a full-factorial setup to assess their relative importance for invasion success. An experimental approach like this will be necessary to arrive at a generalised understanding of the invasion process. However, previous experimental studies focused mainly on the earlier stages of invasion and thus, generalized insights that include landscape spread are still missing (cf. Alzate, Onstein, Etienne, & Bonte, 2020; Kempel, Chrobock, Fischer, Rohr, & van Kleunen, 2013).

For generalizing invasion processes, islands can be useful model systems. Firstly, islands are highly susceptible to invasion-related degradation. For example, invasive predators have caused multiple species extinctions on islands (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016), and there have been observed cases of complete “invasional meltdown” after native keystone species were displaced (O’Dowd, Green, & Lake, 2003). Secondly, their small size, isolation, and comparatively simple ecological dynamics mean that islands are popular study systems in ecology in general (Patiño et al., 2017). These characteristics therefore lend themselves to comprehensively study biological invasions in the context of the stages of invasion (Theoharides & Dukes, 2007). Unfortunately, even for islands, exhaustive data to investigate invasion factors are difficult to obtain and conducting systematic experiments is often unfeasible.

As an alternative, mechanistic models offer a powerful approach to supplement field studies. Such models have previously been used in invasion biology, although usually in the context of specific invaded sites (e.g. Buckley, Brieese, &

94 Rees, 2003). However, they also hold great promise for exploring fundamental
 95 processes within a more generalised setting (Cabral, Valente, & Hartig, 2017;
 96 Grimm & Railsback, 2005; Leidinger & Cabral, 2017), and are very useful for
 97 gaining a mechanistic understanding of complex ecological patterns (Grimm &
 98 Railsback, 2011). The fact that mechanistic models allow both complete con-
 99 trol over all environmental variables, as well as complete knowledge of every
 100 individual's traits makes them an ideal tool to help us better understand the
 101 intricacies of the invasion process.

102 Here, we therefore used a recently developed trait-explicit, individual-based
 103 mechanistic model of island plant communities (Leidinger & Cabral, 2020) to
 104 investigate the relative roles of propagule pressure, productivity, and distur-
 105 bance, as well as the traits of invasive species relative to natives. Guided by the
 106 framework of Theoharides and Dukes (2007), we wanted to know which factors
 107 and trait syndromes increase the success of alien species during the stages of
 108 invasions on islands (cf. Pyšek et al., 2015). The specific questions we asked are
 109 found in table 1, covering all stages of invasion and including both trait-based
 110 and environmental factors. Our experimental setup enabled us to go both broad
 111 (covering a wide range of ecological factors) and deep (analysing the resulting
 112 species communities down to the trait level) in our investigation of the invasion
 113 process. We find that propagule pressure and trait syndromes relative to the
 114 native community are the most influential factors promoting invasion success,
 115 and discuss how these factors relate to the stages of invasion.

Figure 1: The four stages of invasion (from top to bottom) with their associated filters and abiotic (left label) and trait (right label) factor groups (Theoharides & Dukes, 2007). Apart from the transport factor groups, all factor groups were explicitly modelled (transport factors were combined in a single “introduction” process.)

Table 1: Questions regarding species invasions to be explored with the model.

No.	Stage	Question	Expectation
1	<i>Transport</i>	How important is propagule pressure for invasibility and why?	Very, because it helps to establish a minimum viable population (Lockwood et al., 2005)
2	<i>Colonisation</i>	Do invasives share a common trait space with native species?	Yes, as they need to be sufficiently adapted to the environment (Carboni et al., 2016)
3	<i>Establishment</i>	How do productivity and disturbance affect invasibility?	Maximum invasibility should be reached at high productivity and high disturbance levels (Huston, 2004)
4	<i>Establishment</i>	Do invasives have a higher fitness than natives?	Yes, as they have to outcompete the natives to establish successfully (Hui et al., 2016)
5	<i>Landscape spread</i>	Are invasives more generalistic and dispersive than natives?	Yes, as this enables them to spread after introduction (Rejmánek, 2000)

116 Methods

117 The model

118 We extended the model of Leidinger and Cabral (2020) to simulate species in-
119 vasions to plant communities on a virtual oceanic island (fig. 2). The island
120 consisted of a 5×5 grid depicting a radial elevation (and corresponding temper-
121 ature) gradient. Additionally, there was a linear (lee-luv) precipitation gradient,
122 which is typical for many oceanic islands. We chose to call this second gradient
123 “precipitation” for simplicity, although it could also be interpreted as any other
124 environmental characteristic like soil type. Each grid cell was assumed to be
125 one hectare in size, with a biomass carrying capacity of two tonnes. Each cell
126 could hold its own community, comprised of individuals belonging to one or
127 more species. Individual body sizes could range between 150 g and 1.2 tonnes,
128 which puts our system along a range between grassland and shrubland (cf.

129 Deshmukh, 1984). Island geometry and extent were chosen arbitrarily to ensure
130 computational feasibility and to provide different environmental combinations,
131 to increase coexistence of native species (see Armstrong & McGehee, 1980).
132 In the model, each individual had a genome consisting of multiple genes that
133 code for a set of traits, which in combination determine the individual's phe-
134 notype. These traits were functional for one or more processes (i.e. traits as
135 parameters of biological functions, table 2). They encompassed environmental
136 optima and tolerances to temperature and precipitation conditions, seed size,
137 reproductive (adult) size, and mean and shape parameters of a logistic dispersal
138 kernel (Bullock et al., 2017). Reproduction only takes place with adult members
139 of the same species within the same grid cell and includes genetic recombination.
140 The probabilities for growth, density-independent mortality, and seed numbers
141 were determined using the Metabolic Theory of Ecology (MTE, Brown, Gillooly,
142 Allen, Savage, & West, 2004), which links yearly biological rates to body mass
143 and to the local temperature. An individual's adaptation to the local grid
144 cell temperature additionally scaled the metabolic density-independent mortal-
145 ity probability, whereas adaptation to local precipitation was used to compete
146 individuals when determining density-dependent mortality.
147 At the initialisation, two species pools were formed with randomly generated
148 species (i.e. each species was characterized by a random combination of genomic
149 and ecological traits). One species pool was used to initialise the island com-
150 munity, and was allowed to stabilise during a "burn-in period" of 500 years.
151 This period length was enough to ensure quasi-equilibrium. Depending on the
152 scenario, native species numbers per island and replicate ranged between one
153 and 15, with a mean of six (Supporting Information, fig. 2). As additions to
154 the original model, the second (alien) species pool had a fixed number of 100
155 species and was used as a source of alien seeds. After the burn-in period, a

Figure 2: Schematic representation of the simulated island. Temperature decreased with altitude, giving a radial gradient with a step size of 2°C per unit of height (greyscale). A second gradient of an abstract environmental resource (termed “precipitation” for simplicity) was applied longitudinally. The green grid cell denotes the point of entry for alien species. Pictograms show the three factors that were varied in the experimental setup, namely temperature, disturbance, and propagule pressure.

156 fixed number of individuals, regardless of species identity, was drawn from this
 157 alien pool and introduced to a specified grid cell on the island (“point of entry”,
 158 fig. 2). To further mimic human activities, disturbances also started after the
 159 burn-in period, consisting of a given percentage of individuals being randomly
 160 removed from each grid cell every year, in addition to the previously mentioned
 161 causes of mortality. The model was allowed to run for a total of 1500 years.
 162 For the choice of parameter values, etc., the reader is referred to the full model
 163 description in the ODD format (Grimm et al., 2010), found in the Supporting
 164 Information. The source code for the model was written in Julia (Bezanson,
 165 Edelman, Karpinski, & Shah, 2017), and is available at [https://github.com/](https://github.com/lleiding/gemm)
 166 [lleiding/gemm](https://github.com/lleiding/gemm), along with its documentation.

Table 2: Ecological and life-history processes included in the invasion model, in the order of execution.

Process	Details
<i>Survival</i>	Density-independent mortality relative to an individual's temperature adaptation.
<i>Growth</i>	Individuals increase in body size until they reach reproductive size.
<i>Competition</i>	If the total biomass in a grid cell exceeds its carrying capacity, compete pairs of individuals and kill the one with the lower precipitation adaptation (density-dependent mortality).
<i>Reproduction</i>	Sexual reproduction including recombination of the parents' genomes by meiosis, produces multiple seeds.
<i>Disturbance</i>	Species- and density-independent mortality of a given percentage of individuals in each grid cell.
<i>Transport</i>	Introduction of aliens (i.e. individuals from the alien species pool) into the point of entry.
<i>Dispersal</i>	Dispersal of seeds produced during reproduction, the distance is calculated with a dispersal kernel.

167 Experimental design

168 We varied the three factors propagule pressure, productivity, and disturbance
169 in a full-factorial design across two levels of each factor to give a total of eight
170 scenarios (cf. Catford et al., 2009; fig. 2). 60 replicates of each scenario were
171 run, resulting in 480 simulations.

172 We used temperature as a proxy for productivity, varying the base (lowland)
173 temperature between 15°C and 35°C. These values were arbitrary but provided a
174 sufficiently large contrast while maintaining realism. Due to our use of the MTE,
175 higher surrounding temperatures lead to an increase in growth and reproduction
176 rates and thus satisfy the general requirements for productivity (Huston, 2004).
177 Propagule pressure (1 or 10 individuals per year) and disturbance (1% or 10%
178 mortality per year) were explicitly implemented in the model, as described above
179 (cf. Buckley, Bolker, & Rees, 2007; Kempel et al., 2013, for factor values).

Figure 3: **a)** Island map after the burn-in period ($t = 500a$), and **b)** at the end of the simulation ($t = 1500a$) for one example run. Each marker represents one population, colours signify species. Natives are circles, aliens triangles. The green grid cell is the point of entry, grey scale denotes temperature (cf. fig. 2).

180 Data recording and analysis

181 Every year, the model recorded a log file with the mean and variance of each
182 population's trait values. All data analyses were carried out in R 3.2.3 using
183 ggplot2 for visualisation (R Core Team, 2017; Wickham, 2016).

184 To quantify the effect of the varying factors on the success of species invasions
185 (study questions 1 and 3, table 1), we classified species as native, alien, or
186 invasive (species type). Natives were species from the original island species
187 pool that were still extant at the end of the burn-in period. Aliens were all
188 species introduced to the island from the alien species pool. Invasives were the
189 subset of alien species that had established at least one population outside of
190 the point of entry, i.e., had undergone landscape spread (Ricciardi & Cohen,
191 2007). We then identified all species that became invasive across all replicate
192 runs and summed these up by scenario. During each run, we generated island
193 maps at regular intervals, showing size, location, and species of all populations
194 (e.g. fig. 3).

195 To compare the environmental adaptation A_{ind} of natives, aliens, and invasives,
196 (study question 4, table 1) we combined the model's internal calculation of
197 adaptation to temperature and precipitation as follows:

$$A_{ind} = G(T_{opt}, T_{tol}, T_{env}) \times G(P_{opt}, P_{tol}, P_{env}) \quad (1)$$

198 where $G(b, c, x)$ is the Gauss function at point x with mean b and a standard
199 deviation of c ; T is the temperature and P the precipitation; N_{opt} the indi-
200 vidual's niche optimum value, N_{tol} its niche tolerance, and N_{env} the actual
201 environmental niche value in the individual's grid cell.

202 For trait comparisons between alien, invasive and native species (study questions
203 2 and 5, table 1), we pooled population data per species type ('alien', 'invasive'
204 or 'native') from all scenarios. From this pooled data, we used native popu-
205 lations at the onset of invasion (year 500), and invasive and alien populations
206 over the entire invasion period. The traits we were interested in comprised mean
207 dispersal distance, long distance dispersal, precipitation tolerance, temperature
208 tolerance, adult biomass in grams, and seed biomass in grams. Since precipita-
209 tion and temperature optima traits were primarily influenced by geography and
210 the particular temperature scenarios, we omitted them from our analysis of the
211 pooled data. Furthermore, we $\log(x + 1)$ -transformed all trait and adaptation
212 values to improve normality, because the original distributions were left-skewed
213 and contained values < 1 . We then performed a principal component analysis
214 (PCA) on standardized trait medians of that data to investigate general pat-
215 terns of trait space by comparing the size and location of 95% confidence interval
216 ellipses corresponding to the different species types. For the PCA, we omitted
217 alien populations, since their increased spread in trait values made comparison
218 of natives versus alien species unfeasible. To assess how the trait characteristics
219 in single traits of native species differed from invasives and identify the most

important traits that distinguish native species from invasives, we performed linear mixed models with the particular trait as response, species type as fixed effect, and the specific replicate as random effect, using the R package `lme4` (Bates, Mächler, Bolker, & Walker, 2015). We do not report statistical significance of results, since this is mostly meaningless for mechanistic simulation models, as spurious significance emerges by simply increasing replicate number (White, Rassweiler, Samhouri, Stier, & White, 2014).

Results

A total of 28 species became invasive over all runs, one of them across two different scenarios. We found a strong link between propagule pressure and invasibility, with almost four times as many invasives occurring in high-pressure compared to low-pressure scenarios (fig. 4). Temperature also had a strong influence, with a two- to three-fold difference between levels. There was no clear relationship between invasibility and disturbance.

In terms of the total trait space, invasive populations exhibit a larger spread than natives (fig. 5). The center of the invasive populations' trait space is shifted along the second PCA dimension towards higher long distance dispersal, higher mean dispersal distance, and higher precipitation tolerance compared to native populations.

The difference in total trait space is associated with specific differences of the particular traits between species category. Specifically, mean dispersal distance (fig. 6a), long distance dispersal (fig. 6b), precipitation tolerance (fig. 6c), temperature tolerance (fig. 6d), and adult biomass (fig. 6e) were all increased in aliens and invasives compared to natives. Seed biomasses were increased in aliens, but slightly decreased for invasives (fig. 6f). For long distance dispersal,

Figure 4: Cumulative number of invasive species observed in each of the eight scenarios (60 replicate runs per scenario).

precipitation tolerance, temperature tolerance, and adult biomass, the differences in means between natives and invasives were smaller than between natives and aliens. The differences in precipitation and temperature tolerance resulted in the lowest adaptation values for aliens and highest adaptation values for natives, while invasives shows intermediate adaptation value (fig. 6g). The results from the linear mixed models revealed what traits were most important to distinguish invasive species from native (table 3). The difference in biomass explained by far the most variance, followed by precipitation tolerance, temperature tolerance, long distance dispersal and seed biomass. Mean dispersal distance explained only a small amount of variance.

Discussion

Although not explicitly imposed by the model, we observe the filtering functions of the stages transport, colonisation, establishment, and landscape spread (fig.

Figure 5: Principle component analysis (PCA) showing the distribution of population trait medians in the trait space. Each axis arrow represents one trait, each marker is one population. All traits were $\log(x + 1)$ transformed and normalized before PCA calculation. Natives in purple, invasives in yellow. Ellipses represent 95 % confidence envelopes.

Table 3: Results of linear mixed-effects model fits comparing the means of species' traits with the type of species (native or invasive, with invasive as reference) as fixed effect and replicate as random effect. Note that invasive species were more dispersive and generalist with heavier adults, but lighter seeds than native species. Std. Error: standard error, D.f.: degrees of freedom, Mean Sq: mean squares.

Trait	Estimate	Std. Error	D.f.	t value	Mean Sq
Mean dispersal distance	-0.044	0.003	32467	-16.915	8.668
Long distance dispersal	-0.148	0.004	32438	-41.012	96.768
Precipitation tolerance	-0.360	0.005	32502	-68.964	572.091
Temperature tolerance	-0.214	0.005	32521	-40.307	203.051
Adult biomass (g)	-1.040	0.025	32519	-41.395	4790.100
Seed biomass (g)	0.144	0.028	32521	5.130	92.142

Figure 6: Distributions of single trait values. (a) Mean dispersal distance, (b) long distance dispersal, (c) precipitation tolerance, (d) temperature tolerance, (e) adult biomass in grams, (f) seed biomass grams, (g) adaptation to local temperature and precipitation conditions. All values were $\log(x + 1)$ transformed before visualisation. Boxes show medians and interquartile range. Red lines highlight the means. Blue: populations of native species, red: populations of alien species, yellow: populations of invasive species.

1). Therefore, the general patterns of our model results conform to current knowledge from the empirical and theoretical literature (Theoharides & Dukes, 2007). In line with the requirements of the pattern-oriented modelling paradigm (Grimm & Railsback, 2011), these emergent patterns are found at different ecological levels (individual, population, community, and metacommunity).

Propagule pressure

Concerning the question on the importance of propagule pressure for the success of invasions (question 1, table 1), our findings mirror ample evidence from empirical studies, including macroecological analyses (e.g. Carr, Hooper, & Dukes, 2019; Seebens et al., 2018). Indeed, propagule pressure is well-known as the leading driver of invasion success in the current literature (Cassey, Delean, Lockwood, Sadowski, & Blackburn, 2018; Lockwood et al., 2005). This is mainly due to Allee effects in introduced populations (Keitt, Lewis, & Holt, 2001; Taylor & Hastings, 2005). Only sufficiently large populations will grow fast enough to overcome adverse abiotic conditions and inter-specific competition by native species. As described in Allee effects theory, this relation of population growth to density is typically hump-shaped, and will decrease again beyond a critical density (Courchamp, Clutton-Brock, & Grenfell, 1999; Stephens, Sutherland, & Freckleton, 1999). Thus, increasing propagule pressure will not increase invasion success indefinitely.

Indeed, Cassey et al. (2018) found a sigmoidal relationship between propagule pressure and establishment success. This was also reflected in additional post-hoc experiments with our model. With propagule pressure increased to 100 individuals per year, we did not observe an increase in the number of successful invasions (Supporting Information, fig. 1). Unfortunately, a direct comparison of our values with those of Cassey et al. (2018) is difficult. This is because

284 Cassey et al. (2018) do not relate their measure of propagule pressure to time,
 285 but assume a single initial release, which runs counter to the design of our study.
 286 Rather, the repeated introductions in our model increase our *de facto* propagule
 287 pressure beyond the one or ten individuals introduced in one year; but the
 288 stochastic nature of introductions makes it impossible to quantify exact values
 289 per species. Nevertheless, the results of our subsequent simulations indicate that
 290 we did reach propagule saturation as well. The reason for this is likely increased
 291 intra- and interspecific competition among juvenile alien individuals in already
 292 saturated communities. This saturation is an effect of our initial simulation
 293 conditions, where we initialize communities with more species populations than
 294 they will eventually hold. Given that real islands are known to have lower
 295 species richness than continents (Whittaker & Fernández-Palacios, 2007) and
 296 are thus likely un-saturated in terms of species numbers, they will therefore be
 297 much more susceptible to increased introductions than saturated continental
 298 systems. This highlights again the vulnerability of island biota to global change
 299 processes.

300 Temperature and disturbance

301 The interaction between temperature (our surrogate for productivity) and dis-
 302 turbance was not as straight-forward as we had expected (question 3, table
 303 1). The dynamic equilibrium model (Huston, 2004) predicts that invasibility
 304 approximately increases with native diversity, which is high when both produc-
 305 tivity and disturbance are high, or when both are low. This is because high
 306 productivity with low disturbance leads to population extinction through com-
 307 petitive exclusion, while low productivity with high disturbance means small
 308 populations that go extinct stochastically (Huston, 2004). Indeed, as described
 309 by Huston (2004), we did observe a clear peak of mean native species rich-

ness in the low-temperature, low-disturbance scenarios (Supporting Informa-
tion, fig. 2). Despite this, maximum invasibility did not coincide with either low-
temperature/low-disturbance or high-temperature/high-disturbance scenarios,
but was driven almost entirely by temperature (fig. 4). This apparent mis-
match of our model with theory may raise some questions at first, but can be
explained by a closer look at disturbance and its influence on invasion processes.
The interplay between productivity and disturbance and its effect on species
richness and composition has long been discussed in the theoretical literature
(e.g. Catford et al., 2012; Chesson, 2000) and shown in multiple empirical stud-
ies (e.g. Huebner, Regula, & McGill, 2018; O'Connor, Falk, Lynch, Swetnam,
& Wilcox, 2017). However, these interactions are subject to several precondi-
tions. Firstly, Buckley et al. (2007) point out that disturbance may increase the
invasibility of a habitat, but can also be a cause of mortality for alien species, re-
ducing invasibility again. Thus, if disturbance affects natives and aliens equally,
these two contrary effects may cancel each other out, leaving no net change.
This was the case in our model, as disturbance-driven mortality was species-
agnostic. Secondly, the effects of disturbance on native and alien communities
are likely to change over the full gradient of disturbance intensity (Catford et
al., 2012). Analysing that many disturbance levels was beyond the scope of
this study, however. Therefore, our experiment only reflects two points on this
gradient and may thus give an incomplete picture. And thirdly, an invaded
community's response to disturbance can be strongly modulated by the trait
composition of its native and alien species (Kempel et al., 2013; Mata et al.,
2013). This includes traits that are represented in our model, which will be
discussed in the next section.

335 Traits of invasive species

336 Although sometimes questioned in studies on species invasions (cf. Catford et
337 al., 2009, but see Thuiller et al., 2006), our results provide some insights into an
338 “invasion syndrome” relative to the native community and the stages of invasion
339 (question 2, table 1; Novoa et al., 2020). In fact, invasive species are more
340 similar to native species than alien species in terms of their trait characteristics
341 (cf. Küster et al., 2010). This suggests that invasive species have to pass
342 similar environmental filters to natives in order to complete the colonization
343 and establishment stages.

344 However, this trait similarity is not sufficient to surpass native species in terms
345 of environmental adaptation (question 4, table 1). Instead, invasive species have
346 on average lower environmental adaptation. The fact that some invasive species
347 are still successful, and even end up replacing native species, again highlights the
348 importance of propagule pressure. This might offset some of the maladaptation
349 and the priority effect advantage enjoyed by native species (Chase, 2003). Such
350 interaction of traits and propagule pressure is in line with recent evidence from
351 field and laboratory experiments (Alzate et al., 2020; Kempel et al., 2013). Still,
352 propagule pressure alone does not explain why invasives also manage the fourth
353 phase, landscape spread.

354 In order for invasives to spread, we expected increased dispersal abilities and a
355 rather generalistic niche strategy (question 5, table 1). Indeed, invasive species
356 in our simulations not only feature increased mean and long distance dispersal,
357 but also have higher environmental tolerances on average (see Grotkopp & Re-
358 jmánek, 2007; Schultz & Dibble, 2012). These latter trait characteristics suggest
359 the generalist nature of invasive species, at least in comparison to natives. A
360 larger biomass and thus reduced mortality in invasives additionally makes them
361 stronger competitors (cf. Kempel et al., 2013). This circumstance will also help

offsetting relative maladaptation, besides propagule pressure.

Furthermore, the difference in trait characteristics between species categories might also indicate different evolutionary backgrounds. In this respect, our island communities are the result of several hundreds of years of ecological interactions between species and the environment. This is especially evidenced by their decreased dispersal ability, which is a typical island adaptation (Burns, 2019). They are, therefore, sensitive toward invasive species that (1) were not restricted by those interactions, and (2) exhibit trait syndromes different from those represented in the community. Additionally, invasive species are bigger than natives, but not as big as (unsuccessful) alien species. Thus, the invasion syndrome features adaptation to similar conditions as the invaded native community, but sufficiently different other key traits (e.g. biomass), unbounded by the local evolutionary history, to fill areas of the trait space with the least overlap with native species. If this overlap is enough to induce competitive exclusion, superior competitive abilities allow invasive species to outperform, and thus replace, native species, which we could observe in some of our simulations (cf. Flory & Clay, 2010; Pyšek et al., 2012).

Future considerations

In our simulations, we could not account for most biological interactions except for competition. Mutualisms between native species will likely lead to secondary extinctions, or even extinction cascades, if keystone species get lost (Christian, 2001; Schachtschneider & February, 2013). Trophic interactions can also allow effects like enemy-release of alien species. Therefore, the effects of invasions on our simulated communities might be very conservative and underestimated. We anticipate that the consideration of additional interactions into our modeling framework will further increase the impact of species invasions on the native

388 communities.

389 In this study, we corroborated the importance of propagule pressure for the
 390 invasion success. It is important to point out, however, that previous studies
 391 frequently conflated this with the related but separate concept of colonization
 392 pressure, i.e., the number of species (rather than individuals) introduced per
 393 time (Lockwood, Cassey, & Blackburn, 2009). Although the two may interact
 394 and are difficult to differentiate in the field, they do in fact address two quite
 395 dissimilar mechanisms: propagule pressure determines how quickly a minimum
 396 viable population can be established, whereas colonization pressure increases the
 397 chances of introducing a suitable species. Our experiment does not completely
 398 disentangle these two aspects, but by using an alien species pool of constant size,
 399 we still arguably test the more specific understanding of “propagule pressure”.
 400 However, future investigations could use a model such as ours to fully separate
 401 the effects of both these factors in designated experiments.

402 Increasing the runtime of the model may lead to additional insights. A number of
 403 studies have pointed to the impact of longer time scales on the invasion process.
 404 For example, Pyšek et al. (2015) and Carr et al. (2019) show a link between
 405 residence time or sustained propagule pressure and establishment rates. On the
 406 other hand, Sheppard and Schurr (2019) observed an increase in biotic resistance
 407 over time, which decreases the performance of alien species. Investigating such
 408 long-term and large-scale effects of invasion factors further is possible with our
 409 model, although this will require significant computational resources.

410 Although beyond of the scope of this study, the current model allows us to
 411 consider genomic traits in the characterisation of species. In a previous study,
 412 Leidinger and Cabral (2020) show how environmental variation interacted with
 413 the number of genes and genomic variation of communities. Similarly, inva-
 414 sive species might display particular genomic profiles which enable them to

quickly adapt to novel environments, for example by high standing variation or phenotypic plasticity (Zenni, Lamy, Lamarque, & Porté, 2014). To increase computational feasibility and preclude possible confounding effects, we chose not to include these effects in the present study. However, we expect future experimental designs to account for variation in genomic traits and to allow for mutations when investigating species invasions.

This study demonstrates the utility of individual-based mechanistic models for understanding biological invasions. Our results hold relevance for policy and management, as they reinforce the importance of reducing the import of alien species. This is true of alien species in general, but even more so for those showing high environmental tolerances and dispersal abilities, as well as those coming from habitats with similar conditions as native ecosystems.

Conflict of interests

The authors declare no conflict of interests.

Data Accessibility

All data should be reproducible by using the simulation codes found at <https://github.com/lleiding/gemm>.

Author contributions

DV, LL, and JSC conceived the ideas and designed methodology; DV performed simulations; DV and LL analysed the data; DV led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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