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ORIGINAL PAPER

Prior adaptation, diversity, and introduction frequency mediate the positive relationship between propagule pressure and the initial success of founding populations

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Abstract Propagule pressure is often considered the most consistent predictor of the success of founding populations. This relationship could be mediated by the composition of the founding group (e.g. level of prior adaptation to the recipient environment or its diversity) as well as the introduction scenario (i.e. the frequency, size and timing of discrete introduction events). We introduced groups of *Tribolium castaneum* (red flour beetle) eggs across three levels of propagule pressure (n = 15, 30, 60), of three possible compositions (single, adapted lineage; single, unadapted lineage; mixed lineages) to a novel environment using six unique introduction scenarios, in a fully factorial design to evaluate the importance of composition and introduction scenario in influencing the relationship between propagule pressure and establishment. In our system, prior adaptation to the environment, including having some adapted individuals in mixed groups, rivaled the importance of propagule pressure in determining the establishment success and size of founding populations. More frequent introduction events resulted in fewer individuals that initially survived founding, but introduction scenario did not significantly influence establishment success or population size. This experimental evidence demonstrates the importance of context, both of the founding group and the recipient environment, in understanding how propagule pressure influences the success of founding populations.

Keywords Propagule pressure · Colonization · Genetic diversity · Invasive species · Adaptation

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Introduction

Understanding why founding populations establish or fail to establish is of fundamental importance in explaining the abundance and distribution of organisms across landscapes (MacArthur and Wilson 1967). Within the field of invasion ecology, the total number of individuals introduced in a founding group, or "propagule pressure," is one of the most consistent predictors of establishment success (i.e. whether or not populations establish; Williamson 1996; Lockwood et al. 2005; Colautti et al. 2006; Simberloff 2009; Blackburn et al. 2015). Propagule pressure has also been shown to influence other aspects of the success of founding populations, including population size (Hufbauer et al. 2013) and fitness (Elam et al. 2007). However, groups founded with the same number of individuals can still vary widely in whether or not they successfully establish and their ability to persist once established. It is critically important to better understand what drives differences in outcomes in addition to numbers of individuals, particularly in the first few generations of founding, during which effective management of invasive species is crucial (Gurevitch et al. 2011; Hufbauer et al. 2013). Important aspects influencing the positive effect of propagule pressure on the success of founding populations, as well as the variation around those predictions, include: whether individuals within a founding group are adapted to the environment to which they are introduced (e.g. Hufbauer et al. 2012); how diverse founding groups are (e.g. Crawford and Whitney 2010; Szűcs et al. 2014); and the timing and frequency of discrete introduction events (e.g. Grevstad 1999; Shea and Possingham 2000).

Founding groups vary in the composition of their individuals. Clearly, populations will fail to establish if *none* of the individuals within the founding group can survive in the recipient habitat. If at least some individuals in a founding group can survive, the number of individuals in the founding group can mediate establishment success and the size of the population once established (Blackburn et al. 2015). Prior adaptation to the recipient environment promotes higher fitness, as traits that were advantageous in the native environment are similarly advantageous in the recipient environment (Sol 2007; Hufbauer et al. 2012). The fitness of individuals in the recipient environment can mediate the magnitude and shape of the positive relationship between propagule pressure and success, with fewer individuals needed to successfully establish if environmental conditions promote survival and reproduction (Crawley 1986; D'Antonio et al. 2001; Rouget and Richardson 2003; Szűcs et al. 2014). Thus, establishment success is more likely if all individuals in a founding group exhibit prior adaptation to the recipient environment.

In reality, founding groups often consist of a mix of adapted and unadapted individuals. As diversity increases from monocultures to polycultures, average establishment success and resulting population size can increase, as groups have an increased probability of containing an individual that exhibits prior adaptation to the recipient environment (i.e. sampling effect; Loreau and Hector 2001). This is considered an *additive* diversity effect when individuals in mixed groups perform the same as they would in monoculture (Hughes et al. 2008; Crawford and Whitney 2010). A diverse founding group acting through additive effects alone would not outperform a founding group of individuals that all exhibit prior adaptation to the recipient environment. However, if individuals perform better in mixture than they would in monoculture (*non-additive* diversity effect), more diverse founding groups could outperform a group that is adapted, but lacking diversity, if the non-additive effects outweigh the effect of pre-adaptation. Examples of positive non-additive effects of diversity include complementarity, admixture, and facilitation (Hughes et al. 2008; Crawford and Whitney 2010).

Genetic diversity generally increases as propagule pressure increases, from a purely probabilistic standpoint (Ahlroth et al. 2003). Thus, to assess the impact of genetic diversity on the positive relationship between propagule pressure and the success of founding populations, it is necessary to experimentally separate demography and genetics. A growing body of experimental work suggests that increased genetic diversity can match or even outweigh the effect of an increased number of individuals in the first few generations of founding (Ahlroth et al. 2003; Elam et al. 2007; Agashe et al. 2011; Hufbauer et al. 2013; Hedge et al. 2014; Szűcs et al. 2014), but that sometimes larger founding groups, regardless of their diversity, are more likely to successfully establish than smaller groups (Wootton and Pfister 2013).

Beyond the composition of founding groups, how individuals are introduced can also influence establishment success. Propagule pressure is intrinsically the product of the number of individuals introduced in a single introduction event (hereafter: cohort) and the frequency of those events (Lockwood et al. 2005; Fauvergue et al. 2012). Recent studies have addressed whether fewer introductions of larger cohorts are more successful in establishing than more frequent introductions of smaller cohorts (Shea and Possingham 2000; Drake et al. 2005; Hedge et al. 2012; Britton and Gozlan 2013; Drolet and Locke 2016; Sinclair and Arnott 2016; Koontz et al. 2017). The optimal cohort size and frequency of introduction events is not consistent as it can vary across species, environmental contexts, and whether introduction events are separated by space or time (Grevstad 1999). Further, the timing of introduction events can affect establishment success (Yamamichi et al. 2014). For example, on a large temporal scale, annual fluctuations in temperature or precipitation moderate bioclimatic niches for invasive species (e.g. opening safe-sites; Kowarik 1995). Similar patterns likely also exist on a smaller temporal scale; for example, introducing individuals of different ages during colonization can influence success (Järemo and Bengtsson 2011).

To more fully understand the variation in success of founding populations, it is necessary to jointly address the importance of adaptation to the recipient environment, diversity of the founding group, and introduction scenario (i.e. frequency, size and timing of introduction events), as these components could also interact. For example, less diverse populations could benefit from more frequent introduction events by mediating the reduction in diversity linked to bottlenecks in population size that many founding populations experience (Dlugosch and Parker 2008; Koontz et al. 2017). These potential interactions could explain the divergent conclusions regarding the importance of prior adaptation of individuals and diversity within founding groups and the importance of size, frequency and timing of introduction events.

Here, we sought to better understand how the level of adaptation and diversity of founding groups, together with the size, timing and frequency of introduction events, influence the relationship between propagule pressure and the initial success of founding populations. We used founding groups of *Tribolium castaneum* (red flour beetles) to assess how these factors influence (1) establishment success (whether or not founders successfully reproduced, thus avoiding immediate extinction) and (2) size of populations that had established two generations after introduction.

Methods

Source lineages

Large (500 to > 2000 individuals) panmictic populations of six unique lineages of *T. castaneum* were reared in standard densities in incubators at 31 °C for a minimum of 10 discrete generations prior to the start of the experiment. Lineages were maintained in replicate 4 × 4 × 6 cm plastic boxes (hereafter: patches), containing 30 mL of medium (described below). Adults at standard densities were allowed 24 h to mate and oviposit, and then were removed and discarded. Offspring were allowed five weeks to develop into adults, and then given fresh media to re-initiate the cycle. Three of these lineages were maintained on a nutritionally rich media (95% wheat flour, 5% brewer's yeast) and three were maintained on a challenging media (98.2% corn flour, 1.71% wheat flour, 0.09% brewer's yeast) that used a novel source of carbohydrate (corn flour) and had a reduced amount of nutritional yeast. Previous experiments using similarly nutritionally challenging corn media show that adaptation to a challenging corn environment can occur, and includes the evolution of increased cannibalism, faster development, and smaller body size (Agashe et al. 2011; Szűcs et al. 2014, 2017). Three lineages that were maintained on corn flour media will be hereafter referred to as "adapted" because the recipient environment in this experiment was mostly corn, and three lineages that were maintained on the natal, wheat environment will be referred to as "unadapted".

One generation before the experiment began, individuals within source lineages were introduced to a novel environment (99.0% corn flour, 0.95% wheat flour, 0.05% brewer's yeast) at a constant density to standardize maternal environment carryover effects, which can be strong in *T. castaneum* populations (Van Allen and Rudolf 2013, 2016; Hufbauer et al. 2015). The next generation of adults was then allowed to mate on fresh media for 24 h and their eggs were sifted out of the media. These eggs were used to create experimental founding groups.

Experimental design

We founded experimental groups of *T. castaneum* eggs on nutritionally challenging media (99.9% corn flour, 0.095% wheat flour, 0.005% brewer's yeast), to simulate an introduction where successful establishment was difficult, potentially even for adapted lineages. Founding groups were composed either of eggs from a single, adapted lineage (one of three lineages previously adapted to a high proportion corn media), a single, unadapted lineage (one of three lineages not previously adapted to a high proportion corn environment), or of eggs randomly drawn from a pool of all six lineages, with each lineage providing the same number of eggs to the pool. Random draws from that pool resulted in variation across replicates of the same propagule pressure and allowed for levels of propagule pressure that were odd numbers (e.g. n = 15). We consider single and mixed treatments to be biologically representative of lower and higher genetic diversity treatments, respectively [as supported by data on microsatellite loci in Szűcs et al. (2014)].

Groups were founded at three levels of propagule pressure: 15, 30, or 60 eggs, and were introduced to the patches in one of six, week-long introduction scenarios, which varied in timing (which day of the week introductions occurred), frequency (how many introduction events occurred), and cohort size (number of individuals at each introduction event) (Fig. 1). Propagule pressure levels of 15, 30, and 60 were chosen as they are each divisible by both three and five, and thus, founding groups could be evenly split for introduction scenarios of varying frequencies. We tested the effect of varying cohort size and the number of introduction events jointly, as well as the timing of the introduction events. For example, for introduction scenario 1 (Fig. 1), for a propagule pressure of 15 eggs, five eggs were introduced each on Monday, Tuesday, and Wednesday. Given that beetle populations were restricted to a 35-day life cycle from egg to adult, differences in frequency and timing of introduction events on the magnitude of a few days represent a considerable portion of a full cycle and were postulated to influence competition within a founding group. We implemented a full-factorial design (3 composition treatments × 3 levels of propagule pressure × 6 introduction scenarios = 54 treatment combinations). As single lineage treatments

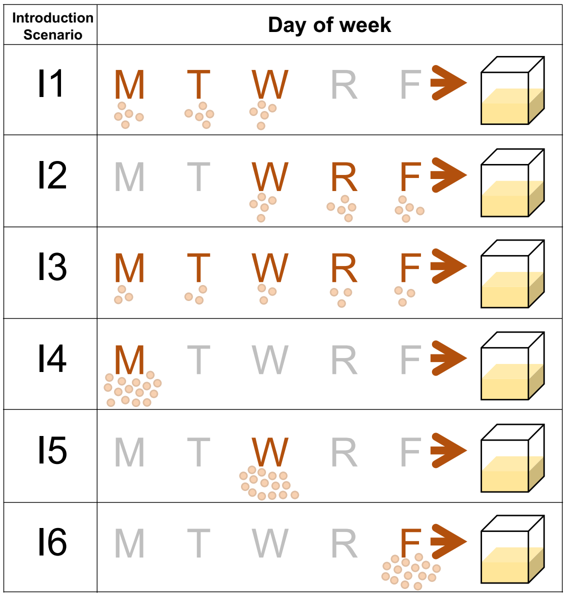

Fig. 1 Experimental introduction scenarios each varying in frequency (number of discrete introduction events), size (proportion of individuals in each introduction event), and timing [what day(s) of the week beetles are introduced]. Days of the week for each scenario are listed in consecutive order and are represented by letters such that *WRF* represents individuals being introduced on Wednesday, Thursday, and Friday. Note: this depicts propagule pressure n = 15, but in the experiment, 3 levels of propagule pressure were used (n = 15, 30, 60) using the same proportion of eggs for each introduction event

were divided into single:adapted and single:unadapted post hoc, our design had 9 replicates of each treatment combination for single lineage treatments and 18 replicates of each treatment combination for mixed treatments.

Beetles that reached adulthood in each founding group were censused after a five-week development period, placed on fresh media, allowed to mate for 24 h, and were then removed. Offspring were censused an additional five weeks later. We recorded the number of individuals that survived from egg to adulthood. We evaluated the effect of propagule pressure, adaptation, diversity, and introduction scenario on *establishment success* (the probability of avoiding population extinction) and the *size* of extant populations at the end of the second generation.

Statistical analyses

All statistical models were fitted in R version 3.4.2 (R Core Team 2017). For all models, we estimated the significance of interactions and main effects by comparing a full model (i.e. with model terms of the same order) to a reduced model without the interaction or main effect of interest.

We assessed the probability of establishment using a generalized linear mixed model (binomial distribution with a logit link) with a binary response of extant or extinct after two generations using propagule pressure, composition, introduction scenario, all possible two-way interactions, and temporal block as fixed effects. A three-way interaction between experimental factors could not be included as it did not allow model convergence. An interaction between lineage (i.e. one of the six lineages or mixed) and block was included as a random effect to account for replicate populations within each lineage by block combination. For multiple treatment combinations, all replicate populations successfully established and as such, there was no variation in establishment (i.e. the separation problem, Albert and Anderson 1984). We applied a Bayesian maximum a posteriori approach using the package *blme* (version 1.0.4) to the generalized linear mixed model, assigning uninformative priors to fixed effects [i.e. $N(\mu = 0, \sigma^2 = 9)$], which allowed for model fit despite complete separation. Likelihood ratio tests were used to evaluate the significance of model terms and we present Wald confidence intervals around predicted means.

We evaluated treatment differences for the size of extant populations after two generations with a linear mixed model using the package *lme4* (version 1.1.14) with a Gaussian error distribution using propagule pressure, composition, introduction scenario, their interactions, and block as fixed effects as well as an interaction between lineage and block as a random effect. Population sizes were log-transformed to meet the assumption of homogeneity of variance. Parametric bootstrap methods [*pbkrtest* (version 0.4.6)] with 10,000 iterations were used to evaluate the significance of interactions and main effects (Halekoh and Hojsgaard 2014). Confidence intervals (CI) were estimated using the adjusted bootstrap percentile method with 10,000 iterations using *boot* (version 1.3.18).

To understand how the initial survivors of the colonization event influenced population size after two generations, we modeled the growth rates of extant populations using a linear mixed model with a Gaussian error distribution. Growth rates were log-transformed to meet the assumption of homogeneity of variance. As the propagule pressure level determined the possible number of adults that survived from egg to adult and *T. castaneum* growth rates are strongly density-dependent (Birch et al. 1951; Halliday et al. 2015), we modeled growth rates of extant populations using composition, introduction scenario, number of adults at first census (density), their interactions, and block as fixed effects. Density was log-transformed to meet the assumption of linearity. The random effect structure was the same as for the establishment and population size models. A significant effect of treatment (composition or introduction scenario) or an interaction between these treatments and density would indicate that there is a mechanism moderating population growth beyond what is explained by the number of adults at the first census. We evaluated significance and estimated confidence intervals using the same bootstrap methods as in the population size analysis.

Results

Larger founding groups were more likely to establish than smaller founding groups ($p < 0.001$; Fig. 2; Table S1), as predicted. Mixed and adapted founding groups were more likely than unadapted groups to establish ($p < 0.001$; Fig. 2; Table S1), and prior adaptation and diversity did not mediate the effect of propagule pressure on establishment success (composition by propagule pressure interaction $p = 0.57$; Fig. 2; Table S1). There were no differences in establishment success between populations founded with different introduction scenarios ($p = 0.24$; Figure S2; Table S1).

The sizes of the populations that established varied depending on the composition of founders, with mixed and adapted founding groups growing larger on average than unadapted founding groups ($p < 0.001$; Fig. 3; Table S2). Populations composed of unadapted or adapted lineages were relatively similar in size regardless of initial propagule pressure but interestingly, propagule pressure was important in predicting the population size of mixed founding groups (composition by propagule pressure interaction, $p = 0.05$; Fig. 3; Table S2). For example, founding groups with the fewest individuals resulted in populations that were 37.8% (CI 23.9–49.1%) smaller than populations

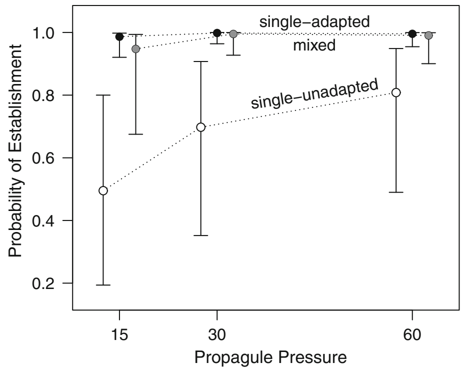

Fig. 2 Probability of population establishment after introduction and one generation of mating for adapted single lineage, unadapted single lineage, and mixed founding groups at three levels of propagule pressure (15, 30, 60 eggs). Back-transformed model means and 95% confidence intervals are reported. Points for each composition group are jittered for ease of interpretation

from groups with the most individuals. There was no effect of introduction scenario on population size by the second generation ($p = 0.77$, Table S2).

Differences in population size after two generations were partially driven by negative density-dependent growth: as the number of individuals that survived the founding event increased, population growth rates decreased ($p < 0.001$; Figure S3; Table S3). At average density, mixed and adapted founding groups still exhibited 118.7% (CI 53.1–211.5%) and 150.6% (CI 81.3–244.4%) higher population growth rates respectively, than unadapted founding groups.

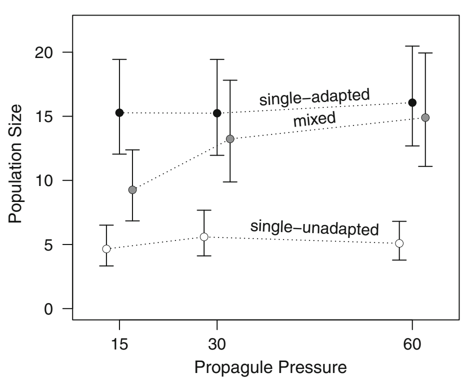

Fig. 3 Population size of extant populations after introduction and one generation of mating for adapted single lineage, unadapted single lineage, and mixed founding groups at three levels of propagule pressure (15, 30, 60 eggs). Back-transformed model means and 95% confidence intervals are reported. Points for each composition group are jittered for ease of interpretation

However, the density-dependent regulation of growth rate was weaker for mixed groups than for adapted groups (Figure S3; difference in slope on log-scale 0.47 [CI 0.17–0.78]; composition by density interaction $p = 0.01$; Table S3).

Discussion

Propagule pressure

Our results validate the empirically supported positive relationship between propagule pressure and establishment success, but weakly: only the smallest founding groups (n = 15) had a significantly lower establishment success (Fig. 2). Further, only for diverse founders did introducing smaller groups result in smaller population sizes than introducing larger groups. Propagule pressure strongly influenced the number of individuals that survived initial founding and negative density dependence was important for determining the number of survivors (Figure S1). Negative density dependence is strong in our experimental system (Birch et al. 1951; Halliday et al. 2015); increases in density can reduce survival from egg to adult because there is proportionally lower nutrient availability during development (Wong and Lee 2011). This effect can also be exacerbated by an increase in cannibalism, which helps mitigate the nutritional deficit (Mertz and Cawthon 1973). Negative density dependence likely influenced the impact of propagule pressure on establishment success and population size following establishment in our experiment. This is a biologically reasonable scenario for some invasive species (Hui and Richardson 2017), as competition for limited resources can be common.

Prior adaptation and diversity

Diversity and prior adaptation strongly influenced the success of founding populations. Both adapted and mixed founding groups were more likely to establish than unadapted groups and had a similarly high probability of establishment (on average > 95%), indicating that only a proportion of individuals in the founding group need be adapted to the recipient environment to establish successfully. Population size following establishment was contingent on propagule pressure, the composition of founding groups, and the number of individuals that survived the initial founding event (density) as evidenced by the growth rate analysis (Figure S3; Table S3). At the lowest level of propagule pressure, final population size reflected the patterns of founding group survival (Figure S1): adapted founding groups were larger than mixed groups, and mixed groups were larger than unadapted groups. However, for larger founding groups (n = 30, 60), adapted and mixed groups performed similarly to each other and better than unadapted groups (Fig. 3). Similarities in sizes of mixed and adapted populations for larger founding groups can be explained by two possible, non-mutually exclusive, mechanisms in the context of our experiment.

First, a positive diversity effect from mixing unadapted and adapted individuals could be more beneficial to founding groups of larger sizes. However, this more positive effect of genetic diversity on larger rather than smaller populations runs counter to theory and empirical evidence, which suggest that increased diversity should be most advantageous to smaller populations that are prone to inbreeding (e.g. Lande 1988; Szűcs et al. 2014). Second, negative density-dependent growth could explain why large, mixed founding groups were of similar population size as large, adapted groups. Fewer individuals from mixed groups survived the first generation than individuals from adapted groups (Figure S1), meaning they should experience less negative density dependence and exhibit higher growth rates, allowing populations to increase their size close to the size of adapted populations. There is also evidence that increased diversity can decrease population sensitivity to density-dependent regulation (Johnson et al. 2016). We see this pattern here, as growth rates of mixed groups were less influenced by density than were those of adapted groups (Figure S3; Table S3). No matter what the mechanism, we provide evidence that increasing the number of adapted individuals in a founding group increases establishment success and the size of extant populations.

We found that adaptation to the novel environment seemed to outweigh the overall effect of propagule pressure. This result contributes to the growing body of literature assessing the relative importance of habitat suitability and propagule pressure in predicting the success of founding populations (Rouget and Richardson 2003; Maron 2006; Nuñez et al. 2011; Erfmeier et al. 2013; Hufbauer et al. 2013; Szűcs et al. 2014; Duncan 2016). For example, Hufbauer et al. (2013) conducted experimental introductions of *Bemisia* (whitefly) that included host suitability and propagule size (the number of individuals in one introduction event), factorially. In that experiment, host suitability explained the probability of establishment and population growth rate. However, population size was influenced by an interaction between propagule size and host suitability. In contrast, propagule size was found to be more important than habitat suitability in predicting colonization success for founding groups of *Hypericum perforatum* (Maron 2006). There is not yet a consensus in the literature on how propagule pressure and habitat suitability interact to drive colonization success, and our research contributes to that discussion.

The context-dependence of the effect of propagule size on establishment success was further verified in dung beetles by Duncan (2016): the importance of the size of the founding population for different species relied on the variability of the recipient habitat. Similarly, the relative importance of prior adaptation and propagule pressure in our experiment is likely driven by the fact that our recipient environment was very harsh and our choice of propagule pressure levels was relatively narrow. Clearly at low enough levels of propagule pressure, founding groups would always fail to establish (fewer than two beetles as *T. castaneum* is a sexual species), and in that case, propagule pressure would always be more important to establishment success than prior adaptation and diversity. This same notion applies to the relative contribution of introduction scenario to establishment and population size. Thus, we do not contend that prior adaptation and diversity will always be more important than propagule pressure, but suggest that demography alone often cannot fully explain establishment outcomes.

Introduction scenario

Neither establishment success nor size of populations that established was influenced by introduction scenario. Interestingly, introducing many, small cohorts resulted in fewer initial survivors than groups founded with other scenarios (Figure S2), but this effect was outweighed by the effects of prior adaptation and diversity by the second generation. This small drop in survival for founding groups that were introduced in the smallest cohorts (and thus most frequently), could be a result of different timings of introduction exacerbating negative density-dependent interactions, such that cohorts introduced at the earliest time may partially deplete resources for the last cohort introduced. Given that adaptation and diversity possibly overwhelmed more subtle effects of introduction scenario in our experiment, future studies should manipulate the frequency, size and timing of introduction events to achieve a better mechanistic understanding of how these factors influence the success of founding populations.

Conclusion

Our results show that multiple factors contribute to the fate of founding populations above and beyond the positive effect of propagule pressure. Propagule adaptation to the recipient environment additionally increases the probability of establishment. Introduction frequency, size and timing play minor roles in mediating establishment success compared to population composition and propagule pressure, at least in the harsh (i.e. where prior adaptation is imperative to survival) environments in the present study. Similar experiments in more benign environments, or for other systems, would allow for a more holistic understanding of how frequency, size and timing influence establishment. Given that many factors can influence the success of founding populations, predictive models for invasive species establishment cannot rely on propagule pressure alone to predict if founding populations will be successful. Further, understanding the population dynamics of a particular invasive species (e.g. strength of density-dependent growth) may be critical in determining how important prior adaptation, diversity, and introduction scenario are in determining probability of establishment and population size in the generations after founding.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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