



# Consequences of hybridization during invasion on establishment success

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## Abstract

Initial colonization by non-native species sometimes occurs in regions already occupied by closely related species, and subsequent hybridization is often inevitable. However, there are several different ways that such hybridization might affect the successful establishment of the non-native species, but many of these remain insufficiently explored. Although there is growing evidence in support of improved local adaptation by genetic rescue, we demonstrate here another way that closely related species can facilitate invasions in which hybridization assists the invading species to overcome Allee effects arising from mate-finding failure. We explore this phenomenon using a simple mathematical model of two closely related diploid insect species, native and non-native, exhibiting differences in mate searching efficacy, relative strength of competition, and mate preference. We find that when the carrying capacity in the invading species is higher than in the native species, invasion success is facilitated. Invasion is also facilitated under parameterization for high hybrid fitness and severe competition between natives and hybrids. In light of these results, we discuss general patterns of how invasion success is affected by the manner in which native, non-native, and hybrids interact with each other and note situations where such conditions might occur in nature.

**Keywords** Allee effect · Hybridization · Mathematical model · Population dynamics

## Introduction

Overall numbers of invading species are increasing worldwide, and there is little indication of declining rates of new invasions (Seebens et al. 2017). The strength of biosecurity

programs vary among countries (Early et al. 2016), and despite the effectiveness of these programs at reducing arrival rates, there remain certain invasion pathways by which non-native species continue to be transported to new regions (Sakai et al. 2001; Hulme et al. 2008).

Though many non-native species arrive in novel regions, few of these successfully establish invading populations. The reasons why some organisms succeed in establishing new populations while others do not are not completely understood. Considerable evidence indicates the importance of propagule pressure; establishment success is closely related to the size of the colonizing population (Lockwood et al. 2005). Invading populations often suffer from a heavy positive density dependence, i.e., the Allee effect, in the initial phase of invasion (Courchamp et al. 1999; Taylor and Hastings 2005). Several mechanisms, such as inbreeding depression, cooperative feeding, and predator satiation, are known to cause Allee effects (Berec et al. 2007), but mate location failure is often one of the most severe in invading populations (Taylor and Hastings 2005; Yamanaka and Liebhold 2009). Invading populations exist at characteristically low densities and are isolated in space; under these conditions, populations characteristically have difficulty to find mates.

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One mechanism by which invading species sometimes may avoid depressed population growth arising from mate-finding failure is mating with closely related native species (e.g., congenics). Relatively small founding populations of non-native species may be able to sustain their genetic material in hybrid populations (Cox 2003; Mesgaran et al. 2016; Wares et al. 2005). Such hybrid populations of course are only possible when a closely related species exists with which they can mate and their hybrid offspring are viable. There are several studies from various invasive taxa exploring how hybridization with a native species can facilitate invasion success (e.g., Cox 2003; Wares et al. 2005). Surprisingly, however, precedent studies mainly focus on genetic advantages of hybridization, such as heterosis (Roman and Darling 2007) or genetic rescue effects (Tallmon et al. 2004). There has been little exploration of the demographic benefits that hybridization can have on relief from mate-finding Allee effects.

Recently, Mesgaran et al. (2016) constructed a theoretical model for plant populations that incorporates demography, mating systems, quantitative genetics, and pollinators. They proposed the novel concept that hybridization itself provides a demographic rescue effect for low-density invading populations in the absence of elevated fitness in hybrids and their progeny. Simulations using their model revealed that even a small founding population of a non-native species may be able to introduce its genes into a native population via hybridization and thereby overcome population size constraints caused by pollen limitation. If the non-native genes are more favorable to pollinators (or even equivalent), the native genes are gradually replaced by the non-native genes and the non-native species thereby becomes established. Non-native species can thus utilize hybridization with native species as a stepping stone for establishment in a new region: a phenomenon we refer to here as “demographic rescue via hybridization” in contrast to “genetic rescue effect” (Barton 1979; Edmonds et al. 2004; Hufbauer et al. 2015).

Even though empirical evidence is still scarce, it is possible that the phenomenon of hybridization demographic rescue may be common in animal as well as in plant populations (Havill et al. 2017; Yara et al. 2007). The limited number of candidate examples includes the parasitoid species, *Torymus sinensis* (Hymenoptera: Torymidae), which is native to China, and is an effective biological control agent of the non-native chestnut pest, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae), introduced to Japan in 1982. The parasitoid was rapidly established and spread quickly throughout Japan resulting in successful biological control (Moriya et al. 1989, 2002). Though there are several plausible explanations for the widespread success and rapid establishment of this species, hybridization with the congeneric native species, *T. beneficus*, was frequently observed. Populations of native *T. beneficus* and the hybrids with *T. sinensis* were gradually replaced by *T. sinensis* (Yara et al. 2007; Yara et al. 2010). The

demographic rescue of *T. sinensis* via hybridization with *T. beneficus* can explain successful rapid establishment of this biological agent. Another example of demographic rescue effect is provided by the invasive lepidopteran pest, *Operophtera brumata* (Lepidoptera: Geometridae), which suddenly spread through the New England region of the eastern USA (Elkinton et al. 2010). *Operophtera brumata* is known to hybridize with the congeneric native species, *O. bruceata*, and there is strong asymmetric fertility among the two species, and their hybrids;  $F_1$  and backcrosses can produce viable offspring when mated with the invasive *O. brumata* (Havill et al. 2017).

Though hybridization may in some cases facilitate establishment of invading species, it could also have adverse impacts. If  $F_1$  and successive hybrids have decreased fitness or are less competitive than their parents, hybridization acts as a sink mechanism in sink-source population dynamics, and the small number of genes from the invading species will be trapped (Coyne and Orr 2004). In such the cases, the Allee threshold is strengthened and invading populations arriving in small numbers will be extremely prone to extinction. There is also a possibility that a small fraction of genes from the invading species can remain in the gene pool otherwise dominated by the closely related native species (Dowling and Secor 1997). In yet another scenario, if hybrids are more fit than either parent species, they may occupy their own ecological niche and create a new gene pool (hybrid speciation) in the invaded habitat (Roman and Darling 2007; Schwarz et al. 2005).

To better understand the ecological conditions under which hybridization with a native species facilitates establishment of a closely related non-native species, we construct a simple theoretical model of two congeneric species, one native species and the other non-native. For simplicity, we assume that both species are diploid and that their biological properties are controlled by a single locus with two alleles, though the results obtained from our model are likely applicable to the other hybridizing organisms with random (non-assortative) mating. We first demonstrate that demographic rescue effect by an invading species can be observed, much as has been shown for plants (Mesgaran et al. 2016). We then use animals as target systems to explore how key parameters of mate searching efficacy, relative strength of competition, and mate preference, affect the conditions for invasion facilitation. Finally, we quantify the speed of invasion success, i.e., how hybridization can accelerate the establishment of the invading species compared to those without hybridization.

## The model

We developed a frequency- and density-dependent deterministic model to explore population dynamics of native and non-

native species as well as their hybrids. The assumption is made that two species (resident and invader) and their hybrids are homogeneously distributed across space. Consider a single locus with two alleles ( $a$  and  $A$ ) in a diploid outbreeding sexual species with non-overlapping generation. Three genotypes,  $AA$ ,  $Aa$ , and  $aa$ , correspond to resident ( $R$ ), hybrid ( $H$ ), and invader ( $I$ ), respectively. We denote  $p(t)$  as the frequency of allele  $A$  in the population censused in generation  $t$ . Hence,  $1 - p(t)$  is the frequency of the  $a$  allele. Frequencies of these genotypes follow from random mating as summarized by the Hardy-Weinberg principle. These basic assumptions are based on classical population genetic models which explain the maintenance of a genetic polymorphism within a single species rather than hybridization of two species (Roughgarden 1971; Charlesworth 1971).

Given a population density  $N(t)$  (individuals per unit area) at generation  $t$ , the absolute number of each genotype in the population can be deduced from the gene frequency:  $N_R(t) = p^2(t)N(t)$ ,  $N_H(t) = 2p(t)(1 - p(t))N(t)$ , and  $N_I(t) = (1 - p(t))^2N(t)$ , where the subscript indicates each genotype. Similarly, we define the absolute fitness of each genotype as  $\lambda_g(t)$  ( $g \in R, H, I$ ) and average absolute fitness of the population as

$$\bar{\lambda}(t) = p^2(t)\lambda_R(t) + 2p(t)(1 - p(t))\lambda_H(t) + (1 - p(t))^2\lambda_I(t) \quad (1)$$

Defined in this way,  $\bar{\lambda}(t)$  also measures the total rate of population growth between the  $t$ th and  $t + 1$ th generations. Thus, the entire population dynamics can be described as  $N(t + 1) = \bar{\lambda}(t)N(t)$ . In addition, the gene frequency of allele  $A$ , expressed as zygotes at generation time  $t + 1$ , is

$$p(t + 1) = \frac{\lambda_R p^2(t) + \lambda_H p(t)(1 - p(t))}{\bar{\lambda}} \quad (2)$$

We assume that the fitness of each genotype  $\lambda_g(t)$  changes over time, and these fitnesses will be functions of total population size  $N(t)$  and allele frequency  $p(t)$ . Using the Ricker's discrete logistic equation (Ricker 1954) to specify this density and frequency dependencies gives

$$\lambda_g(t) = \exp \left[ r_g \left\{ 1 - \frac{N(t)}{K_g} C_g(p(t)) \right\} \right] \times I(N(t)) \quad (3)$$

where  $C_g(p(t))$  corresponds to competition term among genotypes:

$$C_g(p(t)) = c_{g,R}p^2(t) + c_{g,H}2p(t)(1 - p(t)) + c_{g,I}(1 - p(t))^2 \quad (4)$$

and  $I(N(t))$  represents a positive density-dependent factor, i.e., an Allee effect. The term  $c_{g_1,g_2}$  ( $> 0$ ) is the

competition coefficient quantifying the effect of an individual of genotype  $g_1$  on an individual of  $g_2$ . The term  $\exp \left[ r_g \left\{ 1 - \frac{N(t)}{K_g} C_g(p(t)) \right\} \right]$  is a negative density-dependent factor. Variables  $r_g$  and  $K_g$  represent the intrinsic growth rate and the carrying capacity of each genotype population in the absence of the positive density dependence (i.e.,  $I(N(t)) = 1$ ). For an Allee effect due to mate limitation, we let

$$I(N(t)) = \frac{sN(t)}{1 + sN(t)} \quad (5)$$

be the probability of finding a mate where  $s$  ( $s > 0$ ) is an individual's searching efficiency (Dennis 1989; McCarthy 1997; Scheuring 1999).

The basic model shown above will mainly be examined in the later section. In addition, the model can be extended to include assortative mating among genotypes, following frequency-dependent function  $M_g(p(t))$ . Specific forms of the function are:

$$M_R(p(t)) = a_{R,R}(p^2(t))^2 + a_{R,H}p^3(t)(1 - p(t)) + a_{H,H}(2p(t)(1 - p(t)))^2 \frac{1}{4} \quad (6a)$$

$$M_H(p(t)) = a_{R,H}p^3(t)(1 - p(t)) + a_{R,I}p^2(t)(1 - p(t))^2 + a_{H,H}(2p(t)(1 - p(t)))^2 \frac{1}{2} + a_{H,I}p(t)(1 - p(t))^3 \quad (6b)$$

$$M_I(p(t)) = a_{H,H}(2p(t)(1 - p(t)))^2 \frac{1}{4} + a_{H,I}p(t)(1 - p(t))^3 + a_{I,I}(1 - p(t))^4 \quad (6c)$$

The variable  $a_{g_1,g_2}$  ( $> 0$ ) represents the mating preference between genotype  $g_1$  and  $g_2$ . As an example,  $M_R(p(t))$  indicates the degree that offspring are native individuals from assortative matings. The first term on the right-hand side represents the probability of crosses between two natives,  $a_{R,R}(N_R(t)/N(t))^2$ . The second and third terms include crosses between a native and a hybrid, and between two hybrids, respectively. In addition to coefficients of mating preference, a constant is multiplied by each term based on Mendelian inheritance of one-locus two-allele model. When considering frequency-dependent assortative mating, we simply assume that the probability of successful mating is reduced because following initial encounter, pairs sometimes do not mate because of their preferences. Maximum values of  $M_g(p(t))$  vary depending on parameters  $a_{g_1,g_2}$ ; thus, we multiply  $M_g(p(t)) / \max_{0 \leq p(t) \leq 1} (M_g(p(t)))$  which has a value from zero to one, to the intrinsic growth rate  $r_g$ . Otherwise,  $M_g(p(t)) = 1$  (random mating) is assumed in the following result section.

## Results

### Population dynamics and Allee effects

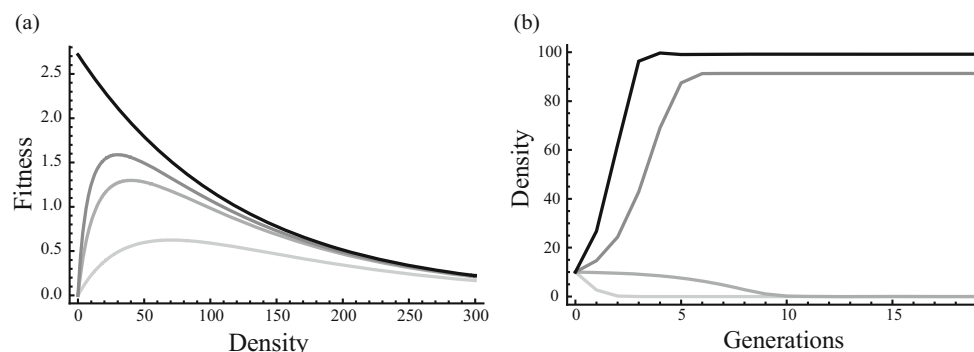
To analyze the invasion-related population dynamics and allele frequency dynamics in this system, we first consider the invader population in isolation by setting the initial population size of the resident species and hybrids equal to zero. When a strong Allee effect exists, there is a possibility that a small invader population cannot establish in the absence of a population of the resident species (Fig. 1). This result implies that a small number of migrants from the original invader population are sometimes insufficient to establish a new population due to mate limitation.

However, when a small number of resident species are present, hybrid individuals can reproduce, and the invader allele can persist in the common gene pool. If there are no differences in parameters such as growth rates and competitive relationships among the three genotypes, and when starting from almost same number of individuals, hybrid individuals become a majority in the population and form a hybrid swarm at equilibrium (Fig. 2). In another example, when the resident population vastly outnumbers the invading population, it is robust against invasion. In this case, invaders are maintained at a very low frequency, or competitive exclusion occurs depending upon the initial number of individuals. The invader alleles will remain in the population at low levels as hybrid individuals and may be maintained in the gene pool (see Fig. S1).

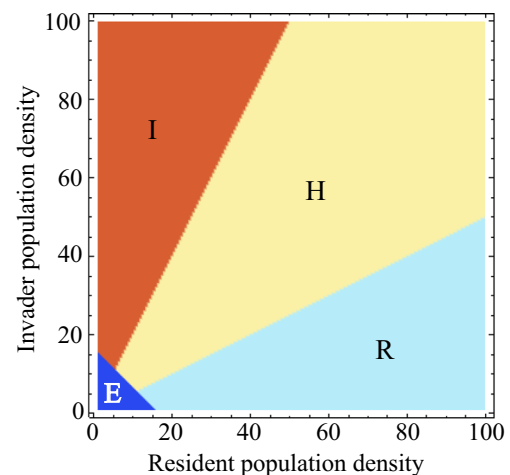
The patterns above describe dynamics in the absence of differences in fitness and mate preference among the three genotypes. In the following section, we explore conditions under which the invader species succeeds in colonizing by overcoming competition with the resident species and the Allee effect through the formation of hybrid individuals.

### Invasion facilitation through mating with hybrids

Here, we investigate the outcome of an invasion when resident and invader populations have different ecological properties.



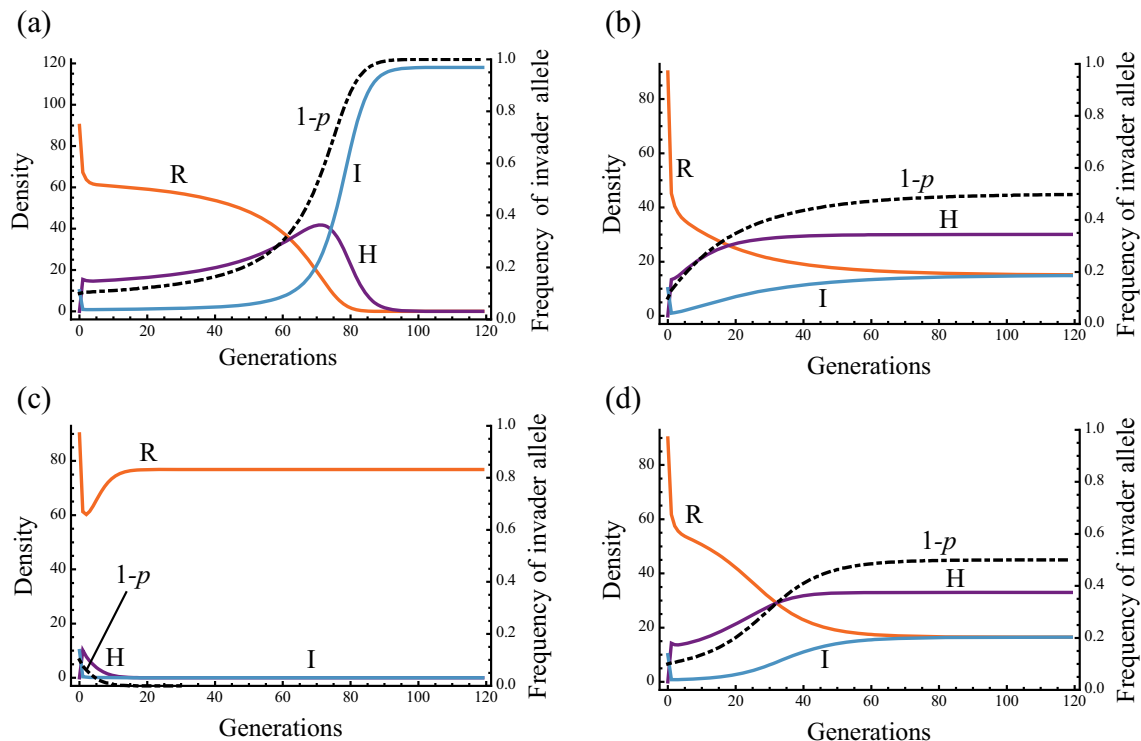
**Fig. 1** **a** Fitness function with different strengths for the Allee effect.  $s = 0.01, 0.05, 0.1$ , and  $1$  from bottom to top. **b** Dynamics of the invader population under the Allee effect shown in **a** setting the initial condition



**Fig. 2** Dependence of equilibrium states on initial resident and invader population densities when assuming no ecological parameter differences among all genotypes (equal fitness). Regions in the parameter space are categorized by the genotype that is dominant in the population; R resident, H hybrid, I invader, E extinction. All parameters are as in Fig. 1 except for  $s = 0.035$

In a scenario representative of the classical invasion ecology literature (e.g., Parker et al. 2013), we assume that the invader species has a larger intrinsic growth rate  $r_g$  or carrying capacity  $K_g$  compared to the resident species. In Fig. 3a, a greater carrying capacity in the invader species resulted in the facilitation of invasion success even when the initial population size of the invader was much smaller than the resident, and the growth rate of the hybrid was slightly lower than that of either species. In this example, the population size of the invading species initially declined and hybrid individuals became more abundant. Although there was little change in the dynamics after this phase, the hybrid population size gradually grew. Then, the invasion rapidly progressed as the invader population increased, while simultaneously, hybrid individuals decreased in abundance. In our model, the value of the intrinsic growth rate had little effect on the long-term behavior of the population dynamics, but it did influence the transient behavior as the system approached equilibrium (Case 2000).

as  $N_R(0) = N_H(0) = 0$  and  $N_I(0) = 10$ . In cases of  $s = 0.01$  and  $0.05$ , the population went extinct within ten generations. Parameters are  $r_R = r_H = r_I = 1.2$ ,  $K_R = K_H = K_I = 100$ ,  $c_{R,R} = c_{R,H} = c_{R,I} = c_{H,H} = c_{H,I} = c_{I,I} = 1$



**Fig. 3** Temporal variation in population densities (R resident, H hybrid, I invader) and invader allele frequencies ( $1-p$ ). **a** Invasion succeeded under the condition that the carrying capacity of the invader is larger than that of the resident. **b** A hybrid swarm occurs when intraspecific competition is stronger than interspecific competition. **c** Competitive exclusion results when interspecific competition is stronger than intraspecific competition. **d** A hybrid swarm results even under strong interspecific competition with heterosis. The following parameters are

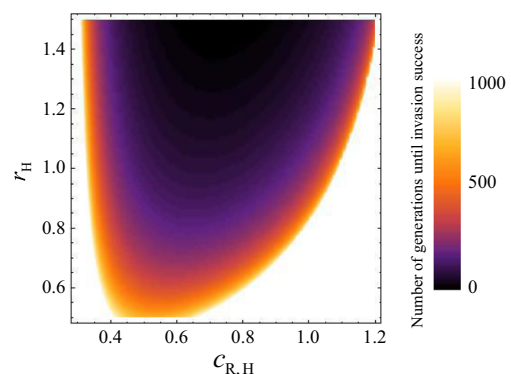
used for all figures as shared values:  $r_R = r_I = 1$ ,  $K_R = 100$ ,  $s = 0.05$ ,  $N_R(0) = 90$ ,  $N_H(0) = 0$  and  $N_I(0) = 10$ . The other parameters are case-dependent: **a**  $r_H = 0.9$ ,  $K_H = 100$ ,  $K_I = 140$ ,  $c_{R,R} = c_{R,H} = c_{R,I} = c_{H,H} = c_{H,I} = c_{I,I} = 1$ ; **b**  $r_H = 1$ ,  $K_H = K_I = 100$ ,  $c_{R,R} = c_{H,H} = c_{I,I} = 1.5$ ,  $c_{R,H} = c_{R,I} = c_{H,I} = 1$ ; **c**  $r_H = 1$ ,  $K_H = K_I = 100$ ,  $c_{R,R} = c_{H,H} = c_{I,I} = 1$ ,  $c_{R,H} = c_{R,I} = c_{H,I} = 1.5$ ; and **d**  $r_H = 1$ ,  $K_H = 140$ ,  $K_I = 100$ ,  $c_{R,R} = c_{H,H} = c_{I,I} = 1$  and  $c_{R,H} = c_{R,I} = c_{H,I} = 1.5$

As the population size grew larger, density dependence became stronger. Therefore,  $K_g$  is the main factor determining the equilibrium state of the dynamics (cf. Asmussen and Feldman 1977; Case 2000).

Next, we varied competition coefficients in order to examine the convergence of the equilibrium for all genotypes. If intraspecific (intra-genotypic) competition is stronger than interspecific (inter-genotypic) competition, this resulted in a hybrid swarm in which the resident and invader coexisted (Fig. 3b). In contrast, under strong interspecific competition, competitive exclusion occurs depending upon the initial population density (Fig. 3c). Even under this condition, heterosis can facilitate coexistence of different genotypes in the hybrid swarm (Fig. 3d).

With hybridization, some combinations between hybrid fitness and competition relationships may facilitate invasion in a relatively short time. We define the time point of “invasion success” as the point at which population sizes of resident and invader are reversed. If this reversal occurs, the invader population density can reach an equilibrium value that is higher than the resident. In Fig. 4, we calculated the time to invasion success with different values of growth rates in

hybrids and competition coefficients between resident and hybrids,  $c_{R,H}$ . As expected, high values of growth rates in hybrids resulted in rapid invasion success. On the other hand,

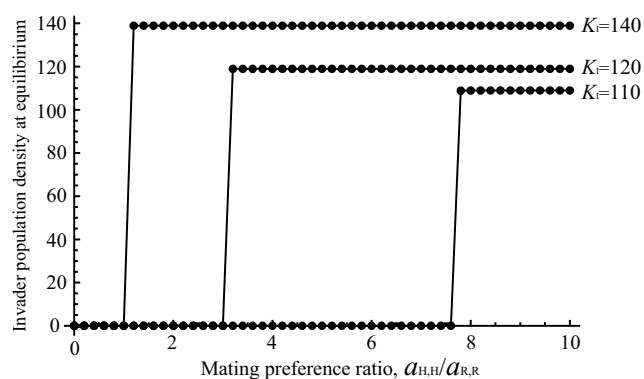


**Fig. 4** Dependence of generation time until the invasion success (see main text for definition) on the hybrid growth rate  $r_H$  and competition coefficient between resident and hybrid  $c_{R,H}$ . Dark regions indicate a rapid invasion success, while lighter colored regions indicate delayed invasion success. White regions indicate invasion failure. Rapid invasions were likely when  $c_{R,H}$  had an intermediate value. Parameters are  $r_R = r_I = 1.0$ ,  $K_R = K_H = 100$ ,  $K_I = 160$ ,  $c_{R,R} = c_{R,I} = c_{H,H} = c_{H,I} = c_{I,I} = 1$ ,  $s = 0.05$ ,  $N_R(0) = 90$ ,  $N_H(0) = 0$ , and  $N_I(0) = 10$

there existed an optimal intermediate value of the competition coefficient between residents and hybrids that minimized the waiting time to successful invasion. To understand this counter-intuitive result, it is better to separate the initial and the later phase of the invasion. With a small initial numbers of invaders, accumulation of hybrid individuals is more likely to result in successful invasion. At this stage, a low value of  $c_{R,H}$  is more likely to yield establishment. By contrast, when the resident population is excluded following accumulation of numerous hybrid individuals, a high value of  $c_{R,H}$  is necessary for establishment to occur. Thus, competition between residents and hybrids has the opposite effect on invasion speed during the initial and the later phases of the establishment process.

### Effects of assortative mating

Finally, we investigated the effects of assortative mating on invasion success. Considering first the case where mating preference is high within each species, the initial population size is the main determinant of whether establishment is successful. Under assortative mating, populations of the resident species are generally robust to invasion when its population size is larger than the invader. As we emphasized in the previous result sections, accumulating hybrid individuals is important for successful invasion. Figure 5 illustrates the equilibrium density of the invader population and the effect of the relative strength of mating preference between residents  $a_{R,R}$  and hybrids  $a_{H,H}$ . If  $a_{R,R}$  is lower, it is likely that residents easily mate with invader individuals. This argument can also be applied to  $a_{I,I}$ , not only  $a_{R,R}$ . After this hybridization, high  $a_{H,H}$  values result in the accumulation and maintenance of hybrid individuals. Thus, when the asymmetry of the ratio  $a_{H,H}/a_{R,R}$  is sufficiently large, hybridization can facilitate invasion. In addition, Fig. 5 also



**Fig. 5** Invader population densities at equilibrium under various degree of assortative mating as defined by the ratio of mate preferences,  $a_{H,H}/a_{R,R}$ . A high  $a_{H,H}$  can facilitate invasion success. If the carrying capacity of hybrids becomes smaller, a higher value of the ratio is necessary to lead to successful invasion. Parameters are  $r_R = r_H = r_I = 1.0$ ,  $K_R = K_H = 100$ ,  $c_{R,R} = c_{R,H} = c_{H,H} = c_{H,I} = c_{I,I} = 1$ ,  $a_{R,H} = a_{R,I} = a_{H,I} = a_{I,I} = 1$ ,  $s = 1$ ,  $N_R(0) = 80$ ,  $N_H(0) = 0$ , and  $N_I(0) = 20$ . Values of  $K_I$  are shown in the figure

describes the existence of a tipping point along the horizontal axis, which is the boundary of invasion success and failure. This threshold value of  $a_{H,H}/a_{R,R}$  is affected by the parameter  $K_I$ . Under a larger value of  $K_I$ , a relatively small  $a_{H,H}/a_{R,R}$  is sufficient to promote invasion because the invader population already has a fitness advantage.

### Discussion

In our study, we successfully reproduced the phenomena of invasion facilitation through hybridization using specific parameter values in a simple extension of the classic Lotka-Volterra competition model (Volterra 1938) representing three genotypes at a single locus with two alleles. The structure of our model is similar to that of earlier population genetic models (Asmussen and Feldman 1977; Anderson and Arnold 1983) except for the incorporation of the Allee effect and assortative mating. These earlier models focused on equilibrium states that maintain polymorphisms rather than establishment success or failure of an invading species described in the current paper. Specifically, we found facilitation of invasion success when the carrying capacity of the invading species exceeded that of the native species. If the invading species has a broader range of hosts that it can utilize compared to the native species or if it can utilize environmental niches more efficiently than the native species, then we can expect it to have a greater carrying capacity (Levins 1966). We found that invasion is also facilitated when the native species can mate with invaders and hybrids prefer to mate with other hybrids. In this situation, relatively small numbers of invader individuals can overcome the mate-finding Allee effect and successfully establish when the invader and hybrids are attractive to the native species and also the hybrids are substantially competitive with the native species.

As previously mentioned, the rapid establishment and spread of the parasitoid species, *Torymus sinensis*, in Japan may be attributed to their ability to hybridize with the native wasp *T. beneficus* (Moriya et al. 1989, 2002). Populations of native *T. beneficus* and the hybrids with *T. sinensis* were gradually replaced by *T. sinensis* (Yara et al. 2007, 2010), and the rate of invasion spread of *T. sinensis* was as fast as ca. 2 to 50 km per year (Dr. S. Moriya personal communication). It is known that *T. sinensis* and *T. beneficus* readily hybridize and  $F_1$  females are fertile (Yara et al. 2000). Our model can explain this rapid establishment given that *T. sinensis* is currently much more abundant than the native *T. beneficus* in the host *D. kuriphilus* populations (Murakami 1977). The current higher abundance of the invasive *T. sinensis* than the native *T. beneficus* indicates that they have a high carrying capacity. Given that native *T. beneficus* readily hybridize with *T. sinensis*, it appears likely that in this case, the invading species can utilize the native species for demographic rescue as can be seen in Fig. 3a.

In the other example of *O. brumata* suddenly spreading through the eastern USA, we also suspect that hybridization with the congeneric native species, *O. bruceata*, has played an important role in promoting successful establishment through hybridization (Elkinton et al. 2010). Again, *O. brumata* often reaches high densities in their native and invaded ranges while *O. bruceata* ordinarily remains at an endemic state (Havill et al. 2017) indicating that the invasive *O. brumata* has a greater carrying capacity than the native *O. bruceata*. Havill et al. (2017) also reported that  $F_1$  and backcrosses can produce viable offspring when mated with the non-native *O. brumata* but not with native *O. bruceata*. Though we have not fully explored the parameter values related to the asymmetric viability among resident, hybrid, and invasive species, such asymmetric hybridization might accelerate the rapid replacement of *O. brumata* from *O. bruceata* because the asymmetric relationship facilitates the accumulation of hybrids and the elimination of the native species.

Though we mainly focus here on the facilitation of invading species establishment through hybridization, our model can be used to explore various other consequences related to the hybridization of invading species with closely related native species. Our model predicts that hybrid swarms will take place under strong interspecific competition among hybridizing, native, and invading species if there is heterosis (Fig. 3d). This conclusion is consistent with previous population genetic research that emphasized that heterosis of the carrying capacity in heterozygote individuals promoted allelic polymorphism (Asmussen and Feldman 1977; Anderson and Arnold 1983). Evidence supporting this conclusion comes from reports that hybrid swarms form in the presence of heterosis, especially during the early phase of invasion and that hybridization may lead to the rapid replacement of the native species (Drake 2006; Perry et al. 2000). Also if the invading and native species do mate but do not produce viable offspring, this acts as a trap, diminishing population growth of both species and possibly leading one or both to extinction. Disadvantages caused by hybridization may be much more severe than has been recognized in the theory of competitive exclusion. Such detrimental effects of interspecific mating are also known as reproductive interference and were recently brought into an argument related to its ubiquity (Kuno 1992; Kyogoku 2015). For example, Yukawa et al. (2007) reported that the invasive stinkbug *Nezara viridula* (Hemiptera: Pentatomidae) in Kyushu Island is now expanding its distribution and excluding the congeneric native species, *N. antennata*. The species *N. viridula* and *N. antennata* often mate but never produce viable offspring. They suspect that such the infertile matings facilitated the rapid displacement of *N. viridula* from *N. antennata*.

We also considered the time to invasion success, defined as the point at which population sizes of resident and invader were reversed. With high competition rates between native-species

and hybrids, we expected that rapid invasion success was more likely to occur because competition would lead to exclusion of the native species. However, surprisingly, we found an optimal intermediate value of the competition coefficient between residents and hybrids that minimized the waiting time to successful invasion. By separating out the initial and the later phase of the invasion, we were able to verify that a low value of  $c_{R, H}$  can yield accumulation of hybrid individuals at the first stage. Once the accumulation phase is over, severe competition between residents and hybrids can lead to rapid replacement. It is noteworthy that very little relevant information about typical ranges of parameters to forecast any particular invasion is available. This important prediction should be testable in experimental studies in the future.

We made several simplifying assumptions in this study that warrant more exploration in future work. In our model, we simplified the genetics inherent to both the native and non-native species' genotypes. Specifically, we assumed that each species is distinguished by a single gene. In reality, species are composed of thousands or millions of genes. This means that once hybridization occurs, their descendent may have genes with mixtures of alleles from each parent species and it would be unlikely for pure genotypes to emerge again. Nevertheless, from the perspective of non-native genes, the hybridization mechanisms described here still represent potentially important processes by which invasion by non-native alleles may occur. It should also be noted that our model did not include any representation of stochasticity, and this may limit the ability of the model to realistically represent dynamics. For example, if native and non-native alleles are of equal fitness, then one may be expected to ultimately become fixed due to genetic drift rather than both persisting in gene pools indefinitely. Another logical extension of this model would be to include spatially explicit dynamics in order to investigate the spatial spread of the invading species.

We believe our simple theoretical approach will contribute to the comprehensive understanding about the consequences emerging from differences in fitness, mate preference, and competitive ability among native and non-native species and their hybrids. We believe that this study represents only an initial first step to more fully understanding the mechanisms by which hybridization can facilitate invasions.

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