

# Neutral hybridization can overcome a strong Allee effect by improving pollination quality

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**Abstract** Small populations of plant species can be susceptible to demographic Allee effects mainly due to pollen limitation. Although sympatry with a common, co-flowering species may somewhat alleviate the problem of pollinator visitation (pollination quantity), the interspecific pollen transfer, IPT, (pollination quality) may remain a barrier to reproduction in small populations such as new introductions. However, if the two species are crosscompatible, our hypothesis is that neutral hybridization can help the small founding population overcome the Allee effect by improving the quality of pollination. We tested this hypothesis by using a novel modelling approach based on the theory of kinetic reactions wherein pollinators act as enzymes to catalyse the reaction between the two substrates: pollen and unselfed ovule. Using a single locus, two-allele genetic model, we developed a generic model that allows for hybridization between the invading and the native genotypes. Analysing the stability properties of the trivial equilibria in hybridization model as compared with the single genotype invasion model, we found that hybridization can either remove or reduce the Allee effect by making an otherwise stable trivial equilibrium unstable. Our study suggests that hybridization can be neutral but still be the key driver

of a successful invasion by mediating pollen limitation. Conservation programmes should therefore account for this cryptic role that hybridization could play in plant invasions.

**Keywords** Introgression · Invasion facilitation · Allee effect · Pollination quality · Ordinary differential equations · Phase plane analysis

## Introduction

A small population size can have dire ecological and genetic consequences (Ellstrand and Elam 1993; Willi et al. 2005; Blackburn et al. 2015). Such situations arise in many circumstances, such as new introductions (Simberloff 2009), the leading fronts of active invasions (Taylor and Hastings 2005), recovery from severe disturbances (Copson and Whinam 1998; Chapuisa et al. 2004), peripheral or isolated populations of an abundant species (Busch 2005) and in rare species (Pickup and Young 2008). While both large and small populations may be vulnerable to environmental stochasticity (extreme weather events, floods, etc.), small populations are particularly subject to extinction risks related to demographic Allee effects (Ellstrand and Elam 1993; Lewis and Kareiva 1993; Liebhold and Bascombe 2003; Simberloff 2009). In plants, outcrossing species are very likely to experience Allee effects because they rely on pollinator services, which become less reliable when the population size is small (Seeley et al. 1991; Kunin 1993, 1997; Ghazoul and Shaanker 2004; Ghazoul 2005). Reproduction may be limited by the low availability of pollen or the ineffective transfer of the pollen to the small number of plants. Further, a genetic Allee effect can arise if outcrossing is governed by self-incompatibility systems where finding a compatible mate carrying unmatched S alleles becomes a

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further hurdle to reproduction (Willi et al. 2005; Pickup and Young 2008; Levin et al. 2009; Young and Pickup 2010; Young et al. 2012). Plants in small populations, however, may overcome some of these challenges if they occur in sympatry with a common species.

When a common species co-occurs with a less abundant species and their flowering periods overlap (they “co-flower”), its presence can increase pollinator visitation rate to the rare species through either increased attraction of their joint floral display (Ghazoul 2006; Robson 2013) or via the “magnet effect” where one species with a very attractive floral display acts as a lure to pollinators and thus enhances visits to its neighbouring, less attractive species (Thomson 1978; Lavery 1992; Johnson et al. 2003). However, the rare species may still be pollen limited because most pollen that it now receives is from the common species and thus is unable to fertilize its ovules (the pollen is “improper”, *sensu* Rathcke 1983). These interspecific pollen grains may even interfere with its own and hence increase the abortion rate (e.g. Randall and Hilu 1990, Carney et al. 1996). The presence of a co-flowering species may thus, to some extent, reduce Allee effects driven by the low *quantity* of pollination (*sensu* Kunin 1993), i.e. the low number of pollinator visits, but the *quality* of pollination (*sensu* Kunin 1993), i.e. deposition of proper pollen, remains a limiting factor to seed production.

An interesting demographic situation arises if heterospecific pollen arriving on the stigma of the rare species can effectively fertilize ovules and, as a result, produce hybrid seeds. The quality of pollination can be argued to have increased, but the offspring are neither one species nor the other. These hybrids have often been found to increase in abundance and then spread, becoming a naturally occurring taxon or an invasive entity in their own right, while the rare species remains rare (Rieseberg 1997; Ellstrand and Ka 2000). The mechanism for this has almost exclusively been assumed to be genetic, with the hybrid genotypes having greater fitness than either parent (Ellstrand and Ka 2000; Hovick and Whitney 2014). If, instead, the rare/newly arriving species increases in abundance and the hybrids decline, at least two genetic explanations arise. Firstly, the hybrids might be less fit than their parents and have been outcompeted by a species whose increase was inevitable. Secondly, as a result of backcrossing, they might have increased the fitness of the rare species, through either introgression of locally adapted alleles or by allowing selection to act upon new genetic combinations. But there is at least one other, purely demographic possibility requiring no change in fitness of genotypes but where hybridization is an essential part of overcoming Allee population thresholds. The plausibility of this mechanism has been demonstrated using a simulation model verified by a case study (Mesgaran et al. 2016). Hybridization, followed by preferential backcrossing

to an incoming species at low abundance, was shown to facilitate an invasion by improving both the quantity and quality components of pollination. While the high local density of the common species increases the visitation rate to the mixed patch (i.e. increased quantity), hybridization allows heterospecific pollen grains to contribute to seed production (i.e. increased quality). The relative importance of pollination quality, however, remains an aspect deserving attention, since interspecific pollen transfer, rather than visitation rate, is the component that is directly affected by hybridization.

The possibility for *quantitative* facilitation in co-flowering (but non-hybridizing) species has been investigated theoretically (Feldman et al. 2004; Hanoteaux et al. 2013) and empirical data supporting such a facilitation mechanism have been reported from several experimental and natural plant communities (Ghazoul 2006; Duffy and Stout 2011; Sieber et al. 2011; Seifan et al. 2014). We are unaware of any study exploring the possibility for a *qualitative* facilitation that can result from a neutral hybridization with no changes in the fitness (in the sense of equal competitive ability and reproductive output of the colonizing species, the common species, and/or hybrid offspring). While interspecific (i.e. improper) pollen transfer, IPT, (Waser 1978; Caruso and Alfaro 2000; Morales and Traveset 2008) is known as an interface mechanism in mixed stands of co-flowering species, we hypothesize that hybridization can turn those *improper* (*sensu* Rathcke 1983) pollen grains into viable seeds and that crossing between the resultant hybrid offspring or backcrossing with the parental species can ultimately result in the recovery of virtually pure parental genotypes (Huxel 1999). That is, if we assume a biallelic locus with *II*, *IN* and *NN* indicating invading, hybrid and native genotypes receptively, then 50 % of offspring resulting from a (back)cross between the heterozygote (hybrid) and the invading genotype and 25 % of offspring from hybrid × hybrid crosses are expected to be homozygous for the invader locus. Over just a few generations of such preferential crossings, the invading genotypes will be recovered.

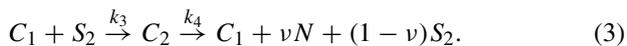
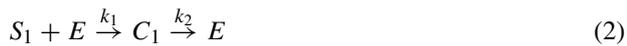
Using a novel modelling approach based on chemical kinetic reactions, our objective of this study was to test whether the hybridization enhancement of the pollination quality can rescue an invading genotype that may otherwise fail to establish because of Allee effects.

## Models

In this section, we derive qualitative models, using the law of mass action from kinetic reaction theory (e.g Murray 2002, chapter 6), to characterize the dynamics of an invading plant as related to the breeding system and pollinator behaviour.

## Mass-action model for plant-pollinator dynamics

The law of mass action states that the rate at which a reaction occurs is proportional to the concentration of reactants. Although originally designed for chemical reactions, the concept and methodology can be applied to other disciplines such as ecology (multiple species models) and epidemiology (SIR models) (Murray 2002, chapters 3 and 10). In this study, we used this approach to model the dynamics in an annual plant system where the ovules and the pollen act as two reactants to produce seeds. We assumed a mixed breeding system where a plant species can produce seeds through both self-fertilization and outcrossing. The relative contribution of selfing and outcrossing to seed output is variable and can range from a fully selfing (with zero outcrossing) to an obligate outcrossing (with zero selfing) mating system. The seed production through outcrossing is assumed to depend entirely on animals (pollinators) as the agents of pollen transfer between plants (assuming no wind or other means of pollination) and hence pollinators can be considered as enzymes: necessary agents for the reaction to occur. Let  $S$  stands for the reactant with  $S_1$  being the pollen and  $S_2$  the ovule;  $E$  indicates the pollinator (enzyme),  $C_1$  is the complex of pollinator with pollen (the enzyme and substrate  $S_1$ ),  $C_2$  is the complex of pollinator depositing pollen loads on the ovule of a recipient plant (the enzyme and the two types of substrate  $S_1$  and  $S_2$ ) and  $N$  is the seed (product). The kinetic reactions are written:



where reaction (1) represents the production of seeds through self-fertilization. Reaction (2) happens when a pollinator ( $E$ ) picks up pollen and forms the complex  $C_1$  (pollinator + pollen): this complex is unstable and pollen may become unloaded after some time and thus not available for fertilization. In reaction (3), a pollinator already loaded with pollen (complex  $C_1$ ) brings the pollen into contact with the ovules of the recipient plant to form complex  $C_2$  (pollinator + pollen + ovule). The complex will result in successful fertilization of ovules and thus produce seeds,  $N$ , with probability  $\nu$  or abortion with probability  $1 - \nu$ . In this last reaction, we always assume that the pollinator does not deposit all of its pollen load to each flower. The biological interpretations for the rate parameters  $k_i$  ( $i \in \{0, 1, \dots, 4\}$ ) are given in Table 1.

Equations 1–3 describe qualitatively the dynamics of seed production, via self-fertilization (1) and outcrossing (2) and (3). Using a quasi-steady-state approximation (Appendix A.1), we first derived a quantitative model of ordinary differential equations, ODEs, to explore the dynamics of  $N$  with respect to time. Both the dependent and independent variables were then rescaled to obtain non-dimensional ODEs (Appendix A.2) then used to derive three different models: a model with a single invading species, a model with two non-hybridizing species (Appendix B) and the model that includes two hybridizing species.

### Model of a single invading species

As discussed in Appendix A, we simplified the model by considering  $n$  to stand for the density of species without regard to any within season life-cycle events. Whether  $n$  is

**Table 1** Description and units for rate parameters used in kinetic reactions of the plant-pollinator model (1–3)

Parameters	Descriptions	Units
$k_0$	Selfing rate <sup>a</sup> , i.e. ovules fertilized by the pollen from the same flower	Ovules per unit time
$k_1$	Rate of pollen uptake by pollinators from the pollen donor plants (a measure of the attractiveness of the male partner to pollinators)	Pollen load per unit time per unit of pollinator
$k_2$	Rate of pollen loss by the pollinator (a measure of the efficiency of the pollinator in carrying pollen)	Pollen load per unit time
$k_3$	Rate of pollen deposition on the stigmas of the recipient plant (a measure of the attractiveness of the female partner to pollinators)	Pollen load per unit time per unit of pollinator
$k_4$	Crude outcrossing rate <sup>a</sup> , i.e. the rate of cross pollination irrespective of the fertilization (cross pollination may or may not result in successful fertilization)	Complex per unit time
$\nu$	Fertilization success, also representing the compatibility between pollen and ovule	Dimensionless

<sup>a</sup>Note that in ecology literature, selfing and outcrossing rates are usually referred to as the proportion of ovules fertilized by the pollen from flowers on the same plant or the pollen from another conspecific plant respectively but here by rate, we mean the number of ovules fertilized per unit of time

treated as seeds or as mature plants has no effect on the results derived from the model. Here, we will refer to  $n$  as plant density but plant is used as a general term rather than in the sense of a specific developmental stage such as the contrast between a plant vs. seed stage. Following from Eq. 24 derived in Appendix A, the simplified model for a single invading species can be written as follows:

$$\underbrace{n'(t)}_{\text{rate of change}} = n \left( \underbrace{A}_{\text{self-fertilization}} + \underbrace{B \frac{n}{1+n+n^2}}_{\text{outcrossing}} - \underbrace{(1+n)}_{\text{death}} \right) = F(n), \tag{4}$$

where

$$A = \frac{d_2 k_0 k_4}{d_1^2 k_3}, \text{ a measure of fertile selfing rate} \tag{5}$$

and

$$B = \frac{v k_4 e_0 d_2}{d_1^2}, \text{ a measure of fertile outcrossing rate.} \tag{6}$$

Equation 4 thus describes the rate of changes in plant density  $n$  over time, as a function of the reproduction through self-fertilization (parameter  $A$ ) and outcrossing (parameter  $B$ ), while assuming density-dependent and density-independent death rates. The kinetic reaction framework thus allowed us to mechanistically incorporate the breeding system of plants into a population dynamics model. This model was further extended to include more than one species where the heterospecific crosses were either infertile (Appendix D) or fertile and thus could form hybrids (see below).

### Model of two hybridizing genotypes

We expanded our model (4) to a system of two hybridizing genotypes (species), namely the native (resident) genotype  $N$  and a new incoming (invading) genotype  $I$ . The two genotypes interact with each other through density-dependent regulations, e.g. death rate is a function of the total population size. We also suppose that the pollen and ovule of the two genotypes are compatible and hence they can produce viable hybrid offspring  $H$  in the sympatric zone. Let  $N$  and  $I$  be the two co-dominant alleles of a locus that can result in three genotypes:  $NN$  native,  $II$  invading and  $IN$  hybrid. We derive the following system of ODEs for the native ( $NN$ ), hybrid ( $NI$ ) and invading genotype

( $II$ ) with respective densities  $n_N$ ,  $n_H$  and  $n_I$  (extending Eq. 4):

$$\underbrace{n'_i(t)}_{\text{rate of change}} = \underbrace{\sum_j A_j n_j(t) P(i|j, j)}_{\text{self-fertilization}} + \underbrace{\sum_{j,k} \frac{B_{jk} n_j(t) n_k(t)}{1 + n_j(t) + n_j(t) n_k(t)} P(i|j, k)}_{\text{outcrossing}} - \underbrace{n_i(t) \left( 1 + \sum_j n_j(t) \right)}_{\text{death}}, \tag{7}$$

where  $i \in \{I, H, N\}$ ,  $\mathbf{A} = (A)_{j=I,H,N}$  is a  $3 \times 1$  vector,  $\mathbf{B} = (B_{jk})_{j,k=I,H,N}$  is a  $3 \times 3$  symmetric matrix and  $P(i|j, k)$  is the probability of producing an offspring with genotype  $i$  from a cross between parents  $j$  and  $k$ . The first term in Eq. 7,  $\sum_j A_j n_j(t) P(i|j, j)$ , represents the reproduction from selfing, where the product  $A_j n_j(t)$  indicates the birth rate through selfing for genotype  $j$ , while  $P(i|j, j)$  is the probability of the selfed parent  $j$  producing offspring of genotype  $i$ . The second term in Eq. 7,  $\frac{B_{jk} n_j(t) n_k(t)}{1 + n_j(t) + n_j(t) n_k(t)}$ , indicates the growth rate through outcrossing between pollen from genotype  $j$  and ovules from genotype  $k$ , which can result in genotype  $i$  with the probability given by  $P(i|j, k)$ . The last term in Eq. 7 stands for the death rate, which depends on the size of the combined population consisted of the three genotypes. Following a Mendelian genetic model for a biallelic locus, the probabilities for three offspring genotypes given the genotype of their parents are the following:

$$P(I|\cdot, \cdot) = P_I = \begin{pmatrix} I & H & N \\ 1 & 1/2 & 0 \\ 1/2 & 1/4 & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{matrix} I \\ H \\ N \end{matrix} \tag{8}$$

$$P(H|\cdot, \cdot) = P_H = \begin{pmatrix} I & H & N \\ 0 & 1/2 & 1 \\ 1/2 & 1/2 & 1/2 \\ 1 & 1/2 & 0 \end{pmatrix} \begin{matrix} I \\ H \\ N \end{matrix} \tag{9}$$

$$P(N|\cdot, \cdot) = P_N = \begin{pmatrix} I & H & N \\ 0 & 0 & 0 \\ 0 & 1/4 & 1/2 \\ 0 & 1/2 & 1 \end{pmatrix} \begin{matrix} I \\ H \\ N \end{matrix} \tag{10}$$

Matrix  $P_I$  contains probability values for the production of offspring of the invading genotype,  $II$ , from all nine possible crosses between the three genotypes.  $P_H$  includes the

probabilities for offspring with the hybrid genotype while those for the native offspring are given in the matrix  $P_N$ .

Using Eq. 7, we investigated the effect of hybridization when a new genotype invades an equilibrium population of the native genotype and can hybridize with the native genotype as compared with the scenario where there is no native genotype in the habitat (4). Biologically, it is realistic to assume that the native genotype is at equilibrium at the time of the introduction (this is also mathematically demonstrated in the “Model of a single invading species” section). Thus, as a first step, we studied the dynamics of the hybrid and invading genotypes at the time of the introduction to understand whether the invading genotype can establish in the environment. For this first step, we assumed that the native genotype is at equilibrium, i.e.  $n_N(t) = \bar{n}_N$  for all  $t \geq 0$ , and focused on the dynamics of invading  $n_I$  and hybrid  $n_H$  genotypes, as a function of  $A$  and  $B$  parameters and their respective  $P(I; \cdot, \cdot)$  and  $P(H; \cdot, \cdot)$  matrices, which can be described by the following:

$$\begin{aligned}
 n'_I = & \left[ n_I \left( A_I + \frac{B_{II}n_I}{1+n_I+n_I^2} - (1+\bar{n}_N+n_I) \right) \right] \\
 & + \left[ n_I n_H \left( \frac{B_{IH}}{2(1+n_I+n_I n_H)} + \frac{B_{HI}}{2(1+n_H+n_I n_H)} - 1 \right) \right] \\
 & + \left[ n_H \left( \frac{A_H}{4} + \frac{B_{HH}n_H}{4(1+n_H+n_H^2)} \right) \right] \tag{11}
 \end{aligned}$$

$$\begin{aligned}
 n'_H = & \left[ n_H \left( \frac{A_H}{2} + \frac{B_{HH}n_H}{2(1+n_H+n_H^2)} - (1+\bar{n}_N+n_H) \right) \right] \\
 & + \left[ n_H \left( \frac{B_{HN}\bar{n}_N}{2(1+n_H+n_H\bar{n}_N)} + \frac{B_{NH}\bar{n}_N}{2(1+\bar{n}_N+\bar{n}_N n_H)} \right) \right] \\
 & + \left[ n_H n_I \left( \frac{B_{HI}}{2(1+n_H+n_I n_H)} + \frac{B_{IH}}{2(1+n_I+n_H n_I)} - 1 \right) \right] \\
 & + \left[ n_I \left( \frac{B_{NI}\bar{n}_N}{1+\bar{n}_N+\bar{n}_N n_I} + \frac{B_{IN}\bar{n}_N}{1+n_I+n_I\bar{n}_N} \right) \right]. \tag{12}
 \end{aligned}$$

Note that we have dropped the  $t$  from our notation but it should be clear that  $n_I$  and  $n_H$  are functions of  $t$  and that  $n_N \equiv \bar{n}_N$  is a constant. In Eq. 11, the first term on the right, denoted by  $I \times I$ , indicates the generation of genotype  $I$  by  $I \times I$  crosses either through selfing or outcrossing. The second term of the right-hand side in Eq. 11, denoted by  $I \times H$ , groups all the intercrossings that can result in offspring genotype  $I$ , either the invading genotype acting

as the male, i.e. pollen donor, ( $IH$ ) or as the female, i.e. pollen receiver, ( $HI$ ) partner. As shown in  $P(I; \cdot, \cdot)$ , one fourth of the offspring produced by a cross between two hybrids (either a selfing hybrid or outcrossing between two hybrid plants) will have the identity of the invading genotype: this is reflected in the third term of Eq. 11. The same interpretation applies to the four terms in Eq. 12.

For this two-dimensional system of ODEs, we have nine parameters, including the coefficients related to seed production through selfing ( $A_I$  and  $A_H$ ) and the coefficients related to outcrossing:  $B_{IH}, B_{HI}, B_{II}, B_{HH}, B_{IN}; B_{NI}$  and  $B_{HN}$ . We assumed that the matrix  $\mathbf{B}$  is symmetric, i.e.  $B_{IH} = B_{HI}$  and  $B_{IN} = B_{NI}$ . We also assumed that

$$A_I=A_H=A_N=A \in \mathbb{R}^+, \quad B_{II}=B_{HH}=B_{NN}=B \in \mathbb{R}^+, \tag{13}$$

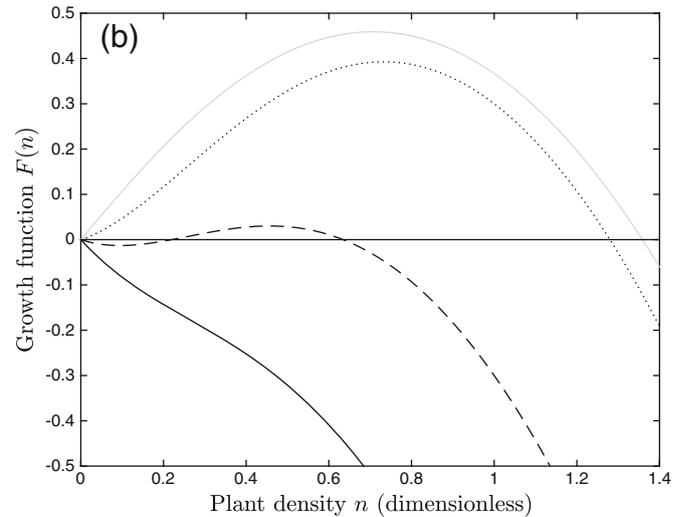
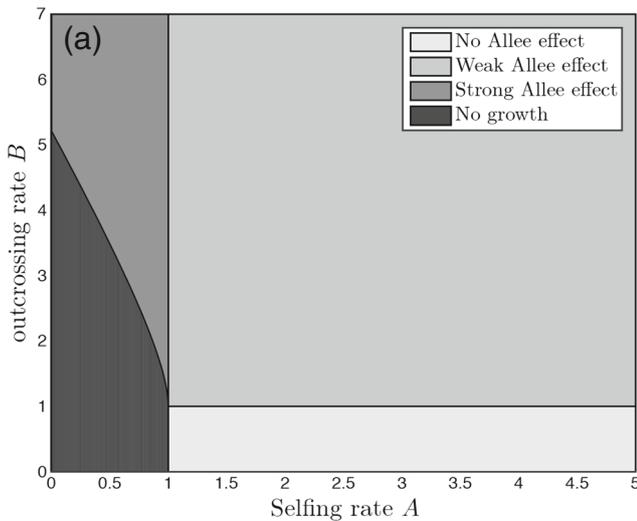
meaning that the three genotypes have the same selfing rate as well as the same within-genotype outcrossing rate, so that the three genotypes do not differ in fitness characters (this equality in these fitness characters is necessary to be able to extract the pure effect of hybridization).

In this section, we first derived the model of a single invading genotype on the basis of plant-pollinator kinetics (4). Then, in the framework of interacting species, we incorporated hybridization and developed a system of three ODEs, to model the rate of changes in the populations with invading, hybrid and native genotypes (7). From this last model, we also derived a sub-model (11–12) that describes the dynamics of invading and hybrid genotypes only, while the native population is assumed to stay at equilibrium, in order to understand the dynamics of the system at the time of the introduction. We also included in Appendix B the derivation and the analysis of a model considering two non-hybridizing species.

As shown in Eq. 11, the death rate of the invading genotype (as well as other genotypes) increases in the presence of the other genotypes; however, the occurrence of hybridization when another genotype is present will provide an additional means for generation of the invader genotype, i.e. increasing birth rate through fertile crossings such as  $H \times H$  and  $I \times H$ . Can this augmented birth rate brought about by hybridization compensate for, or exceed, the increased mortality and thus facilitate the invasion? We explore the possibility of such an outcome as will be discussed in the following analysis.

### Analysis

Using the theory of dynamical systems and numerical simulations, we analysed the properties of the models introduced above to determine whether interspecific pollen transfer can help the establishment of the invading genotype.



**Fig. 1** A qualitative bifurcation diagram for Eq. 4 as related to changes in parameter values of  $A$  (representing selfing rate) and  $B$  (representing outcrossing rate) (a), and respective growth curves for different parameter values of  $A$  including 0 (solid black line, negative

growth), 0.7 (dashed line, strong Allee effect) and 1.3 (dotted line, weak Allee effect), when  $B = 3$  and  $A = 2.1$ ,  $B = 0.8$  (solid light grey line, no Allee effect) (b)

### Model of a single invading species

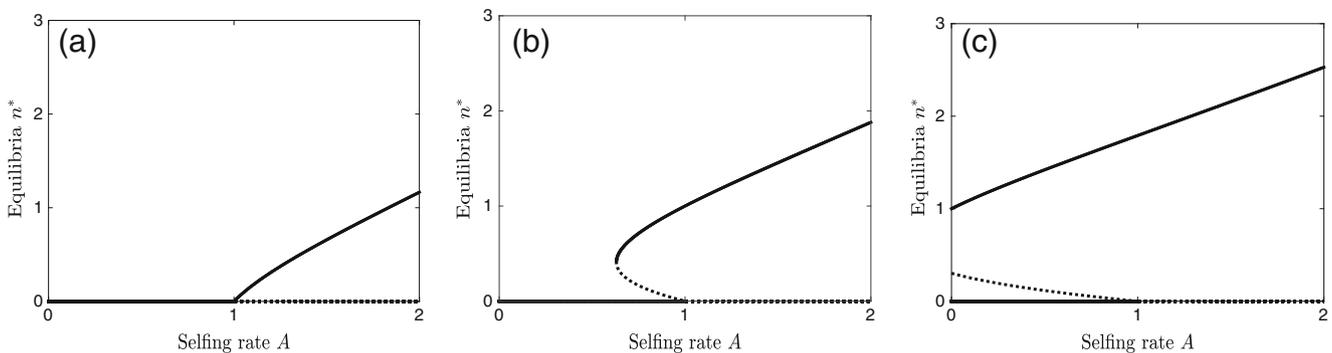
The dynamics modelled by Eq. 4 represents the invasion of habitat by a single species in absence of any competitors. The long term behaviour of  $n$  (i.e. population size of the invader) depends on the shape of  $F$  which can be a logistic function or can include Allee effects (weak or strong), depending on the values of  $A$  and  $B$  (see Figs. 1 and 2). Indeed, analysis of the function  $F$ , detailed in Appendix C.1, provided information on the number of positive roots along with the sign of  $F$ . From these different analyses, we reached conclusion about the existence of non-negative equilibria of Eq. 4 and on their stability properties.

Four different outcomes can be deduced from the function  $F$  as related to the values of the parameters  $A$  and  $B$ . When  $A < 1$  (i.e. the chance of seed production through

selfing is low), the outcrossing rate  $B$  is a bifurcation between no growth or a strong Allee effect with an Allee threshold. An Allee threshold exists when the density of population must be above a positive value to gain a positive growth: this positive value is then defined as the Allee threshold. When selfing provides some degree of reproductive assurance, i.e.  $A > 1$ , then outcrossing rate,  $B$ , determines if the population can grow without the challenges of an Allee effect or subjected to a weak Allee effect.

### Model of two hybridizing genotypes

Now, we consider the model with hybridization between the invading and native genotypes. We first analyse the model assuming that the native population stays constant (at equilibrium), that is  $n_N(t) = \bar{n}_N$  for all  $t \geq 0$ . Then we study the



**Fig. 2** Equilibria of Eq. 4  $n^* \geq 0$  as a function of  $A$  for three  $B$  values of 0.5 (a), 3 (b) and 6 (c). Solid and dotted lines represent the stable and unstable equilibria, respectively

behaviour of the full system taking into account the dynamics of the three populations: native ( $n_N$ ), invading ( $n_I$ ) and hybrid ( $n_H$ ), through numerical simulations.

*Analytical solution*

We analysed the impact of hybridization in a system of two interacting genotypes, using model (11)–(12), which describes changes in the invading and hybrid genotype populations, assuming that the native genotype stays at equilibrium.

We computed the equilibrium value  $\bar{n}_N$  using the model of a single invading genotype described in the previous section. That is we used Eq. 4 to compute the non-trivial equilibrium  $n_N^*$  and set  $\bar{n}_N = n_N^*$ . We chose to investigate the stability of the (0, 0) equilibrium of Eqs. 11–12 (i.e. when  $n_I = 0$  and  $n_h = 0$ ), as this analysis reflects the situation wherein the invading genotype occurs at low density and thus is prone to Allee effects. Further, a low propagule pressure is known to be very common in most introductions (Simberloff 2009). We therefore choose values of parameter  $A$  such that  $F$  in Eq. 4 is either always negative or bistable, i.e. exhibits strong Allee effect:

$$A < 1 \tag{14}$$

In other words, we analysed a situation under which the trivial steady state 0 is a stable equilibrium for the single genotype model (4). If our analysis shows that this stable equilibrium can become unstable in the presence of hybridization, we can conclude that neutral hybridization has facilitated the invasion as the invader has been able to escape from a stable zero growth state to a positive growth state, even if this period of growth is very brief.

The stability properties of (0, 0) can therefore provide some insights into the potential rescue effects of hybridization, i.e. whether hybridization can reduce the risk of extinction or Allee effect in the invading genotype. Indeed, the linear stability of an equilibrium point provides information on the behaviour of the non-linear system, at least

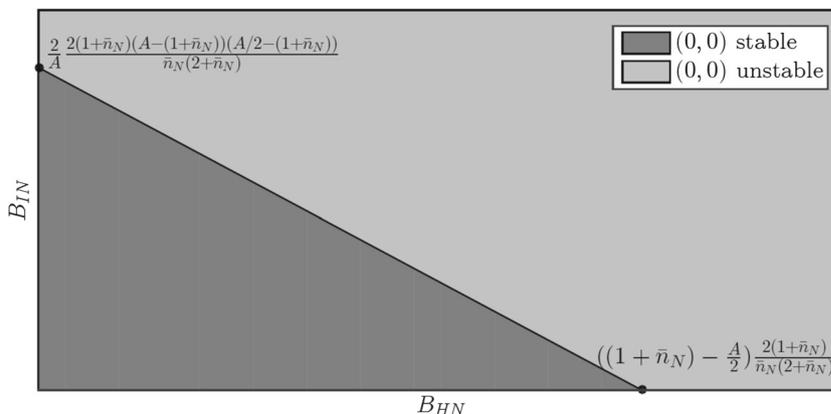
in the vicinity of the equilibrium point (Edelstein-Keshet 1988, chapter 4), which could be determined by the sign of the eigenvalues of the Jacobian matrix at the equilibrium point (Edelstein-Keshet 1988, chapters 5–6). The stability properties of (0, 0) can be inferred from the sign of the trace and the determinant of the Jacobian of the system at (0, 0), denoted by  $J^0$ . The trivial equilibrium is stable if  $tr(J^0) < 0$  and  $det(J^0) > 0$ . The trivial equilibrium is unstable if ( $det(J^0) > 0$  and  $tr(J^0) > 0$ ) or ( $det(J^0) < 0$  only). A detailed analysis of the Jacobian at (0, 0) is provided in Appendix D.1. From this analysis, we note that the trace and the determinant of the Jacobian at (0, 0) (39) only depend on  $B_{IN}$  (a measure of intercrossing rate between the two parental genotypes) and  $B_{HN}$  (a measure of intercrossing rate between the hybrid and the native genotype), given that  $A_H = A_I = A$  were chosen to be fixed. Our goal is to determine the parameter space under which either the trace and the determinant are positive (and (0, 0) will then be an unstable node) or the determinant is negative (and (0, 0) will be an unstable saddle): if any of these conditions ( $tr(J^0), det(J^0) > 0$  or  $det(J^0) < 0$ ) are met, the trivial equilibrium (0, 0) will become unstable, suggesting a rescue effect for hybridization

When hybridization was allowed, the trivial equilibrium (0, 0) was either a stable node ( $det(J^0) > 0$  and  $tr(J^0) < 0$ ) or an unstable saddle ( $det(J^0) < 0$ ) (Appendix D.1). The trivial equilibrium (0, 0) is unstable and thus facilitation is warranted, if and only if the determinant becomes negative, i.e. when  $B_{IN}$  and  $B_{HN}$  are such that

$$B_{IN} > \frac{4(1 + \bar{n}_N)(A - (1 + \bar{n}_N))}{A\bar{n}_N(2 + \bar{n}_N)} \left[ \frac{A}{2} - (1 + \bar{n}_N) + \frac{\bar{n}_N(2 + \bar{n}_N)}{2(1 + \bar{n}_N)} B_{HN} \right]. \tag{15}$$

An illustration of the stability property of the trivial steady state as a function of  $B_{IN}$  and  $B_{HN}$  is shown in Fig. 3. One needs to compute the eigenvectors associated with the

**Fig. 3** Stability of the trivial steady state (0, 0) as a function of the parameters  $B_{HN}$  (a measure of intercrossing rate between hybrid and native genotypes) and  $B_{IN}$  (a measure of intercrossing rate between invading and native genotypes) for Eqs. 11 and 12



two real eigenvalues of the Jacobian at  $(0, 0)$ , to better understand the behaviour of the solution near the trivial equilibrium (Edelstein-Keshet 1988, chapter 5.7). That is, by introducing a few individuals of the invading genotype (hybrid genotype density is zero in the first generation) and calculating the eigenvector of the trivial steady state  $(0, 0)$ , we can determine the direction along which the solutions are converging to or diverging from  $(0, 0)$ .

To understand the bifurcation of the trivial equilibrium from a stable node to an unstable saddle, we computed and analysed the null clines of problems (11)–(12), i.e. the points  $(n_I, n_H)$  in the phase plane  $(n_I, n_H)$  such that  $n'_I \equiv 0$  and  $n'_H \equiv 0$  (Appendix D.2).

Two general conclusions can be made based on the stability statuses of the  $(0, 0)$  equilibrium. If  $(0, 0)$  is stable (i.e.  $\det(J^0) > 0$ ), there exist either no or two non-trivial equilibrium points, including  $n^1 = (n_I^1, n_H^1)$  and  $n^2 = (n_I^2, n_H^2)$ . If  $(0, 0)$  is unstable, there exists only one non-trivial equilibrium point  $n^2$ , which is always stable (see also Appendix D.3).

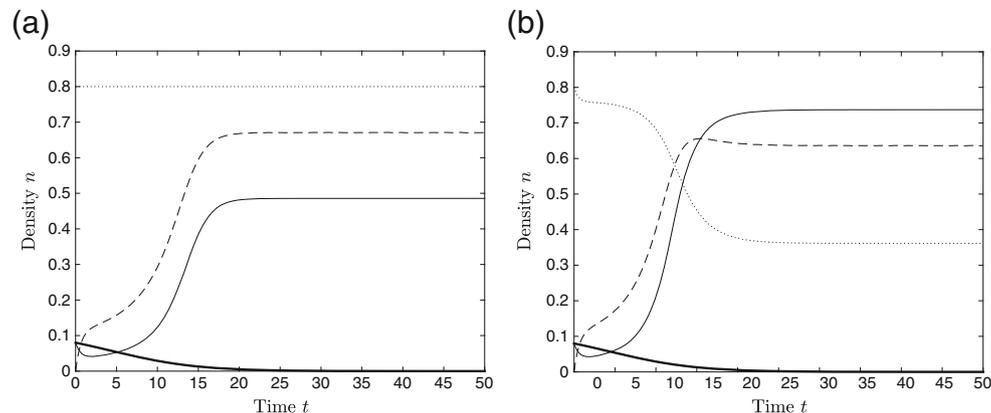
Our general conclusion from this analysis is that the pollination quality improvement due to hybridization can facilitate the establishment of the invading genotype either by reducing the Allee threshold or removing it (Appendix D.1). Hybridization reduces the Allee threshold when there are two non-trivial equilibria  $n^2$ , which is stable, and  $n^1$ , which approaches  $(0, 0)$  with increasing  $B_{IN}$  and/or  $B_{NH}$ , and removes the strong Allee effect by making the trivial equilibrium  $(0, 0)$  unstable (Appendix D.2 and D.3). From this analysis, we can conclude that the parameters that affects the existence of an Allee threshold and thus a strong Allee

effect are only the interspecific crossing rate between native and invading genotypes  $B_{IN}$  and the one between hybrid and native genotypes  $B_{HN}$ .

#### Numerical simulations

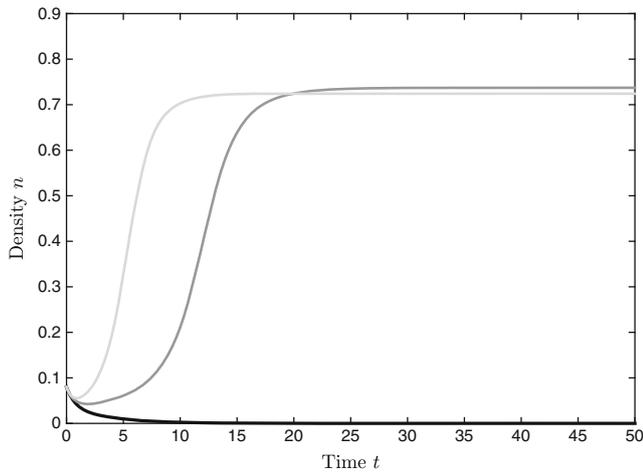
So far, we have assumed that the density of  $n_N$  is at equilibrium and does not change over time. The equilibrium assumption is biologically realistic, but that the native population remains constant even after the invasion by a second species may not represent a likely scenario in the real world. This assumption can make the appropriateness of non-trivial equilibrium analysis questionable. Therefore, a more realistic analysis of the time evolution of the three genotypes was performed numerically by relaxing the assumption of a constant  $n_N$ . As before, we maintained the assumption that the native genotype is at equilibrium at the time the new genotype arrives, but the new model allows the density of the native genotype to change with time. This model also allows for hybridization between the invading and native genotypes.

As before, we assumed that the three genotypes have the same phenotypic values with regard to  $A$  (selfing rate) and  $B$  (within-genotype outcrossing rate) parameters:  $A_N = A_I = A_H = A$  and  $B_{NN} = B_{II} = B_{HH} = B$ . When  $A$  and  $B$  were chosen so that the trivial equilibrium was stable in the single species model (Fig. 1) and thus the species could not invade the environment (Fig. 4 – thick solid line), neutral hybridization with the native genotype allowed successful establishment of invader under the same parameter settings as with single species scenario (Fig. 4a when the  $n_N$



**Fig. 4** Temporal changes in the density ( $n$ ) of the invading genotype when it occurs alone (**bold solid line**) compared to the situation where it can intercross (**solid line**) with the native genotype (**dotted line**) to form hybrids (**dashed line**) when the native population is assumed to stay constant (model (11)–(12)) (**a**) or considering the full model (**b**). The outcrossing rates were fixed at  $B_{IH} = 2$ ,

$B_{IN} = 2$  and  $B_{HN} = 1.2$ . For the hybridizing scenario, the density of the native was either held constant ( $n_N \equiv 0.8$ ) (**a**) or starting at equilibrium ( $n_N(0) = 0.8$ ) (**b**) while no hybrid existed in the first generation ( $n_H(0) = 0$ ) and the density of the invading genotype, at  $t = 0$ , was 10 % of the native. Other parameters were  $A = 0.8$  and  $B = 3$

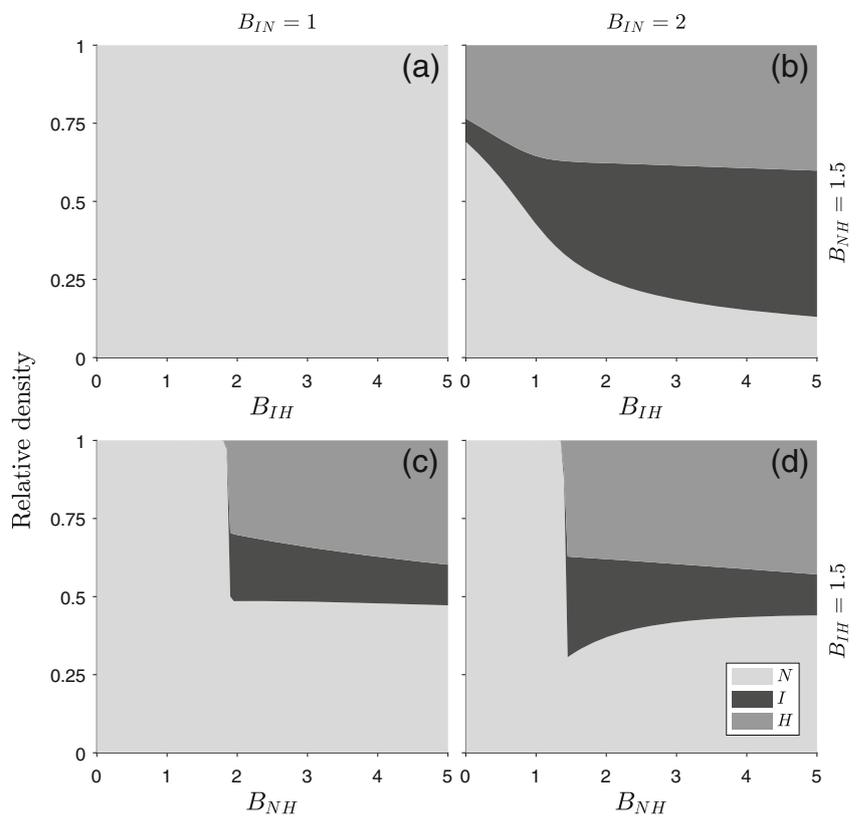


**Fig. 5** Temporal changes in the density of the invading genotype for different  $B_{IN}$  values including 1 (solid black line), 2 (solid grey line) and 3 (solid light grey line) with  $B_{IH} = 2$  and  $B_{HN} = 1.2$ . The density of the native was at equilibrium at the beginning of the simulation ( $n_N(0) = 0.8$ ), no hybrid existed in the first generation ( $n_H(0) = 0$ ) and the density of the invading genotype was 10 % of the native. Other parameters were  $A = 0.8$  and  $B = 3$

is assumed to be constant, Fig. 4b for the full hybridizing model). Moreover, as shown with the analysis of the simplified hybridizing model, the growth rate of the invading

**Fig. 6** Relative density of native ( $N$ ), invading ( $I$ ) and hybrid ( $H$ ) genotypes after 100 generations, as a function of  $B_{IH}$  (top panel) and  $B_{NH}$  (bottom panel) for three different hybridization rates,  $B_{IN}$ , of 1 (a and d), 2 (b and e) and 3 (c and f).

Interbreeding parameters  $B_{ij}$  ( $i \neq j$ ) were fixed at 1.5 if not used as an independent variable (i.e.  $B_{HN} = 1.5$  for the top panel and  $B_{IH} = 1.5$  for the bottom panel). The density of native was at equilibrium at the beginning of the simulation ( $n_N(0) = 0.8$ ) while that of the invading genotype was 1 % of the native. No hybrid existed in the first generation ( $n_H(0) = 0$ ). Other parameters were  $A = 0.8$  and  $B = 3$



genotype became positive when the reproduction barriers between the native and invading genotypes became weaker (i.e. larger  $B_{IN}$ ) (Fig. 5). Notice that when the native population was assumed to stay constant over time, the hybrid population outnumbered the invading genotype (Fig. 4a), whereas the invading genotype became the dominant genotype when the full model, which allows for changes in population of native, was considered (Fig. 4b). Thus, the analysis of the simplified hybridizing genotype (holding  $n_N$  constant over time) is useful for interrogating the effects of parameters on the establishment of the invading genotype, but the full hybridizing model is necessary to understand the equilibrium frequencies of native, hybrid and invading genotypes.

We also studied the dynamics of the three genotypes as a function of  $B_{HN}$  or  $B_{IH}$ , representing the degree of symmetry in the direction of backcrossing between the hybrid and parents, and for different values of  $B_{IN}$ , representing the rate of hybridization (Fig. 6). When  $B_{IN}$  and  $B_{HN}$  were small, the invader will go extinct whatever the values of  $B_{IH}$  (Fig. 6a). The invader can establish and become dominant only if  $B_{IH}$  is large, implying a large asymmetry in introgression where hybrids backcross with the invading genotype more than the native genotype (Fig. 6b). The increase in  $B_{NH}$  also allows the invader to establish

(Figs. 3 and 6) but only to a limited extent: beyond a specific threshold, increasing  $B_{NH}$  will reduce the frequency of the invader in the population while that of the native genotype is increasing (Fig. 6c, d). However, when  $B_{IN}$  is large (Fig. 6b, d), the effect of asymmetric backcrossing is less profound.

## Discussion

Our kinetic model highlighted the possibility for a *qualitative* facilitation of pollination in a system of two interacting species that share pollinator services and can hybridize. Hybridization improvement of the pollination quality not only allowed the invading genotype to avoid extinction but also enabled it to maintain a positive growth and even become dominant in the mixed population (e.g. Fig. 6b). In this study, we only investigated the potential role of hybridization in improving the quality of pollination while keeping the pollination quantity constant: this allowed us to underpin the pure facilitative effect of hybridization compared to our previous study that included the positive effect of a co-flowering species on a visitation rate too (Mesgaran et al. 2016). We achieved a constant pollination quantity by assuming that the density of pollinators,  $e_0$ , is a fixed parameter and independent of the population size so the visitation rate in the invading genotype (and other genotypes if they exist) is not affected by the density of population (see Eq. 26). Our model suggests that hybridization as a process that exploits interspecific pollen transfer, IPT, can be sufficient to drive a facilitative effect with no requirement for additional benefits of increased visitation rate that can be provided by a co-flowering species.

When hybridization is possible, the native genotype interacts with the invading genotype both negatively and positively. On the one hand, the individuals of the native genotype compete with the invading genotype and reduce its survival rate through density-dependent regulation. On the other hand, the native individuals act as potential mates for the invading genotypes, thus alleviating the problem of pollen limitation. The net outcome of these two processes will be positive, leading to facilitation, when the interbreeding rates (designated as  $B_{ij}$  in our model) are high. A high interbreeding rate reduces fertilization failure (caused by heterospecific pollen-ovule encounter) and thus results in a birth rate that exceeds the mortality.

This conclusion was derived by observing that hybridization made the stable trivial equilibrium in the single species model unstable with the solution diverging from (0, 0). More specifically, a large value of interbreeding parameter  $B_{IN}$  or  $B_{NH}$  resulted in an unstable trivial equilibrium (Fig. 3) suggesting the possibility for growth from the same low densities. A stable trivial equilibrium, however, implies

that the invading genotype will always go extinct if it is introduced at low densities. It might seem unexpected that the backcrossing rate between the native and hybrid genotypes,  $B_{NH}$ , was found to be more important than  $B_{IH}$  (backcrossing rate between the invader and hybrid) for alleviation of a strong Allee effect in the invader given that the latter crossing can produce more homozygous invading genotypes (i.e.  $II$ ) than the former one. Since both the invader and the hybrid occur at very low densities at the time of introduction, they need to interact (cross) with the native population, which already has a high density, to be able to establish. The increase in intercrossing between the invader and hybrid, i.e.  $B_{IH}$ , will not be effective in removing the strong Allee effect as they both have densities close to the trivial equilibrium in the beginning of invasion.

The heterospecific mating rate in sympatric zone depends on a variety of pre- and post-pollination factors such as the temporal distribution of flowering, pollinator behaviour and compatibility of pollen-stigma or pollen-ovule complex (Campbell and Aldridge 2006). The first requirement for interspecific mating is an overlap in flowering timing of the co-occurring species. However, ethological isolation caused by preference and constancy of pollinators may still prevent pollen transfer between co-flowering species (e.g. Esfeld et al. 2009, Schemske and Bradshaw 1999). Even after the successful deposition of heterospecific pollen on the stigma, the pollen may fail to germinate or grow down the style (e.g. Lee et al. 2008) or may be outcompeted by the conspecific pollen (Carney et al. 1996). The above mechanisms not only affect the likelihood and rate of interbreeding but can also cause a bias in the direction of crossing and introgression (e.g. Aldridge and Campbell 2006). Our previous model showed that bias in the direction of hybridization (introgression) can have important demographic and genetic consequences (Mesgaran et al. 2016). In this study, we also found a similar effect from an asymmetric introgression. As predicted by our kinetic model, increasing the crossing rate between the hybrid and invading genotype ( $B_{IH}$ ) increased the growth rate of the invading genotype which ultimately resulted in a population structure that mainly consisted of the invading genotype (Fig. 6b). This can be explained by the Mendelian genetic model: every time that a hybrid crosses with the invader, 50 % of the resultant offspring will have the identity of the invading genotype  $II$ . However, this synergic effect of asymmetric backcrossing can only exist if the interbreeding rate between the parental genotypes ( $B_{IN}$ ) is already high enough to allow the establishment of the invader: when it is low there is no chance for the invader to escape the Allee effect as shown in Fig. 6a. At the genome scale (with no assumption about the number of loci), the amount of genetic material from the native species is halved in the progeny with each successive backcross generation while that from the

invading genotype increases following  $(2^b - 1/2)/2^b$  with  $b$  indicating the backcross generation. It therefore takes only six backcross generations to produce an individual in which >99 % of its genome descends from the invading species. In this study, we included only three genotypes in the model assuming a simple Mendelian genetic inheritance. Huxel (1999) used the same single locus, two-allele genetic model but with no account of population demography. Wolf et al. (2001) also used three genotype classes but incorporated various ecological parameters. However, their model included no explicit genetic component with hybrids acting as an absorbing class, i.e. any cross between parents and hybrid results in hybrid offspring. This assumption may artificially inflate the hybrid class. It is unlikely that our qualitative results be affected by the choice of the number of genotype classes (locus) or the model of inheritance. An alternative approach is to consider genotype as a continuous variable as was implemented in the hybridization model of Hall et al. (2006) and Mesgaran et al. (2016).

A variety of models have been developed to explore the genetic consequences of hybridization, usually by tracking the changes in the frequency of invasive alleles in a fixed population size (e.g. Durrett et al. 2000, Hu 2005, and Huxel 1999 also see the review by Hall and Ayres 2008). Only very few hybridization models, however, have combined genetics processes with ecological or demographical parameters. Previous models of hybridization have mainly focused on the extinction risks of native species by hybrids (e.g. Epifanio and Philipp 2000; Hall et al. 2006; Wolf et al. 2001). None of these models included Allee effects. Allee effects have been incorporated into many population models of invasions but the majority are single species models (e.g. Kanarek 2012, Kot et al. 1996, and Lewis and Kareiva 1993 also see the review by Boukal and Berec 2002). Using the theory of kinetic reactions, we were able to integrate these two seemingly unrelated biological phenomena, i.e. hybridization and Allee dynamics, into a population dynamics model. The advantage of this modelling approach is that many well-established mathematical techniques and theories (e.g. see Appendix D) can be used to address complex biological questions such as those raised in this study.

The selection of the trivial equilibrium as the basis of our analysis was both for mathematical and biological reasons. First, the use of a trivial point makes the model more tractable and amenable to mathematical techniques that biologists are familiar with, e.g. Jacobian linearization commonly used in stability analysis (Edelstein-Keshet 1988). Other equilibria, if they could be solved, were rather complex and difficult to analyse. Second, perturbation about the trivial equilibrium simulates the dynamics of a small founding population, which is a common phenomenon in many systems including biological invasions (Taylor and Hastings 2005; Elam et al. 2007; Simberloff 2009). This assumption

about having a small founding population also validates the mass-action approach used in our modelling process, where the production of seeds is proportional to the abundance (concentration) of reactants (pollen and ovule) and agent (pollinator). We expect the outcome to be different if we include pollinator satiation or pollen saturation, especially if the saturation threshold stands below the Allee threshold.

While “invasion pinning” (*sensu* Keitt et al. 2001) from an Allee effect has been suggested as a potential means for managing biological invasions (Tobin et al. 2011), hybridization exploitation of IPT illustrates another mechanism by which an invader can overcome Allee effects and initiate a successful invasion. Hybridization is a growing concern as it can result in genomic swamping of natives by invasive species (Rhymer and Simberloff 1996), and our model shows that with hybridization, the “pure” invader rather than its hybrid lineages (Epifanio and Philipp 2000; Hall et al. 2006; Wolf et al. 2001) can cause rapid decline in the population of native species, while without hybridization, the invader might have gone extinct during the early phases of invasion. Conservation programmes should therefore account for this cryptic role that hybridization may play in invasions.

The interaction between dispersal and hybridization can provide useful insights as to how hybridization can affect the rate of spread, in addition to establishment, in invading populations. Therefore, the incorporation of a spatial component could form the basis of future work.

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## Appendix A: Derivation of the models

In this section, we use a quasi-steady state approximation followed by rescaling of the dependent and independent variables to obtain a dimensionless ordinary differential equation that describes the rate of change in seed number as a function of pollen and ovule density; the dynamics are defined by Eqs. 1, 2 and 3.

### A.1 Kinetic reaction theory and quasi-steady-state approximation

The time-evolution of  $N$  can be obtained through a quasi-steady-state approximation as described in Keener and Sneyd (2009) and Murray (2002). Let  $s_1 = [S_1]$ ,  $s_2 =$

$[S_2]$ ,  $e = [E]$ ,  $c_1 = [C_1]$ ,  $c_2 = [C_2]$ ,  $n = [N]$  be the abundance of pollen, ovules, pollinator without pollen, pollinators with pollen, pollinator with pollen on ovules and seeds, respectively. We derive, from the kinetic reaction (1), (2) and (3), the following system of ODEs:

$$\begin{cases} \frac{ds_1}{dt} = -k_1 s_1 e, \\ \frac{ds_2}{dt} = -k_0 s_2 - k_3 c_1 s_2 + (1 - \nu) k_4 c_2, \\ \frac{de}{dt} = -k_1 s_1 e + k_2 c_1, \\ \frac{dc_1}{dt} = k_1 s_1 e - k_2 c_1 - k_3 c_1 s_2 + k_4 c_2, \\ \frac{dc_2}{dt} = k_3 c_1 s_2 - k_4 c_2, \\ \frac{dn}{dt} = k_0 s_2 + \nu k_4 c_2. \end{cases} \quad (16)$$

Note that

- $n$  will be known once  $c_2$  and  $s_2$  are known and it does not affect the dynamics of the other variables in the system so the equation can be removed from the system,
- $\frac{de}{dt} + \frac{dc_1}{dt} + \frac{dc_2}{dt} = 0$  thus  $e + c_1 + c_2 = e(0) + c_1(0) + c_2(0) = e_0$  and  $e$  can be deduced from  $c_1$  and  $c_2$ , so we can remove  $e$  from the system by replacing it with  $e_0 - c_1 - c_2$ . Rewriting the equations for  $s_1$ ,  $s_2$ ,  $c_1$  and  $c_2$ , we obtain the following new system

$$\begin{cases} \frac{ds_1}{dt} = -k_1 s_1 e_0 + k_1 s_1 c_1 + k_1 s_1 c_2, \\ \frac{ds_2}{dt} = -k_0 s_2 - k_3 c_1 s_2 + (1 - \nu) k_4 c_2, \\ \frac{dc_1}{dt} = k_1 s_1 e_0 - k_1 s_1 c_1 - k_1 s_1 c_2 - k_2 c_1 - k_3 c_1 s_2 + k_4 c_2, \\ \frac{dc_2}{dt} = k_3 s_2 c_1 - k_4 c_2. \end{cases} \quad (17)$$

The quasi-steady state approximation assumes that the rate of formation and breakdown of complexes are essentially equal at all times, that is  $dc_1/dt = 0$  and  $dc_2/dt = 0$ . This approximation can be derived through non-dimensionalization of the system, choosing for example the following dimensionless variables:

$$\tau = k_1 e_0 t, \quad u_1 = \frac{s_1}{s_0}, \quad u_2 = \frac{s_2}{s_0}, \quad v_1 = \frac{c_1}{e_0}, \quad v_2 = \frac{c_2}{e_0},$$

where  $e_0$  and  $s_0$  are the initial number of enzyme (pollinator) and substrate (pollen and ovule), respectively.

Now, writing the equations based on the scaled variables, one gets:

$$\begin{cases} \frac{du_1}{d\tau} = -u_1 + u_1 v_1 + u_1 v_2, \\ \frac{du_2}{d\tau} = -\frac{k_0}{k_1 e_0} u_2 - \frac{k_3}{k_1} v_1 u_2 + (1 - \nu) \frac{k_4}{k_1 s_0} v_2, \\ \epsilon \frac{dv_1}{d\tau} = u_1 - u_1 v_1 - u_1 v_2 - \frac{k_2}{k_1 s_0} v_1 - \frac{k_3}{k_1} v_1 u_2 + \frac{k_4}{k_1 s_0} v_2, \\ \epsilon \frac{dv_2}{d\tau} = \frac{k_3}{k_1} v_1 u_2 - \frac{k_4}{k_1 s_0} v_2, \end{cases} \quad (18)$$

with  $\epsilon = \frac{e_0}{s_0}$ .

Notice that in our framework  $\epsilon \ll 1$  as that there is much more pollen and ovule (substrate) than pollinator (enzyme) in the beginning.

Thus, letting  $\epsilon \rightarrow 0$  while considering the last two equations in Eq. 18, we have

$$\begin{cases} 0 = u_1 - u_1 v_1 - u_1 v_2 - \frac{k_2}{k_1 s_0} v_1 - \frac{k_3}{k_1} v_1 u_2 + \frac{k_4}{k_1 s_0} v_2, \\ 0 = \frac{k_3}{k_1} v_1 u_2 - \frac{k_4}{k_1 s_0} v_2. \end{cases}$$

which after solving for  $v_1$  and  $v_2$ , we obtain the following:

$$\begin{cases} v_2 = \frac{k_3 s_0}{k_4} v_1 u_2, \\ v_1 = \frac{u_1}{u_1 + \frac{k_3 s_0}{k_4} u_1 u_2 + \frac{k_2}{k_1 s_0}}. \end{cases} \quad (19)$$

Scaling back to the initial variables  $c_1$  and  $c_2$ , Eqs. 19 can be written

$$\begin{cases} c_1 = \frac{e_0 s_1}{\frac{k_2}{k_1} + s_1 + \frac{k_3}{k_4} s_1 s_2}, \\ c_2 = \frac{k_3}{k_4} c_1 s_2. \end{cases} \quad (20)$$

Note that these two equations could have been obtained directly by setting  $dc_1/dt = 0$  and  $dc_2/dt = 0$ . Using the last equation in (16):

$$\frac{dn}{dt} = k_0 s_2 + \nu k_4 c_2.$$

and after some substitutions and simplifications, we obtain the following ODE that describes the dynamics of seed production  $n$  as related to the density of pollen,  $s_1$ , and ovules,  $s_2$ :

$$\frac{dn}{dt} = k_0 s_2 + \frac{V_{\max} s_1 s_2}{Q_1 Q_2 + Q_2 s_1 + s_1 s_2}, \quad (21)$$

where

$$V_{\max} = \nu e_0 k_4, \quad Q_1 = \frac{k_2}{k_1}, \quad Q_2 = \frac{k_4}{k_3}.$$

We also obtained equations for the temporal dynamics of  $s_1$  and  $s_2$  but our focus here is on the role of the ovules and pollen on the production of seeds and not the dynamics of these reactants *per se*.

The above Eq. 21 models the birth rate of seeds only: to account for death of individuals, we incorporated a density-dependent mortality component as follows:

$$\frac{dn}{dt} = k_0 s_2 + \frac{V_{\max} s_1 s_2}{Q_1 Q_2 + Q_2 s_1 + s_1 s_2} - d_1 n - d_2 n^2, \quad (22)$$

with  $d_1$  and  $d_2$  being the density-independent and the density-dependent death rates, respectively (Harper and McNaughton 1962).

This last Eq. 22 describes the rate of change in  $n$ , the density of seeds, as a function of  $n$  itself but also that of the pollen and ovule densities. The first term in the right hand side of the Eq. 22 represents reproduction through self-fertilization, whereas the second term indicates seed production via outcrossing. The last term on the right-hand side of Eq. 22 accounts for death that can happen at any stage of the plant's life cycle over the whole growing season. Note that Eq. 22 models changes in plant density over

time as a single stage, so that from a mathematical perspective,  $n$  can be envisioned both as a seed in the seedbank or as a mature plant above the ground. That is, the rate of change in  $n$  is simply the result of the difference between birth and death rates. This simplification is reasonable as our model is based on the life cycle of an annual plant with no persistent seedbank and thus with no overlap between generations. We can therefore further simplify the model by assuming that the other two dynamic variables, i.e.  $s_1$  and  $s_2$  in Eq. 22, are proportional to  $n$  (this results in the final model (4) as will be discussed later).

## A.2 Non-dimensionalization

To reduce the number of free parameters in the system, we scaled the variables and reduced the model to a dimensionless problem (Buckingham 1914; Segel 1972) by strategically choosing

$$t^* = td_1, \quad n^* = \frac{d_2}{d_1}n, \quad s_1^* = c_s^1 \frac{k_1}{k_2} s_1, \quad s_2^* = c_s^2 \frac{k_3}{k_4} s_2,$$

where  $c_s^{1,2}$  are positive constants that will be determined later. Equation 22, after substituting the scaled variables, becomes the following:

$$\frac{dn^*}{dt^*} = \frac{d_2 k_0 k_4}{d_1^2 c_s^2 k_3} s_2^{*2} + \nu \frac{k_4 e_0 d_2}{d_1^2} \frac{s_1^* s_2^*}{c_s^1 c_s^2 + c_s^2 s_1^* + s_1^* s_2^*} - n^* (1 + n^*). \quad (23)$$

For simplicity, we drop the  $*$ , but hereafter the variable  $n$ ,  $s_1$ ,  $s_2$  and  $t$  refer to the non-dimensionalized version of the same variables. We obtain the non-dimensional version of Eq. 22:

$$\frac{dn}{dt} = A \frac{s_2}{c_s^2} + B \frac{s_1 s_2}{c_s^1 c_s^2 + c_s^2 s_1 + s_1 s_2} - n - n^2, \quad (24)$$

where

$$A = \frac{d_2 k_0 k_4}{d_1^2 k_3}, \quad (25)$$

and

$$B = \frac{\nu k_4 e_0 d_2}{d_1^2}. \quad (26)$$

The ratio  $d_2/d_1$  represents the relative contributions of density- and non-density-related factors to mortality, which are not easy to separate and can vary depending on the habitat type and species (Harper 1977). In disturbance-prone habitats such as coastal systems, for example, mortality is mainly due to erosion and is less affected by the density of plants (e.g. Keddy 1981). However, in tropical habitats and forests, where competition could become intensive, density can be a driving force of mortality (e.g. Lambers et al. 2002). Here, we assumed that mortality is mainly caused by

density-independent regulators (as in Watkinson and Harper 1978; Keddy 1981; Watkinson et al. 1989), though the opposed scenario can also be used without the loss of the generality of results. In the annual species *Vulpia fasciculata* plant, for example, mortality due to density-independent factors ranged from 7 to 40 % in the study of Watkinson and Harper (1978). Similarly, fire, as a density-independent factor, killed  $\sim 40$  % of flowering *Sorghum intrans* plants (Watkinson et al. 1989).

If we assume 30 % of plants die due to factors unrelated to the density while competition, i.e. density-dependent processes between plants, accounts for 9 % death over the growing season of 100 days, we will obtain a  $d_2/d_1^2 = 100$  day per unit density. We also assume that pollen deposition and the breakdown of the complex  $C_2$  happen at the same rate, so that  $k_3 = k_4$ . This gives  $k_3/k_4 = 1$  per unit density. The selection of these values is somewhat arbitrary and for mathematical convenience, e.g. parameter  $A$ , which is dimensionless, is now reduced to  $A = k_0 \times 100$  day where 100 is the length of growing season assumed for an annual plant: a longer or shorter growing period will not qualitatively affect the results. Parameter  $A$  now represents the selfing rate ( $k_0$ ) over the season. Nevertheless, the above mortality values are still realistic and fall within the range of reported values. Using the above argument, one also obtains that  $B = \nu \cdot k_4 \cdot e_0 \cdot 100$  day  $\cdot$  m<sup>2</sup>. The parameter  $e_0$  represents the density of pollinators at the time of the introduction and was assumed to be 1 m<sup>-2</sup>, which lies within the range of pollinator abundance in several surveys (e.g. Grixti and Packer 2006; Janovsky et al. 2013; Moreira et al. 2015; Westphal et al. 2008). The density of pollinators,  $e_0$ , can change (positively) with the plant density (Kunin 1993), but as we are mainly interested in the potential effect of hybridization on the quality of pollination, we assumed that this parameter is constant and independent of plant density. Now, the dimensionless parameter  $B$  becomes  $B = \nu \cdot k_4 \cdot 100$  day, which represents the fertile outcrossing rate as function of cross pollination rate,  $k_4$ , and fertilization success rate,  $\nu$ , in a growing season.

Equation 24 is thus a dimensionless equation that describes the rate of change in  $n$  as a function of  $A$  and  $B$ , representing the selfing and outcrossing rates over the season, respectively. This equation was then used to derive two different models: a model with a single invading species and the other with two hybridizing species.

Equation 22 and its dimensionless version Eq. 24 describe the multiple temporal processes within the life cycle of a plant simultaneously as a single phenomenon where  $n$  can be any expression of a plant's developmental stages from seed to seedling to mature plant. We assume that, on average, the ovule density and pollen load density are proportional to the plant density, which, in turn, is proportional to the matured seed density. We choose the

constants of proportionality to be the undetermined constants from the non-dimensionization,  $c_s^1$  and  $c_s^2$ , so that  $s_1 = c_s^1 n$  and  $s_2 = c_s^2 n$ .

### Appendix B: Model of two non-hybridizing genotypes: competition model

#### B.1 The model

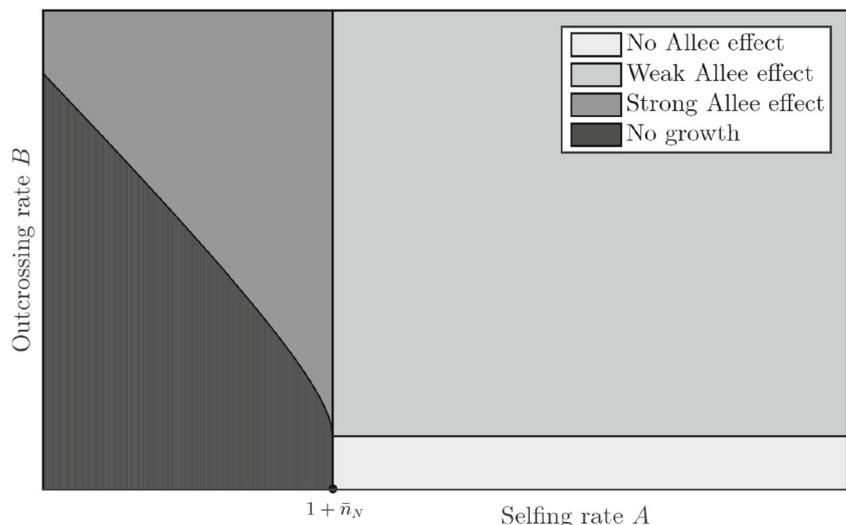
In this section, we expand our single species model (4) to a system of two competing genotypes (species), namely the native (resident) genotype, denoted by  $N$ , and a new incoming (invading) genotype, denoted by  $I$ . The two genotypes interact with each other through density-dependent regulation, e.g. death rate is a function of the total population size  $N + I$ , but they do not intercross, i.e. no hybridization occurs between them. The two genotypes are assumed to vary in their selfing, parameter  $A$ , and outcrossing, parameter  $B$ , rates. Extending the Eq. 4 to include two genotypes results in the system of two ODEs:

$$\begin{cases} n'_I(t) = n_I(A_I + B_I \frac{n_I}{1+n_I+n_I^2} - (1 + n_I + n_N)) \\ n'_N(t) = n_N(A_N + B_N \frac{n_N}{1+n_N+n_N^2} - (1 + n_N + n_I)), \end{cases} \quad (27)$$

where  $n_I$  and  $n_N$  denote the densities of invading and native genotypes, respectively. From Eq. 27, it can be seen that the existence of another genotype will always reduce the growth of either genotype. Now, suppose that the native genotype is at equilibrium (i.e.  $n_N \equiv \bar{n}_N$ ) at the time the propagules of the new genotype arrive at the location. As the density of the native is kept constant, the dynamics of invading can be studied through the following:

$$n'_I(t) = n_I \left( A_I + B_I \frac{n_I}{1 + n_I + n_I^2} - (1 + n_I + \bar{n}_N) \right) = \bar{F}(n_I). \quad (28)$$

**Fig. 7** Bifurcation diagram (27) depicting four dynamic outcomes for the invading genotype as related to parameters  $A$  (representing selfing rate) and  $B$  (representing outcrossing rate). See the “Analysis of the model” section for more details



As we assumed that the native genotype always remains at equilibrium and that it cannot interbreed with the invading genotype, the differential model of the invader in the presence of a resident species is similar to that of the single invading genotype, with the only exception being density-dependent mortality formulation.

#### B.2 Analysis of the model

Similar to the single species dynamics (Appendix C), bifurcation analysis of the above model gave rise to four outcomes, contingent on the value of  $A_I$  with respect to the bifurcation point  $(1 + \bar{n}_N)$  and the value of  $B_I$  with respect to 1 (Fig. 7). When  $A_I > (1 + \bar{n}_N)$ , population grows either with a weak Allee effect (if  $B_I > 1$ ) or with no Allee effect (if  $B_I < 1$ ). In the case of  $A_I < (1 + \bar{n}_N)$ , the invading population will have no growth and go extinct (if  $B_I$  is small) or experience strong Allee effects (if  $B_I$  becomes large).

### Appendix C: Analysis of the dynamics of invasion in the single species model

#### C.1 Single species model

In this section, we derive the analysis performed on the function  $F$  of Eq. 4, in order to characterize its shape and the type of growth for  $n$ .

When  $A > 1$ , using Descartes’ rule of sign (Appendix C.2 or in Pearson (1990), chapter 1), one can conclude that there exists a unique positive root  $n^*$  for  $F$ . Given that when  $n > 0$  is small,  $F(n) > 0$  whereas  $F(n) \rightarrow -\infty$  as  $n \rightarrow +\infty$  we obtain

$$F(n) > 0 \text{ if } 0 < n < n^* \text{ and } F(n) < 0 \text{ if } n > n^*.$$

We can conclude that for  $A > 1$ , the growth function  $F$  is always positive and there exists a stable equilibrium  $n^* > 0$ . Moreover, the per capita growth rate

$$\frac{F(n)}{n} = A - 1 - n + \frac{Bn}{1 + n + n^2}$$

is maximal at 0 if and only if  $B \leq 1$ . The model will thus give rise to a weak Allee effect if and only if  $B > 1$  (Fig. 1).

When  $A = 1$ , the model reduces to

$$F(n) = n^2 \left( \frac{B}{1 + n + n^2} - 1 \right), \tag{29}$$

which is positive for some values of  $n > 0$  if and only if  $B > 1$ . In this case, there exists  $n_B^* > 0$  such that

$$F(n) > 0, \quad \text{if } 0 < n < n_B^* \text{ and } F(n) < 0 \text{ if } n > n_B^*.$$

Lastly, if we assume that  $A < 1$ , the use of Descartes' rule of sign affirms the growth function is always negative if  $B \leq 2 - A$ . To investigate the model behaviour for situations where the population may grow, i.e.  $B > 2 - A$ , we use Cardan's method (Appendix C.3; also see Pearson (1990), chapter 1). We found that the function  $F$  can either be bistable or negative depending on the sign of the so-called discriminant  $\Delta$  (see Appendix C.3). Accordingly, when  $\Delta < 0$ , there exists two positive roots  $0 < n_1^* < n_2^*$  such that

$$F(0) = F(n_1^*) = F(n_2^*) = 0,$$

$$F(n) < 0, \quad \text{if } 0 < n < n_1^* \text{ or } n > n_2^*$$

and

$$F(n) > 0, \quad \text{if } n_1^* < n < n_2^*.$$

Whereas 0 and  $n_2^*$  equilibria are stable, the  $n_1^*$  equilibrium is unstable. The function  $F$  is thus bistable when  $\Delta < 0$  and there is a strong Allee effect. When  $\Delta \geq 0$ ,  $F(n) \leq 0$  for all  $n \geq 0$  and the only non-negative stable equilibrium is 0, implying that there is no growth.

### C.2 Descartes' rule of sign

Descartes' rule of sign is used to obtain an upper bound on the number of positive roots of a polynomial (Pearson 1990, chapter 1). That is, if the polynomial is ordered by descending variable exponent, then the number of sign changes between consecutive non-zero coefficients is greater or equal to the number of positive roots of the polynomials. Moreover, if the number of positive roots is not equal to the number of sign changes of non-zero consecutive coefficient, then it is smaller than it by an even number. Let  $Z$

denotes the number of sign changes of consecutive non-zero coefficients and  $P$  the number of positive roots, then

$$P \geq 0 \text{ and } P = Z - 2k, \text{ for some } k \in \mathbb{N}.$$

This means for example that if  $Z$  is odd then there is at least one positive root and if  $Z = 1$ , then we know that there is exactly one positive root.

This rule can be extended to negative roots also by considering  $-x$  in the polynomial instead of  $x$  and again using the above rule.

In our framework we write  $F$  as follows:

$$F(x) = \frac{x(-x^3 + (A - 2)x^2 + (A - 2 + B)x + (A - 1))}{1 + x + x^2}. \tag{30}$$

As the denominator in (30) is positive when  $x$  is non-negative, using Descartes' rule of signs for the third order polynomial in the numerator, we found that if  $A > 1$  then there is always only one sign change between the coefficients and thus there is exactly one positive root  $x^* > 0$ .

### C.3 Cardan's method

A brief description of Cardan's method can be found in Pearson (1990), chapter 1. Here, we provide more details on the method. We are interested in solving the general cubic equation, using Cardan's method

$$x^3 + ax^2 + bx + c = 0. \tag{31}$$

We first reduce this equation in a degenerate cubic equation of the form

$$x^3 + px + q = 0. \tag{32}$$

This can be done by the following substitution:

$$x = t - \frac{a}{3}.$$

Then Eq. 31 becomes

$$t^3 + pt + q = 0, \tag{33}$$

with  $p = (3b - a^2)/3$  and  $q = (2a^2 - 9ab + 27c)/27$ .

- If  $p = q = 0$ , then the only solution is  $t = 0$ , which is equivalent to  $x = -a/3$ ,
- If  $q \neq 0$  and  $p = 0$ , then  $t = \{\sqrt[3]{-q}, \sqrt[3]{-q}(-\frac{1}{2} - \sqrt{3}\frac{i}{2}), \sqrt[3]{-q}(-\frac{1}{2} + \sqrt{3}\frac{i}{2})\}$ , and  $x = t - a/3$ ,
- If  $p \neq 0$  and  $q = 0$ , then  $t = \{0, -\sqrt{-p}, \sqrt{-p}\}$  and  $x = t - a/3$ ,
- If  $p \neq 0$  and  $q \neq 0$ , then we introduce  $u$  and  $v$  such that  $t = u - v$ . Given that

$$(u - v)^3 + 3uv(u - v) - (u^3 - v^3) = 0 \tag{34}$$

we obtain  $p = 3uv$  and  $q = -(u^3 - v^3)$ . Note that  $u \neq 0$  and  $v \neq 0$ . This implies that  $v = \frac{p}{3u}$  and

$$u^3 - \left(\frac{p}{3u}\right)^3 + q = 0 \Leftrightarrow u^6 + qu^3 - \frac{p^3}{27} = 0,$$

thus,  $u^3$  solves a quadratic equation and

$$u^3 = \frac{-q \pm \sqrt{\Delta}}{2},$$

with  $\Delta = q^2 + 4p^3/27$ . As  $v^3 - u^3 = q$ , it follows that

$$v^3 = \frac{q \pm \sqrt{\Delta}}{2}.$$

Notice that as  $x = t - a/3 = u - v - a/3$ , the same results would be obtain if we change  $+\sqrt{\Delta}$  to  $-\sqrt{\Delta}$ , we can thus consider, without loss of generality, only the case with  $+\sqrt{\Delta}$  and

$$u^3 = -\frac{q + \sqrt{\Delta}}{2}, v^3 = \frac{q + \sqrt{\Delta}}{2}.$$

Depending on the sign of  $\Delta$ , now we can reach conclusion about the nature of the roots  $x$ :

- If  $\Delta = 0$ , then  $u = \{\sqrt[3]{-\frac{q}{2}}, \sqrt[3]{-\frac{q}{2}}(-\frac{1}{2} - i\frac{\sqrt{3}}{2}), \sqrt[3]{-\frac{q}{2}}(-\frac{1}{2} + i\frac{\sqrt{3}}{2})\}$  and using the fact that  $3uv = p \in \mathbb{R}$ , we know that  $u$  and  $v$  must be conjugate. Substituting for  $x$ , we get

$$x = \left\{ \sqrt[3]{\frac{q}{2} - \frac{a}{3}}, 2\sqrt[3]{-\frac{q}{2} - \frac{a}{3}} \right\}.$$

and the roots are real with  $(2\sqrt[3]{-\frac{q}{2} - \frac{a}{3}})$  being a simple root and  $(\sqrt[3]{\frac{q}{2} - \frac{a}{3}})$  being a double root.

- If  $\Delta > 0$ , then using the same arguments, we obtain

$$u^3 = \frac{-q + \sqrt{\Delta}}{2} \in \mathbb{R}, v^3 = \frac{q + \sqrt{\Delta}}{2} \in \mathbb{R},$$

and

$$u_1 = \sqrt[3]{\frac{-q + \sqrt{\Delta}}{2}} \in \mathbb{R}, v_1 = \sqrt[3]{\frac{q + \sqrt{\Delta}}{2}} \in \mathbb{R},$$

$$u_2 = \sqrt[3]{\frac{-q + \sqrt{\Delta}}{2}} \left(-\frac{1}{2} + i\frac{\sqrt{3}}{2}\right), v_2 = \sqrt[3]{\frac{q + \sqrt{\Delta}}{2}} \left(-\frac{1}{2} - i\frac{\sqrt{3}}{2}\right),$$

$$u_3 = \sqrt[3]{\frac{-q + \sqrt{\Delta}}{2}} \left(-\frac{1}{2} - i\frac{\sqrt{3}}{2}\right), v_3 = \sqrt[3]{\frac{q + \sqrt{\Delta}}{2}} \left(-\frac{1}{2} + i\frac{\sqrt{3}}{2}\right).$$

We can then deduce  $x_1 \in \mathbb{R}, x_2, x_3 \in \mathbb{C}$ .

- If  $\Delta < 0$ , then

$$u^3 = \left(\frac{-q + i\sqrt{-\Delta}}{2}\right) \in \mathbb{C}, v^3 = \left(\frac{q + i\sqrt{-\Delta}}{2}\right) \in \mathbb{C}.$$

Using the trigonometric representation of a complex number, we can write

$$u^3 = r(\cos(\varphi) + i\sin(\varphi)),$$

with  $r^2 = \left(-\frac{q}{2}\right)^2 - \Delta = \left(-\frac{p}{3}\right)^3$  and  $\cos(\varphi) = -\frac{q}{2\sqrt{(-\frac{p}{3})^3}}$ . We know that

$$u = r^{1/3} \left(\cos\left(\frac{\varphi}{3}\right) + i\sin\left(\frac{\varphi}{3}\right)\right)$$

and similarly

$$v = r^{1/3} \left(-\cos\left(\frac{\varphi}{3}\right) + i\sin\left(\frac{\varphi}{3}\right)\right).$$

Then,  $x = \{2r^{1/3}\cos(\frac{\varphi}{3}) - \frac{a}{3}, 2r^{1/3}\cos(\frac{\varphi+2\pi}{3}) - \frac{a}{3}, 2r^{1/3}\cos(\frac{\varphi+4\pi}{3}) - \frac{a}{3}\}$  and the roots of Eq. 31 are distinct and real.

Now, we apply this derivation to our equations:

$$F(n) = \frac{-n(n^3 - (A-2)n^2 - (A+B-2)n - (A-1))}{1 + n + n^2}. \quad (35)$$

We want to find the roots (or at least their sign) of the cubic polynomial on the numerator:

$$P(n) = n^3 - (A-2)n^2 - (A+B-2)n - (A-1), \quad (36)$$

when  $A < 1$  and  $B > 2 - A$ . First, using the Descartes' rule of signs, we know that this polynomial has either two or no positive roots. Moreover, we know that  $P(n) \rightarrow +\infty$  (respectively  $-\infty$ ) when  $n \rightarrow +\infty$  (respectively  $-\infty$ );  $P(0) = -(A-1) > 0$ ,  $P'(0) = -(A+B-2) < 0$ . Now we apply Cardan's method. Using the same notation given in the derivation above, we have

$a = -(A-2) > 0$ ,  $b = -(A+B-2) < 0$ ,  $c = -(A-1) > 0$  and thus

$$q = \frac{2a^2 - 9b + 27c}{27} > 0, \quad p = \frac{3b - a^2}{3} < 0.$$

Denoting  $\Delta$  as the determinant defined in the derivation above, we have:

- If  $\Delta > 0$ , then there is only one real root and thus it cannot be positive. Moreover, as  $P(0) > 0$  and  $P(n)$  do not change sign for  $n > 0$ , we conclude that  $P(n) > 0$  for all  $n > 0$ ,
- If  $\Delta = 0$ , there are only two real roots and the simple one is  $2\sqrt[3]{-\frac{q}{2} - \frac{a}{3}} < 0$ . Denoting  $n_2^*$  as the second real root, we have  $P(n_2^*) = P'(n_2^*) = 0$  and  $P$  only changes sign at the simple root  $2\sqrt[3]{-\frac{q}{2} - \frac{a}{3}} < 0$ . As  $P(0) > 0$ , we have  $P(n) \geq 0$  when  $n > 0$ ,

– If  $\Delta < 0$ , we know that the polynomial has three real roots  $n_0^*$ ,  $n_1^*$  and  $n_2^*$  such that

$$P(n) = (n - n_0^*)(n - n_1^*)(n - n_2^*), \tag{37}$$

and knowing that  $P(0) > 0$  and  $P'(0) < 0$ ; this implies that  $n_0^* < 0 < n_1^* < n_2^*$ ,  $P(n) > 0$  when  $n \in (0, n_1^*)$ ,  $P(n) < 0$  when  $n \in (n_1^*, n_2^*)$  and  $P(n) > 0$  when  $n > n_2^*$ .

As  $F(n) = \frac{-nP(n)}{1+n+n^2}$ , we obtain the required conclusion about the shape of  $F$ .

### Appendix D: Analysis of the dynamics of hybrid and invading genotypes for the hybridization scenario

#### D.1 Stability analysis of trivial equilibria in the hybridization model (11)–(12)

In this section, we detail the analysis of the two-dimensional ODE system (11)–(12) and more precisely the stability analysis of the trivial equilibrium  $(0, 0)$ . We first need to compute the Jacobian of the system at the trivial equilibrium:

$$J(0, 0) = J^0 = \begin{pmatrix} J_{11}^0 & J_{12}^0 \\ J_{21}^0 & J_{22}^0 \end{pmatrix} \tag{38}$$

where

$$J_{11}^0 = A_I - (1 + \bar{n}_N), \quad J_{12}^0 = \frac{A_H}{4}, \quad J_{21}^0 = \frac{B_{IN}\bar{n}_N}{1 + \bar{n}_N} + B_{IN}\bar{n}_N$$

and

$$J_{22}^0 = \frac{A_H}{2} + \frac{B_{HN}\bar{n}_N}{2} + \frac{B_{HN}\bar{n}_N}{2(1 + \bar{n}_N)} - (1 + \bar{n}_N).$$

The stability properties of  $(0, 0)$  can be inferred from the sign of the trace and the determinant of the Jacobian at  $(0, 0)$ :

$$tr(J^0) = J_{11}^0 + J_{22}^0, \quad det(J^0) = J_{11}^0 J_{22}^0 - J_{12}^0 J_{21}^0. \tag{39}$$

Indeed, the trivial equilibrium is stable if  $tr(J^0) < 0$  and  $det(J^0) > 0$ . It is an unstable node or unstable spiral if  $det(J^0) > 0$  and  $tr(J^0) > 0$  and an unstable saddle if  $det(J^0) < 0$ . We know from the positivity of the parameters that  $J_{12}^0, J_{21}^0 > 0$ , thus

$$\left(tr(J^0)\right)^2 - 4det(J^0) = (J_{11}^0 - J_{22}^0)^2 + 4J_{12}^0 J_{21}^0 > 0 \tag{40}$$

and the eigenvalues of  $(0, 0)$

$$\lambda_{1,2}^0 = \frac{tr(J^0) \pm \sqrt{[tr(J^0)]^2 - 4det(J^0)}}{2} \in \mathbb{R} \tag{41}$$

Both eigenvalues are real, which means that the trivial equilibrium is either a node (stable or unstable) or a saddle.

Note that the trace and the determinant of the Jacobian at  $(0, 0)$  only depend on  $B_{IN}$  and  $B_{HN}$ , given that  $A_H = A_I = A$  were chosen to be fixed. Our goal is to determine the parameter space under which either the trace and the determinant are positive (and  $(0, 0)$  will then be an unstable node) or the determinant is negative (and  $(0, 0)$  will be an unstable saddle): if any of these conditions ( $tr(J^0), det(J^0) > 0$  or  $det(J^0) < 0$ ) are met, the trivial equilibrium  $(0, 0)$  will become unstable. For the first case (i.e. both trace and  $det > 0$ ), we have the two following inequations:

$$\begin{aligned} tr(J^0) > 0 &\Leftrightarrow B_{HN} \\ &> -\frac{2(\bar{n}_N + 1)}{\bar{n}_N(2 + \bar{n}_N)} \left(\frac{3A}{2} - 2(1 + \bar{n}_N)\right) \\ &= T^0 > 0 \end{aligned} \tag{42}$$

and

$$\begin{aligned} det(J^0) > 0 &\Leftrightarrow B_{IN} < \frac{4(1 + \bar{n}_N)(A - (1 + \bar{n}_N))}{A\bar{n}_N(2 + \bar{n}_N)} \\ &\times \left[\frac{A}{2} - (1 + \bar{n}_N) + \frac{\bar{n}_N(2 + \bar{n}_N)}{2(1 + \bar{n}_N)} B_{HN}\right]. \end{aligned} \tag{43}$$

But, when  $det(J^0) > 0$  then  $tr(J^0) < 0$ . A  $det(J^0) > 0$  implies that

$$B_{HN} < \left((1 + \bar{n}_N) - \frac{A}{2}\right) \frac{2(1 + \bar{n}_N)}{\bar{n}_N(2 + \bar{n}_N)} < T^0,$$

as we assumed that  $A - 1 < 0$  in Eq. 14, to meet a stable trivial equilibrium in Eq. 4. Thus, when hybridization is allowed, the trivial equilibrium  $(0, 0)$  is either a stable node ( $det(J^0) > 0$  and  $tr(J^0) < 0$ ) or an unstable saddle ( $det(J^0) < 0$ ). The trivial equilibrium  $(0, 0)$  is unstable and thus facilitation is warranted if, and only if, the determinant becomes negative, i.e when  $B_{IN}$  and  $B_{HN}$  are such that

$$\begin{aligned} B_{IN} > \frac{4(1 + \bar{n}_N)(A - (1 + \bar{n}_N))}{A\bar{n}_N(2 + \bar{n}_N)} \\ \times \left[\frac{A}{2} - (1 + \bar{n}_N) + \frac{\bar{n}_N(2 + \bar{n}_N)}{2(1 + \bar{n}_N)} B_{HN}\right]. \end{aligned} \tag{44}$$

Changing the values of the parameters  $B_{IN}$  and/or  $B_{HN}$  to move from a negative determinant to a positive determinant thus generates a saddle node bifurcation at  $(0, 0)$ .

#### D.2 Analysis of the null clines of the hybridization model (11)–(12)

In this section, we examine the mechanisms underlying the saddle node bifurcation of  $(0, 0)$  by computing the null clines of Eqs. 11–12, i.e. the points  $(n_I, n_H)$  in the phase plane  $(n_I, n_H)$  such that

$$n'_I \equiv 0 \text{ and } n'_H \equiv 0. \tag{45}$$

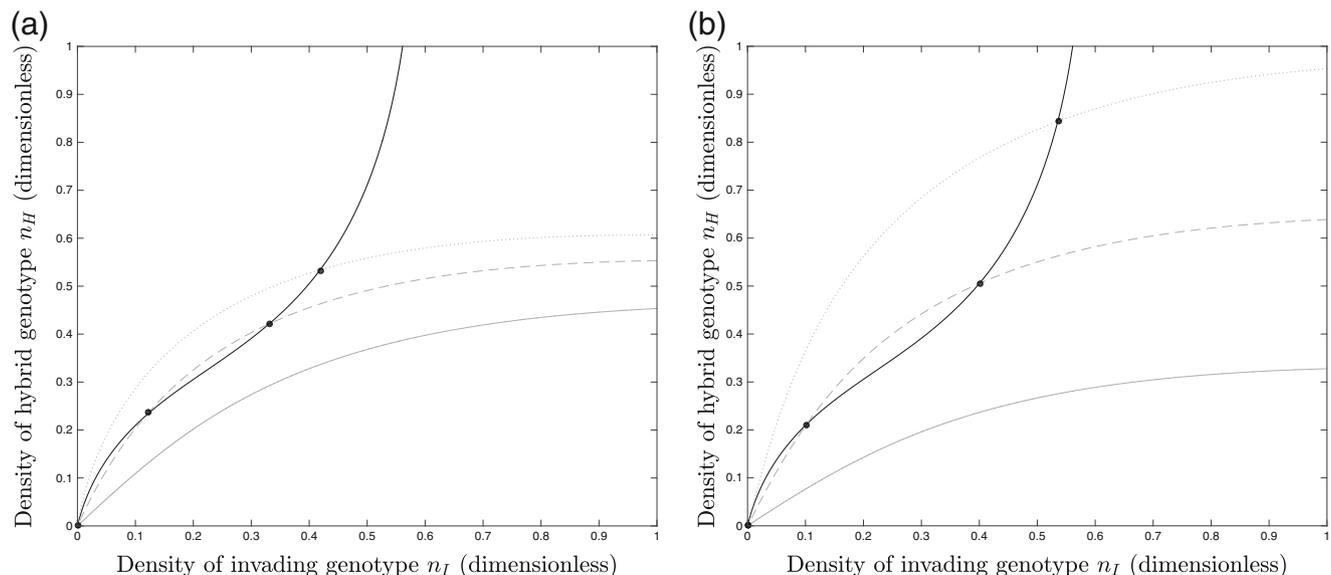
Note that the intersection of these null clines gives the equilibrium point(s). We computed these null clines for  $n_I, n_H > 0$  (Fig. 8) with parameters  $A$  and  $B$  in Eq. 13 chosen so that 0 is stable in the model with a single species (here  $A = 0.8, B = 3$ ). As can be inferred from Eq. 11, as well as shown in Fig. 8, the null cline for  $n_I$ , i.e. the curve such that  $n'_I \equiv 0$ , neither depends on  $B_{HN}$  (Fig. 8a) nor on  $B_{IN}$  (Fig. 8b). Therefore, if we change the values of these two parameters to change the stability of the trivial steady state  $(0, 0)$  of Eqs. 11–12, only the null cline associated with the hybrid population  $n_H$  changes. When  $B_{IN}$  and  $B_{HN}$  are very small (e.g. = 0.5), there is no non-trivial equilibrium, i.e. the null clines of the two genotypes only intersect at the stable equilibrium  $(0, 0)$ . With this parameter setting, the invading genotype will go extinct even if it can hybridize with the native genotype. A small increase in  $B_{IN}$  or  $B_{HN}$  (e.g. = 1) gives rise to three equilibrium points:  $(0, 0)$ ,  $n^1 = (n_I^1, n_H^1)$  and  $n^2 = (n_I^2, n_H^2)$ , where the null clines of the two genotypes intersect (Fig. 8). In this case, the trivial equilibrium is still stable (Fig. 3) but the stability of the two non-trivial equilibria requires further analysis (see below). Here, a low density of the invading genotype will again decline to 0. When large values of  $B_{IN}$  and  $B_{HN}$  were chosen (e.g. = 2), the model resulted in one non-trivial equilibrium  $n^2$  only (the intersection of solid black line and the dotted grey line in Fig. 8). In this case,  $(0, 0)$  is unstable (Fig. 3) but  $n^2$  is stable and the densities of invading and hybrid genotypes will converge to the non-trivial equilibrium  $n^2$  (Appendix D.3). To understand what

happens if the density of invading and hybrid genotype does not converge to the trivial equilibrium  $(0, 0)$ , we need to determine the stability of the non-trivial equilibria. To do so, we analysed the vector field of Eqs. 11–12 in more detail, as shown in Appendix D.3. The transition from a solution with two non-trivial equilibria to a solution with a single non-trivial equilibrium (Fig. 8) corresponds to a saddle node bifurcation at  $(0, 0)$  (Fig. 3). As the parameters  $B_{IN}$  and  $B_{HN}$  increase, the intermediate equilibrium  $n^1$  approaches the trivial equilibrium  $(0, 0)$  (Fig. 8), leading to a saddle node bifurcation. When  $B_{IN}$  and  $B_{HN}$  were large enough so that  $\det(J^0) < 0$ , only two equilibria result, the trivial  $(0, 0)$  which is now a saddle and the non-trivial  $n^2$ , which is stable.

### D.3 Stability analysis of non-trivial equilibria in the hybridization model (11)–(12)

To investigate the stability of the non-trivial equilibrium point(s) of Eqs. 11–12, we analyse the vector field around the equilibria, as outlined in Murray (2002), chapter 7.3. We only provide the details for one scenario, the intermediate equilibrium  $n^1$  (dotted line in Fig. 8), as the procedure is the same, to a large extent, for other non-zero equilibria. At this point  $n^1$ :

$$\left. \frac{dn_H}{dn_I} \right|_{F_I=0} > \left. \frac{dn_H}{dn_I} \right|_{F_H=0} > 0, \quad (46)$$



**Fig. 8** Null clines for invading genotype,  $n'_I \equiv 0$  (solid black line) and hybrid genotype  $n'_H \equiv 0$  (grey lines) for different  $B_{HN}$  values (a) or  $B_{IN}$  values (b) of 0.5 (solid grey line), 1.5 (dashed grey line), 2 (for  $B_{HN}$ ) or 3 (for  $B_{IN}$ ) (dotted grey line). The growth rate of the invading genotype is positive in the areas above its null cline ( $n'_I \equiv 0$ : solid black curve) but negative below it. For the hybrid genotype,

positive growth rate occurs in the areas under the null clines ( $n'_H \equiv 0$ : grey lines) while it is negative above them. The solid circles show the intersections of the two null clines (black and grey curves) which correspond to different equilibria. Other parameters were  $B_{IN} = 1$  (a) or  $B_{HN} = 1$  (b),  $A = 0.8$  and  $B = 3$

where  $F_I$  and  $F_H$  are the “growth” functions for the invading and hybrid genotypes in Eqs. 11–12, that is Eqs. 11 and 12 can be written in term of  $F_I$  and  $F_H$ :

$$\begin{cases} n'_I(t) = F_I(n_I, n_H) \\ n'_H(t) = F_H(n_I, n_H) \end{cases} \quad (47)$$

Given that  $F_I$  is positive above and negative below its null cline,  $n'_I \equiv 0$ , (the black curve in Fig. 8) whereas  $F_H$  is negative above and positive below its null cline,  $n'_H \equiv 0$ , (the grey curve in Fig. 8) we can conclude that at the very vicinity of  $n_1$ ,

$$\frac{\partial F_I}{\partial n_I} \Big|_{F_I=0} < 0, \quad \frac{\partial F_I}{\partial n_H} \Big|_{F_I=0} > 0 \quad (48)$$

and

$$\frac{\partial F_H}{\partial n_I} \Big|_{F_H=0} > 0, \quad \frac{\partial F_H}{\partial n_H} \Big|_{F_H=0} < 0. \quad (49)$$

This implies that  $\det(J(n_1^I, n_1^H)) < 0$  so that the non-trivial equilibrium  $n^1$  is a saddle. Using the same analysis for the other non-trivial equilibrium  $n^2$  yields

$$\frac{dn_H}{dn_I} \Big|_{F_I=0} < \frac{dn_H}{dn_I} \Big|_{F_H=0}, \quad (50)$$

and we can conclude that  $n^2$  is stable. We also conclude from Fig. 8 that there exists a positively invariant set containing the equilibria and observe that there exists no limit cycle in this invariant domain. Using Poincaré-Bendixon theory (as in Murray (2002), chapter 7.3), we conclude that the solutions  $n_I$  and  $n_H$  of Eqs. 11–12 converge to an equilibrium which can only be (0, 0) when it is stable or  $n^2$  (when it exists).

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