

# Biotic Interactions, Rapid Evolution, and the Establishment of Introduced Species

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**ABSTRACT:** The biotic environment can pose a challenge to introduced species; however, it is not known how rapid evolution in introduced and resident species influences the probability that the introduced species will become established. Here, we analyze the establishment phase of invasion with eco-evolutionary models of introduced species involved in predator-prey, mutualistic, or competitive interactions with a resident species. We find that, depending on the strength of the biotic interaction, establishment is impossible, guaranteed, or, in a narrow range, determined by genetic variation. Over this narrow range, rapid evolution of the introduced species always favors establishment, whereas resident evolution may either inhibit or facilitate establishment, depending on the interaction type. Coevolution can also either increase or decrease the chance of establishment, depending on the initial genotype frequencies as well as the interaction type. Our results suggest that the conditions under which genetic variation influences establishment success are limited, but they highlight the importance of considering the resident community's evolutionary response to introduced species as a component of its invasibility.

*Keywords:* invasive species, species interactions, predation, competition, mutualism.

## Introduction

The adage “an ounce of prevention is worth a pound of cure” has become widely associated with species invasions, yet how populations of potentially invasive species initially become established after introduction is still poorly understood (Marsico et al. 2010). In most cases, nonnative species are introduced at low population densities and have a high probability of immediate extinction due not only to the novelty of the habitat but also to consequences of a small population size per se (i.e., demographic stochasticity and Allee effects). Thus, the introduced species is more likely to become established if its population size

can increase quickly. The rate of this increase is expected to depend on the nonnative species' ability to tolerate the abiotic environment as well as on its interactions with resident species. These biotic interactions may either impede or facilitate establishment (Bruno et al. 2005).

Research has tended to focus on identifying ecological traits of potentially invasive species and native communities that characterize a predisposition to invasion (Kolar and Lodge 2001; Mitchell et al. 2006). However, variation in traits could play an important role by strengthening or weakening biotic interactions, both directly and indirectly through the potential for evolution (Bolnick et al. 2011). Rapid evolution from standing genetic variation could increase resistance to nonnative species by reinforcing antagonistic and limiting beneficial interactions, or it could facilitate establishment of nonnatives by alleviating antagonistic and amplifying beneficial interactions.

While introduced species have traditionally been thought to be genetically depauperate (e.g., because of population bottlenecks), evidence is building that species introductions often contain considerable amounts of genetic diversity (Roman and Darling 2007), particularly when multiple introductions lead to hybridization (Ellstrand and Schierenbeck 2000; Schierenbeck and Ellstrand 2009). Consequently, adaptation could occur even in the earliest stages of an invasion. As rapid evolution has the potential to alter population dynamics (Yoshida et al. 2003; Hairston et al. 2005; Becks et al. 2010) and can have an effect size that is significant even when compared to those of the environment and nonheritable variation (Ellner et al. 2011), it is important to assess the role of genetic diversity in establishment of introduced species. Indeed, adaptation to novel abiotic conditions has been predicted to expand the conditions under which introduced species may successfully establish (e.g., Holt et al. 2005; Travis et al. 2005; Gomulkiewicz et al. 2010). Genetic diversity may be expected to play a similar role in expanding the range of biotic environments that permit establishment of non-

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native species. However, it is not yet clear how resident-species evolution and population dynamics influence the establishment of a nonnative species.

Thus, in order to gain insight into the factors determining establishment of introduced species, we develop models of eco-evolutionary dynamics that follow introduction of a species involved in a predator-prey, mutualistic, or competitive interaction with a resident species. We use these models to ask how often and when rapid evolution has a significant effect on the establishment of an introduced species.

## Methods

### General Model Features

We model the joint population and evolutionary dynamics of a resident and an introduced species involved in a predator-prey, mutualistic, or competitive interaction. We analyze models that assume a haploid, diploid, or quantitative-genetic basis of inheritance. The results are, for the most part, qualitatively similar for all three genetic bases, and so we describe only the relatively less complex haploid formulations in the main text. Details of the diploid and quantitative-genetic models can be found in appendix A, available online.

Our models assume that species interactions are genotype dependent and that pairwise interactions between matched genotypes are stronger than those between mismatched genotypes (fig. A1, available online; see also Nuismer et al. 2010). The parameter  $\beta_{ij}$  represents the strength of an interaction between genotype  $i$  of one species and genotype  $j$  of the other. Our assumptions mean that the  $\beta_{ij}$  of matching genotypes ( $i = j$ ) always have a magnitude higher than that of mismatching genotypes ( $i \neq j$ ). Specifically, we set

$$\beta_{ij} = \begin{cases} i = j & \frac{\beta}{K} \\ i \neq j & \frac{\beta}{sK} \end{cases} \quad (1)$$

Genotype-specific interaction coefficients are determined by the base interaction strength,  $\beta$ , scaled by the carrying capacity,  $K$ , to account for the probability of an encounter. The mismatching coefficient is further scaled by the selection factor,  $s > 1$ , which describes the fitness ratio of a genotype match relative to that of a mismatch. To limit the complexity of this haploid model (and of our diploid model in app. A), we assume that each species has two alleles segregating at their respective interaction loci ( $i$  and  $j = 1, 2$ ). These alleles yield the most extreme phenotypes consistent with the selection factor,  $s$ , and thus will be the most informative about whether there is potential for evo-

lution to affect the population dynamics at the given strength of selection.

Below, we describe four introduction scenarios: predator, prey, mutualist, and competitor introduction. The corresponding dynamics are based on modified Lotka-Volterra equations for individual genotypes. In each scenario, we assume that the resident species plays a critical role in the establishment process: it is either necessary for the survival of the introduced species or presents a barrier to growth that must be surmounted. We adopted this assumption in order to capture the cases in which biotic interactions are most likely to have an effect on establishment success or failure.

### Predator-Prey Dynamics

There are two introduction scenarios that could involve a predator-prey interaction, depending on whether the predator or the prey is the introduced species. To emphasize the role of the interaction with a resident prey species, our model of an introduced predator assumes that the predator species must consume the focal resident prey species to reproduce. Genotype matching makes the predator more successful at capturing resident prey. When modeling an introduced prey species, we assume that the resident predator is supported by another resident prey species (whose dynamics are not explicitly modeled). The nonnative prey species will have difficulty establishing if it is unable to evade predation through genotype mismatching.

In both scenarios, the deterministic dynamics of prey ( $V_i$ ) and predator ( $P_j$ ) genotype abundances ( $i$  and  $j = 1, 2$ ) are

$$\frac{dV_i}{dt} = rV_i - \frac{r}{K} V_i \sum_{i=1}^2 V_i - V_i \sum_{j=1}^2 \beta_{ij} P_j, \quad (2a)$$

$$\frac{dP_j}{dt} = \gamma P_j - \frac{\gamma K}{K} P_j \sum_{j=1}^2 P_j + \theta P_j \sum_{i=1}^2 \beta_{ij} V_i. \quad (2b)$$

Prey genotype dynamics (eq. [2a]) depend on birth and death at intrinsic rate  $r$ , intraspecific competition at intensity  $r/K$ , and capture by predators at genotype-specific rates  $\beta_{ij}$  (eq. [1]). In the absence of predators ( $P_1 = P_2 = 0$ ), the combined abundance of prey genotypes has a stable equilibrium  $K$ . Predator genotype dynamics (eq. [2b]) depend on birth and death at intrinsic rate  $\gamma$ , intraspecific competition at intensity  $\gamma K/K$ , and capture of prey at genotype-specific rates  $\beta_{ij}$  (eq. [1]), which are then converted to predator offspring with efficiency  $\theta$ .

We consider an introduced predator species that, in its novel environment, is an obligate consumer of the resident prey species. This biotic effect is modeled by assuming that the predator's death rate exceeds its intrinsic birth rate (net intrinsic rate  $\gamma < 0$ ) and thus that the predator de-

clines in abundance in the absence of resident prey. For simplicity, we also assume no competition among introduced predators ( $\kappa = 0$ ) in this case and thus that predator abundance is regulated by the abundance of the resident prey species. In the scenario of an introduced prey species, the provision that resident predators also exploit a separate resident prey species (that is not explicitly modeled) is implemented by assuming predator growth ( $\gamma > 0$ ) in the absence of the introduced prey. In this case, we assume  $\kappa > 0$ , and so the resident predator's carrying capacity is  $K/\kappa$ . For both introduction scenarios, selection favors genotype mismatching in prey (lower  $\beta_{ij}$ , better chance of escaping a predator) and genotype matching in predators (higher  $\beta_{ij}$ , better chance of capturing prey).

#### Mutualism Dynamics

In our third scenario, a mutualistic introduced species, we once again stress the role of biotic interactions on establishment by assuming that the introduced species will fail to reproduce without rewards supplied by a resident mutualist. Both the introduced and the resident species benefit most from interactions when their genotypes match. Similar to our assumption about a resident predator, we assume that the benefits provided by the introduced species are not required for the resident mutualist to persist.

The dynamics of the resident, facultative mutualist ( $F_i$ ) and the introduced, obligate mutualist ( $M_j$ ) genotype abundances ( $i$  and  $j = 1, 2$ ) are

$$\frac{dF_i}{dt} = rF_i - \frac{r}{K}F_i \sum_{i=1}^2 F_i + \theta F_i \sum_{j=1}^2 \beta_{ij}M_j, \quad (3a)$$

$$\frac{dM_j}{dt} = -\gamma M_j - \frac{\gamma\kappa}{K}M_j \sum_{j=1}^2 M_j + \theta M_j \sum_{i=1}^2 \beta_{ij}F_i. \quad (3b)$$

Resident mutualist genotype dynamics (eq. [3a]) depend on birth and death at intrinsic rate  $r$ , intraspecific competition at intensity  $r/K$ , and rewards from mutualist partners at genotype-specific levels  $\beta_{ij}$  (eq. [1]), which are converted into offspring with efficiency  $\theta$ . Dynamics for the introduced, obligate mutualist genotypes (eq. [3b]) are similar, except that they assume population decline at intrinsic rate  $\gamma > 0$  and intraspecific competition at intensity  $\gamma\kappa/K$ . Thus, the introduced mutualist population will grow only if sufficient benefits are received from the resident mutualist species. Selection favors genotype matching in both mutualists (higher  $\beta_{ij}$ ), to facilitate the interspecific transfer of rewards.

#### Competition Dynamics

The fourth and last scenario involves an introduced species that competes with a resident species for a required, lim-

iting resource. We assume that the nonnative and resident species are equal competitors. Thus, the numerically inferior introduced species will be excluded if competition is too intense (Gotelli 2001). In our model, greater genotype mismatching of these competitors alleviates competition.

The dynamics of the resident competitor ( $R_i$ ) and the introduced competitor ( $I_j$ ) genotype abundances ( $i$  and  $j = 1, 2$ ) are

$$\frac{dR_i}{dt} = rR_i \left( 1 - \frac{1}{K} \sum_{i=1}^2 R_i - \sum_{j=1}^2 \beta_{ij}I_j \right), \quad (4a)$$

$$\frac{dI_j}{dt} = rI_j \left( 1 - \frac{1}{K} \sum_{j=1}^2 I_j - \sum_{i=1}^2 \beta_{ij}R_i \right). \quad (4b)$$

The species are equal competitors; thus, they have the same intrinsic growth rate  $r$ , carrying capacity  $K$ , and genotype-specific interspecific competition coefficients  $\beta_{ij}$  (eq. [1]). Since in our analyses  $\beta_{ij} \leq 1/K$ , the intensity of interspecific competition is never greater than the intensity of intraspecific competition. Selection favors genotype mismatching (lower  $\beta_{ij}$ ; character displacement) in both competitors.

#### Introduction, Selection, and Extinction Probabilities

Equations (2)–(4) were solved numerically (with Mathematica 8.0.0) for the four introduction scenarios described above. In each case, the total population size of the resident species was initiated at its carrying capacity, whereas the dynamics of the introduced species were started with a single pulse of 20 individuals. From there, the deterministic changes of the genotype abundances in both introduced and resident species were projected with the relevant dynamical system (eqq. [2]–[4]).

Because rapid evolution after introduction is most likely to occur through selection on standing genetic variation (Prentis et al. 2008), we assumed that mutation was negligible. We explored the full range of initial standing genetic variation in both resident and introduced species by projecting the deterministic dynamics, starting from genotype frequencies ranging from 0 to 1, at intervals of 0.05. Furthermore, we analyzed the effects of a range of base interaction strengths,  $0 \leq \beta \leq 1$ , which, when scaled by density and conversion efficiency, ranges over per capita interaction strengths observed in ecological networks (Paine 1992; Wootton 1997; Wootton and Emmerson 2005) and used in other theoretical analyses (e.g., Jonsson et al. 2010).

Given genetic variation, selection was driven by the genotype-specific interaction coefficients ( $\beta_{ij}$ ). Selection favors either matching of genotypes (i.e., in predators and

mutualists) or mismatching of genotypes (i.e., in prey and competitors). We considered scenarios in which both species are genetically uniform (and thus incapable of evolving), one species can evolve while the other is fixed, or the species can coevolve. To compare a genetically variable species to a comparable monomorphic one, for each set of parameters and initial conditions we analyzed a genetically uniform species with the same interaction strength as the initial mean interaction strength in the corresponding genetically variable case.

Our primary interest is how adaptive evolution in one or both species affects the probability that an introduced species establishes. However, the deterministic, continuous population dynamics in equations (2)–(4) allow species only to approach, not reach, extinction. Thus, we estimated the probability of species extinction over the time interval from  $t$  to  $t + h$  to be  $e^{-cN(t)}$ , in which  $N(t)$  is the population size at time  $t$  determined with equations (2)–(4) and  $c$  is a scaling coefficient chosen with discrete-time individual-based simulations assuming Poisson-distributed birth and death events. On this basis, we approximated the probability of a species persisting for at least  $n$  time intervals, each of length  $h$ , as

$$P_T = \prod_{i=0}^{n-1} (1 - e^{-cN(t_i)}), \quad (5)$$

where  $t_i = ih$  and  $T = nh$ . This method of estimating the probability of persistence agrees qualitatively with our stochastic simulations of the introduction scenarios.

We have parameterized the models such that the time-scale in our analyses ( $T = 200$ ) corresponds to 20–50 generations, in order to focus on rapid evolution. Given that generations overlap in the models, a simple way to define the length of a generation is as the expected life span, calculated as the reciprocal of the absolute value of the net intrinsic rate of change. Thus, we include fewer generations for long-lived predators and mutualists and more for short-lived prey and competitors. Examples of the population dynamics, evolutionary dynamics, and the probability of species persistence over time are shown in appendix B, available online; they demonstrate the dependence of these dynamics on the introduction scenario and initial genotype frequencies. Figures B1 and B2, available online, show that most of the change in the probability of persistence occurs in the first 5–10 generations after introduction, except when predator-prey cycling leads to repeated periods of low population sizes.

## Results

### Interaction Strength and the Probability of Establishment

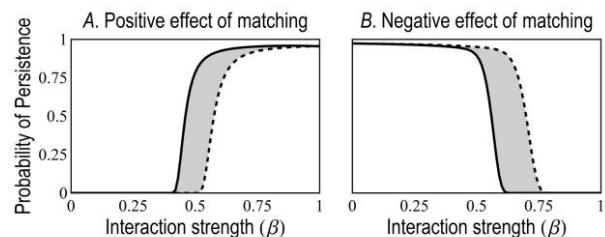
We found that genetic variation in fitness has remarkably little influence on the prospects of species establishment

over the majority of potential strengths of the interaction between introduced and resident species (fig. 1). This pattern holds regardless of whether the introduced species is predator, prey, mutualist, or competitor and even when there is a 30% fitness difference between genotype matching and mismatching (fig. 2).

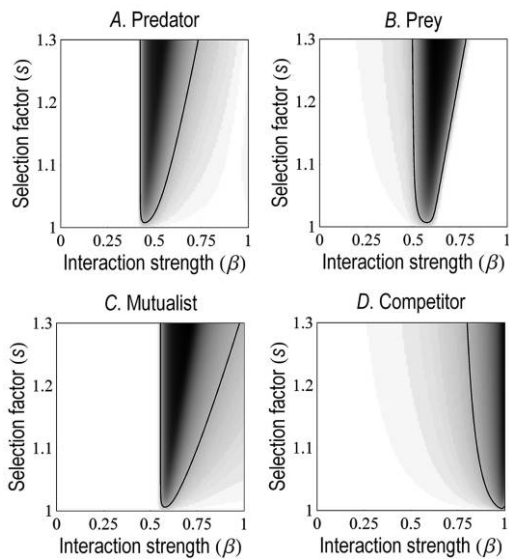
In general, the introduced species will always fail or always succeed in becoming established whether or not it or the resident species can evolve. In these cases, the outcome depends on the type of species introduced and the base strength ( $\beta$ ) of the interaction with the resident species. Failures occur when an antagonistic interaction is too strong, that is, a nonnative prey or competitor species is too strongly harmed by the resident species (fig. 1B; high  $\beta$ ), or when a beneficial interaction is too weak, that is, an introduced predator or mutualist species gains insufficient resources from the resident species (fig. 1A; low  $\beta$ ). By comparison, successful establishment occurs if an introduced species has robust initial growth, that is, a prey or competitor species is only mildly affected by the resident species (fig. 1B; low  $\beta$ ) or a predator or mutualist species reaps substantial benefits from the resident species (fig. 1A; high  $\beta$ ).

### Evolution and the Probability of Establishment

Within the narrow set of conditions where establishment failure or success is uncertain, we found several general patterns of how genetic variation affects the course of the invasion. Genetic variation provides potential for adaptive evolution in both species. Adaptive evolution in the introduced species always increases its probability of persis-



**Figure 1:** Probability of persistence for the introduced species when the demographic effects of genotype matching are positive (A) or negative (B). Genotype matching gives a positive effect for introduced predators (shown) and mutualists and a negative effect for introduced prey (shown) and competitors. The shaded regions show where genetic variation can affect the probability of persistence. These regions are bounded by the probabilities of persistence given by fixed genotype matching ( $i = j$ ; solid line) and fixed genotype mismatching ( $i \neq j$ ; dashed line). Parameter values:  $T = 200$ ,  $h = 1$ ,  $c = 0.2$ ,  $s = 1.25$ ,  $K = 300$ ,  $r = 0.25$ ,  $\theta = 0.4$ ; predator introduction (A):  $\gamma = -0.15$ ,  $\kappa = 0$ ; prey introduction (B):  $\gamma = 0.1$ ,  $\kappa = 3$ .



**Figure 2:** Effect of genetic variation on the probability of establishment, depending on the strength of the interaction and the strength of selection. For each type of introduced species, the panels show the region of interaction strengths ( $\beta$ ) over which there is at least a 5% difference in the probability of establishment between genotypes of the introduced species that do and do not match a fixed resident genotype (darker shading represents a greater difference in the probability of establishment). Parameter values:  $T = 200$ ,  $h = 1$ ,  $c = 0.2$ ,  $K = 300$ ,  $r = 0.25$ ; predator introduction (A):  $\gamma = -0.15$ ,  $\kappa = 0$ ,  $\theta = 0.4$ ; prey introduction (B):  $\gamma = 0.1$ ,  $\kappa = 3$ ,  $\theta = 0.4$ ; mutualist introduction (C):  $\gamma = 0.1$ ,  $\kappa = 2$ ,  $\theta = 0.2$ ; competitor introduction (D).

tence compared to a comparable species that cannot evolve (fig. 3, *left*), whereas the relative effects of resident evolution and coevolution on establishment success depend on the interaction type.

The evolutionary response of a resident species to an introduced species enhances the latter's establishment success when the same interspecific combination of genotypes is favored in both species (i.e., matched mutualist genotypes and mismatched competitor genotypes; fig. 3*Cii* and 3*Dii*, respectively). However, in the predator-prey scenarios, genotype matching is favored in the predator while genotype mismatching is favored in the prey. Thus, resident evolution suppresses fitness in the introduced species, resulting in a lower chance of establishment (fig. 3*Aii*, 3*Bii*).

The effects of resident species evolution on establishment of the nonnative species are less pronounced than those of evolution by the introduced species itself. This is because, in the initial stages of invasion, there are far fewer individuals of the introduced species than of the resident species. Consequently, resident individuals encounter non-

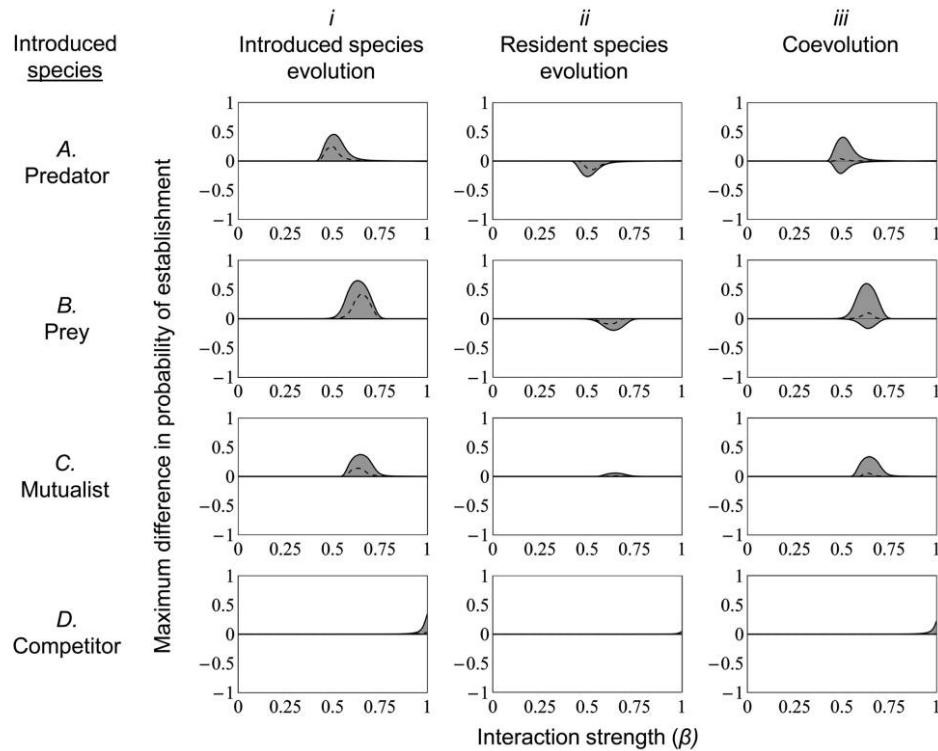
native individuals much less often than the reverse, and so the resident species as a whole experiences much weaker interspecific selection than the introduced species, even when the magnitudes of effects on individuals that do interact are exactly the same.

When both species are genetically variable, the effect of coevolution on the success of the nonnative can depend on the initial genotype frequencies of both species as well as on the interaction type (figs. 3 [iii], B4 [available online]). In the scenarios where resident-only evolution increases fitness of introduced individuals (namely, by favoring genotype matching in mutualism or genotype mismatching in competition), coevolution also increases the chance of establishment (fig. 3*C*, 3*D*) relative to that when both species are monomorphic. Coevolution might be expected to increase the chances of establishment to a greater degree than nonnative-only evolution, and this does occur in our quantitative-genetic model (described in app. A). However, in the haploid model described here, when both the introduced and the resident species are polymorphic, there are two equally beneficial ways to match (or to mismatch). As a result, directional selection is diluted and adaptive evolution is slowed. This Hill-Robertson-like effect (Hill and Robertson 1966) is particularly evident when the genotypes are similar in frequency (fig. B4*Ciii*, B4*Civ*, B4*Diii*, B4*Div*).

With predator and prey introductions, the nonnative species can gain an advantage when initial genotype frequencies are biased toward greater overall genotype matching or mismatching, respectively. Thus, coevolution results in higher or lower probabilities of establishment, depending on whether the introduced species starts with an advantage or a disadvantage due to the initial patterns of genotype frequencies in both species (figs. 3*A*, 3*B*, B4*A*, B4*B*). In addition, predator and prey introductions can cause population and coevolutionary cycling (fig. B2). During these cycles, the introduced species goes through periods of low abundance at which its risk of extinction is increased (fig. B2*A* [*right*], B2*B* [*right*]).

## Discussion

Genetic diversity is thought to be an important factor enabling invasive species to become dominant and widespread in their introduced ranges (Sakai et al. 2001; Allendorf and Lundquist 2003). While it has been suggested that genetic diversity should also play a role in the initial establishment phase of invasion (Facon et al. 2006; Kinnison and Hairston 2007), very little is known about the early dynamics of species introductions (Marsico et al. 2010). Previous theory has investigated whether rapid evolution can enable introduced species to overcome an initially unsuitable novel abiotic environment (Holt et al.



**Figure 3:** Difference in probability of establishment of the introduced species when there is initially genetic variation in at least one species, compared to that in genetically fixed populations with the same mean interaction strengths. The amount of difference depends on the initial genotype frequencies (see fig. B4, available online). The shaded regions show the range of differences in establishment probability across initial genotype frequencies, with the maximum positive and negative differences (solid lines) and the median differences (dashed lines). Parameter values as in figure 2, with  $s = 1.25$ .

2005; Gomulkiewicz et al. 2010). Here, we have focused on novel biotic interactions, considering the consequences of genetic variation in fitness in both the introduced and the resident species.

We found that rapid evolution can sometimes allow an introduced species to overcome unfavorable biotic conditions. However, this occurs only when conditions are slightly unfavorable for growth of the introduced species. We also found that adaptation has virtually no effect on establishment success when biotic conditions initially support rapid growth of the introduced species. Accordingly, there is only a narrow range of “baseline” interaction strengths over which the prospects of persistence for an introduced species are influenced by genetic variation in either the introduced species itself or the resident species. This finding is particularly surprising, given our focus on specialized interactions that play an important role in the population dynamics of the introduced species. Thus, our results suggest that while there is growing evidence of the importance of rapid evolution for species interactions, it

is likely to be of limited importance for the initial stages of species introductions and community assembly.

It is, of course, possible that in the wild, introductions tend to fall within the restricted range of interaction strengths where rapid evolution or coevolution can make a difference. Novel interactions may be stronger or weaker than coevolved interactions, providing an advantage to either the introduced or the resident species, depending on the type and mechanics of the interaction (Verhoeven et al. 2009). Previous studies have suggested that the strengths of novel interactions can be predicted from the similarity of the focal introduced and resident species (Courchamp et al. 2003), as well as from the similarity of the resident community to the community from which the introduced species originated (Sih et al. 2010). However, more extensive empirical documentation of the distribution of interaction strengths between novel species pairings (e.g., Klironomos 2003) is needed to determine how frequently rapid evolution plays a crucial early role in determining the outcomes of species introductions.

We found that ecological barriers to the establishment of an introduced species can result when interactions between introduced and resident species either do not provide enough benefit or are too detrimental. When obligate interactions are too weak, the introduced species may fail to establish because it gains insufficient benefit from the interaction to either survive or reproduce. Failure to establish due to “underexploitation” of an essential biotic interaction could occur for mutualists dependent on partners for reproduction or survival (e.g., figs and fig wasps, pines and mycorrhizae; Richardson et al. 2000; Pringle et al. 2009) or for introduced predators unable to capture novel resident prey (a “novelty disadvantage”; Sih et al. 2010). These considerations also apply to introduced herbivores and parasites.

When antagonistic interactions are too strong, the introduced species may fail to establish because of the costs of the interaction. Introduced species that depend on resources shared with resident species may face “competitive exclusion” if there is too much overlap between the niches of resident and introduced species. This has generally been considered the main mechanism preventing establishment of competitors, although it is recognized that communities may not be so saturated that they can repel all potential invaders (Bruno et al. 2005).

Finally, high consumption of introduced prey by resident predators could make it impossible for nonnative prey to establish because of “overexploitation” (e.g., Nuñez et al. 2008). Analogously, overexploitation of resident prey by introduced predators can lead to the local extinction of the native prey population (reviewed in Bruno et al. 2005; Strauss et al. 2006), which could in turn cause the eventual failure of a nonnative predator to establish, depending on the availability of other resident prey.

In all four scenarios we investigated, it is possible for adaptive evolution of the introduced species, the resident species, or both to alter the probability of establishment of the introduced species by either weakening or strengthening the barriers to establishment described above. Under our model assumptions, selection favors the same outcome for mutualist species (phenotype matching) and competitor species (character displacement). Consequently, in these interactions, both nonnative and resident species evolve toward a common state that facilitates establishment of the introduced species, and this outcome can be approached whether one or both species evolve. Facilitation by resident evolution might be especially important when genetic variation in the introduced species is limited (e.g., because of population bottlenecks). Nevertheless, our findings show that genetic diversity in the introduced species has an even greater effect on establishment success, since an introduced species tends to experience stronger selection (by virtue of being initially outnumbered by the

resident) and speed of adaptation is a critical determinant of its persistence (Gomulkiewicz et al. 2010).

Many introductions are known to be facilitated by mutualistic interactions with resident species (Richardson et al. 2000). Mutualists that are dependent on a highly specialized partner may become able to establish only if their native-range mutualist partner is also introduced. However, most mutualisms are more generalized and may require little adaptation by novel partners (Richardson et al. 2000). If introduced and resident species can each benefit more from a stronger interaction, it is not surprising that selection should favor closer phenotype matching that improves the exchange of rewards, thus further facilitating establishment.

By comparison, the prediction that resident evolution could facilitate establishment of a new competitor may seem counterintuitive, given the antagonistic interaction and the commonly held view of competition contributing to “biotic resistance,” or at least to “biotic containment” (Levine et al. 2004). Residents may respond to introduced competitors through character displacement, increased competitive ability, or development of tolerance to antagonistic traits (Strauss et al. 2006; Goergen et al. 2011). Importantly, different types of evolutionary response vary in their implications for management. Our results from modeling character displacement demonstrate, contrary to the suggestions by Leger and Espeland (2010), that increased genetic variation in resident species facilitates establishment, whereas reduced genetic variation in introduced species diminishes the potential for evolution that would relax competitive pressure on resident species.

In contrast to mutualism and competition, predator-prey interactions have several qualitatively different evolutionary outcomes. Predators may evolve to closely match their prey, increasing their success in capturing prey, or prey may evolve to better escape their predators. Thus, rapid evolution in an introduced predator can facilitate its establishment by increasing its ability to exploit the resident prey. On the other hand, genetic variability in the prey is needed to prevent it from being overexploited and thereby enables establishment of an introduced prey or supports persistence of the resident prey. The threat of overexploitation is particularly severe for prey lacking (similar) native predators, which therefore may lack appropriate defenses and antipredator behaviors (Sih et al. 2010). Finally, when the species coevolve, cycles in allele frequencies change the degree of matching between predator and prey, leading to oscillations in both species' abundances that increase the risk of extinction over time.

A wider community view may expand our assessment of the importance of genetic variation for the establishment of introduced species. Indeed, species outside a particular introduced-resident species pair are likely to influ-

ence how, and how much, the focal resident species responds to the introduced species (e.g., Lau 2008). Interactions among the introduced and several resident species could weaken selection on all species, and interactions among resident species themselves could overwhelm any selection driven by the introduced species until it becomes pervasive (Carlsson et al. 2009).

Another consequence of community interactions is that selection may no longer favor genotype matching or mismatching when both the introduced and a particular embedded resident species are competitors or mutualists. Competitors might not be selected for character displacement if all potential resources are already utilized (Shea and Chesson 2002) or if intraspecific “niche complementarity” favors maintenance of standing genetic variation by reducing competition among resident conspecifics that differ in their resource use (e.g., Crutsinger et al. 2008). While mutualists might be expected to benefit from increased interaction, resident mutualists may be selected to avoid introduced species that are not as rewarding as resident partners, and either species may become an exploiter of the mutualism. In the absence of suitable resident mutualists, introduced species may instead be selected for reduced dependence on partners (Seifert et al. 2009). Likewise, selection on predators and prey need not be frequency dependent (e.g., evolution of increased refuge use; Kiesecker and Blaustein 1997), and predator-prey population dynamics could be more complex in the presence of additional resident prey or predator species.

Our main conclusion is that under a wide range of interaction types and conditions, rapid adaptive evolution is of essentially no consequence for the prospects of establishment success or failure. It is only when interspecific interactions are marginally too strong or too weak that evolution can tip the balance toward or against the introduced species, compared to introductions involving non-evolving interactions. We have shown that genetic variation in the introduced species tends to enhance its chances of successful establishment. More surprisingly, we have shown that genetic variability in a resident species should also often increase, rather than decrease, the probability that a nonnative species is successfully introduced. This result suggests that evolution by a resident community in response to an introduced species may be an important overlooked factor in assessing the community’s vulnerability to exotic invasions, and it highlights the need for a deeper understanding of how immigrant species join co-evolving resident communities.

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# Appendix A from E. I. Jones and R. Gomulkiewicz, “Biotic Interactions, Rapid Evolution, and the Establishment of Introduced Species”

(Am. Nat., vol. 179, no. 2, p. E28)

## Diploid and Quantitative Genetic Models

This appendix shows how we derived the dynamics for diploid and quantitative-genetic systems. We describe in detail only predator-prey dynamics, but equations for the other interactions types are obtained the same way.

First, it is convenient to change variables to track total population size and genotype frequencies for each species. For the haploid model (eqq. [2]), the total sizes are  $V = \sum_{i=1}^2 V_i$  and  $P = \sum_{j=1}^2 P_j$  for prey and predator, respectively. The corresponding genotype frequencies are  $p_v = V_1/V$ ,  $q_v = V_2/V$ ,  $p_p = P_1/P$ , and  $q_p = P_2/P$ . Using equations (2), it follows that

$$\frac{dV}{dt} = rV - \frac{r}{K}V^2 - PV\bar{\beta}_v, \quad (\text{A1a})$$

$$\frac{dP}{dt} = \gamma P - \frac{\gamma\kappa}{K}P^2 + \theta VP\bar{\beta}_p, \quad (\text{A1b})$$

where  $\bar{\beta}_v$  and  $\bar{\beta}_p$  are the average interaction coefficients within each species, assuming random encounters of genotypes. Equations (A1) also describe the population growth rates for the diploid and quantitative-genetic models; however, in each model, the interaction coefficients are derived according to the specific genotype interactions. For the haploid model, these average interaction coefficients are  $\bar{\beta}_v = p_v(p_p\beta_{11} + q_p\beta_{12}) + q_v(p_p\beta_{21} + q_p\beta_{22})$  and  $\bar{\beta}_p = p_p(p_v\beta_{11} + q_v\beta_{21}) + q_p(p_v\beta_{12} + q_v\beta_{22})$ , with each  $\beta_{ij}$  defined according to equation (1). The genotype-specific interaction coefficients are  $\beta_{v_i} = p_p\beta_{i1} + q_p\beta_{i2}$  and  $\beta_{p_j} = p_v\beta_{1j} + q_v\beta_{2j}$ . Note that  $\bar{\beta}_v = p_v\beta_{v_1} + q_v\beta_{v_2}$  and  $\bar{\beta}_p = p_p\beta_{p_1} + q_p\beta_{p_2}$ .

## Diploid Evolutionary Dynamics

From equations (2), the haploid genotype frequency dynamics for prey and predator are, respectively,

$$\frac{dp_v}{dt} = -p_vq_vP(\beta_{v_1} - \beta_{v_2}), \quad (\text{A2a})$$

$$\frac{dp_p}{dt} = p_pq_p\theta V(\beta_{p_1} - \beta_{p_2}). \quad (\text{A2b})$$

Equations (A2) also describe the evolutionary dynamics for randomly mating diploid biallelic prey and predator, given some standard assumptions and natural definitions, as we now describe. In particular, we interpret  $p_v$ ,  $q_p$ , and so forth as allele frequencies and assume that the diploid genotypes are in Hardy-Weinberg proportions at all times, a condition that is approached quickly for continuous-time models if selection is relatively weak (Nagylaki and Crow 1974; Nagylaki 1992).

Interspecific encounters are assumed to be random with respect to genotype, such that the relative interaction

strengths of these genotypes depend on the number of shared alleles. For example, the effects of predators on prey genotypes with two, one, or no “1” alleles are, respectively,

$$\beta_{v_{11}} = b_2 p_P^2 + b_1 2 p_P q_P + b_0 q_P^2, \quad (\text{A3a})$$

$$\beta_{v_{12}} = b_2 2 p_P q_P + b_1 (p_P^2 + q_P^2), \quad (\text{A3b})$$

$$\beta_{v_{22}} = b_2 q_P^2 + b_1 2 p_P q_P + b_0 p_P^2, \quad (\text{A3c})$$

where  $b_n$  is the effect on a prey genotype of an interaction with a predator genotype with which it shares  $n$  “1” alleles. We defined  $b_n = \beta[n + (2 - n)/s]/2K$  so that, as in the haploid model, the strength of interaction between two genotypes is  $b_2 = \beta/K$  if they match perfectly and  $b_0 = \beta/sK$  if they do not match. The strength of an interaction between genotypes that match at a single allele is exactly intermediate:  $b_1 = (b_0 + b_2)/2$ . Equations similar to (A3) describe  $\beta_{P_{11}}$ ,  $\beta_{P_{12}}$ , and  $\beta_{P_{22}}$ , the genotype-dependent effects of prey on their predators. Now, we define the interaction strengths for each allele,

$$\beta_{v_1} = p_V \beta_{v_{11}} + q_V \beta_{v_{12}}, \quad (\text{A4a})$$

$$\beta_{v_2} = p_V \beta_{v_{12}} + q_V \beta_{v_{22}}, \quad (\text{A4b})$$

$$\beta_{P_1} = p_P \beta_{P_{11}} + q_P \beta_{P_{12}}, \quad (\text{A4c})$$

$$\beta_{P_2} = p_P \beta_{P_{12}} + q_P \beta_{P_{22}}, \quad (\text{A4d})$$

and the mean interaction strengths experienced by each population,

$$\bar{\beta}_V = p_V \beta_{v_1} + q_V \beta_{v_2}, \quad (\text{A5a})$$

$$\bar{\beta}_P = p_P \beta_{P_1} + q_P \beta_{P_2}. \quad (\text{A5b})$$

Using definitions (A4) and (A5), equations (A1) and (A2) together describe the joint population and evolutionary dynamics of a diploid prey and predator. Note that these equations can be easily modified to model haploid-diploid interactions.

## Quantitative-Genetic Evolutionary Dynamics

In the quantitative-genetic model, instead of tracking the frequencies of individual alleles, we follow the evolution of the mean trait values  $\bar{z}_V$  and  $\bar{z}_P$  in the prey and predator, respectively. The dynamics of those means are

$$\frac{d\bar{z}_V}{dt} = -\sigma_V^2 P \frac{\partial \bar{\beta}_V}{\partial \bar{z}_V}(\bar{z}_V, \bar{z}_P), \quad (\text{A6a})$$

$$\frac{d\bar{z}_P}{dt} = \sigma_P^2 \theta V \frac{\partial \bar{\beta}_P}{\partial \bar{z}_P}(\bar{z}_P, \bar{z}_V), \quad (\text{A6b})$$

where  $\sigma_V^2$  and  $\sigma_P^2$  are the phenotypic variances around the mean trait value in the prey and predator, respectively (Abrams et al. 1993; Lande 1982), and  $\bar{\beta}_V(\bar{z}_V, \bar{z}_P)$  and  $\bar{\beta}_P(\bar{z}_P, \bar{z}_V)$  are the corresponding mean interaction strengths (see below). Here, we make the simplifying assumption that all variation is additive genetic, and we assume further that this variation is constant over time (for a justification, see Lynch and Lande 1993) in both the prey and its predator.

As in equation (6) of Rossberg et al. (2010), we define the strength of the interaction between a prey

individual with genotype  $z_v$  and a predator individual with genotype  $z_p$  as declining toward 0 as the absolute distance between the genotypes increases,

$$\beta_v = \frac{\beta}{K} e^{-(z_v - z_p)^2 / 2\sigma_w^2}, \quad (\text{A7a})$$

$$\beta_p = \frac{\beta}{K} e^{-(z_p - z_v)^2 / 2\sigma_w^2}, \quad (\text{A7b})$$

where  $\sigma_w^2$  is the width of the fitness function. Selection on prey should minimize the strength of the interaction by maximizing the distance  $z_v - z_p$ , whereas selection on predators favours the opposite. When we define the width of the fitness function as

$$\sigma_w^2 = \frac{1}{2 \ln s}, \quad (\text{A8})$$

interaction strengths (eq. [A7]) become

$$\beta_v = \frac{\beta}{K} s^{-(z_v - z_p)^2}, \quad (\text{A9a})$$

$$\beta_p = \frac{\beta}{K} s^{-(z_p - z_v)^2}. \quad (\text{A9b})$$

Note that both equal  $\beta/K$  when  $z_v - z_p = 0$ , which is the same effect as perfect matching in the haploid and diploid models. There is nothing comparable to a “complete mismatch” in the quantitative-genetics model, but interactions (A9) are defined such that they have strength  $\beta/sK$  when  $z_v - z_p = 1$ . Figure A1 compares interaction strengths for the haploid, diploid, and quantitative-genetics models.

The mean strength of the interaction for each species depends on the mean trait values as well as on the phenotypic variance around those means. Assuming that phenotypes have normal distributions within each species and that encounters are random, it can be shown that the mean interaction strengths are

$$\bar{\beta}_v = \frac{\beta}{K} s^{-[(\bar{z}_v - \bar{z}_p)^2 + \sigma_v^2 + \sigma_p^2]}, \quad (\text{A10a})$$

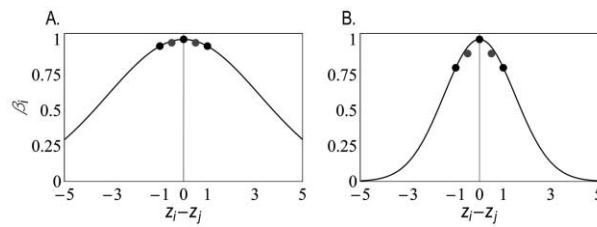
$$\bar{\beta}_p = \frac{\beta}{K} s^{-[(\bar{z}_p - \bar{z}_v)^2 + \sigma_v^2 + \sigma_p^2]}. \quad (\text{A10b})$$

Using definitions (A8) and (A10), equations (A6) become

$$\frac{d\bar{z}_v}{dt} = (2 \ln s) \sigma_v^2 P(\bar{z}_v - \bar{z}_p) \frac{\beta}{K} s^{-[(\bar{z}_v - \bar{z}_p)^2 + \sigma_v^2 + \sigma_p^2]}, \quad (\text{A11a})$$

$$\frac{d\bar{z}_p}{dt} = -(2 \ln s) \sigma_p^2 \theta V(\bar{z}_p - \bar{z}_v) \frac{\beta}{K} s^{-[(\bar{z}_p - \bar{z}_v)^2 + \sigma_v^2 + \sigma_p^2]}. \quad (\text{A11b})$$

Equations (A11), together with equation (A1), describe the joint evolutionary and population dynamics of the prey and predator when interactions are based on quantitative traits.



**Figure A1:** Comparison of interaction strengths  $\beta$ , from the haploid, diploid, and quantitative-genetic models, depending on the distance between traits  $z$  in species  $i$  and  $j$ . In the haploid and diploid models, perfect matching gives  $z_i - z_j = 0$ , whereas perfect mismatching gives  $z_i - z_j = 1$  (black circles). In the haploid model, interaction between a heterozygote and a homozygote leads to intermediate matching, with  $z_i - z_j = 0.5$  (gray circles). In the quantitative model, any distance  $z_i - z_j$  is possible; as this distance becomes greater, the interaction strength becomes weaker (black line). Parameters:  $\beta = 1$ ,  $K = 1$ ; A, relatively weak selection:  $s = 1.05$ ; B, relatively strong selection:  $s = 1.25$ .

### Literature Cited Only in Appendix A

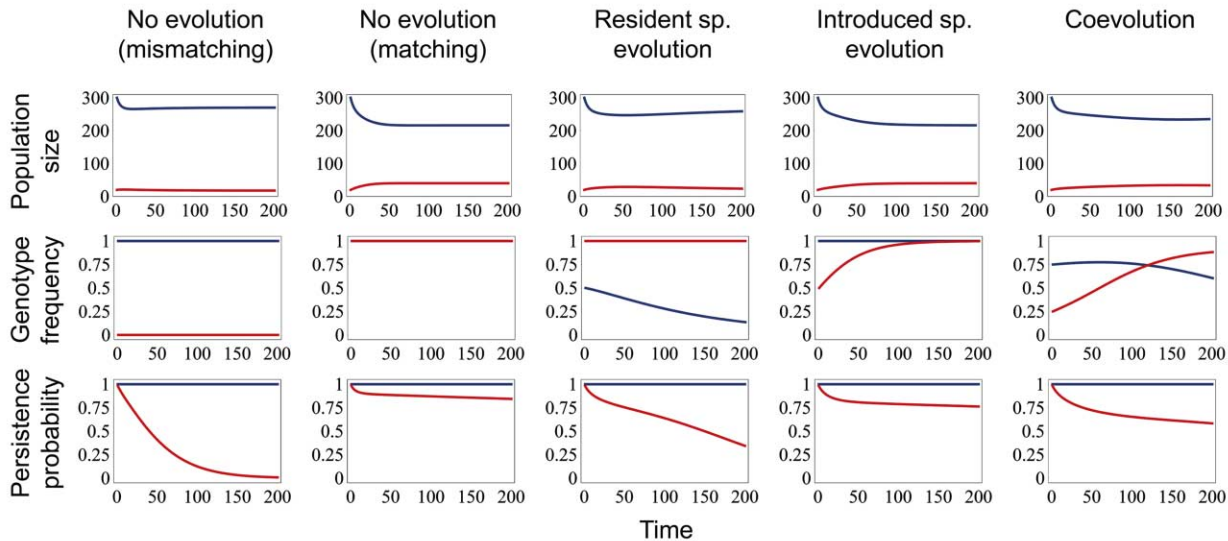
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**Appendix B from E. I. Jones and R. Gomulkiewicz, “Biotic Interactions, Rapid Evolution, and the Establishment of Introduced Species”**  
(Am. Nat., vol. 179, no. 2, p. E28)

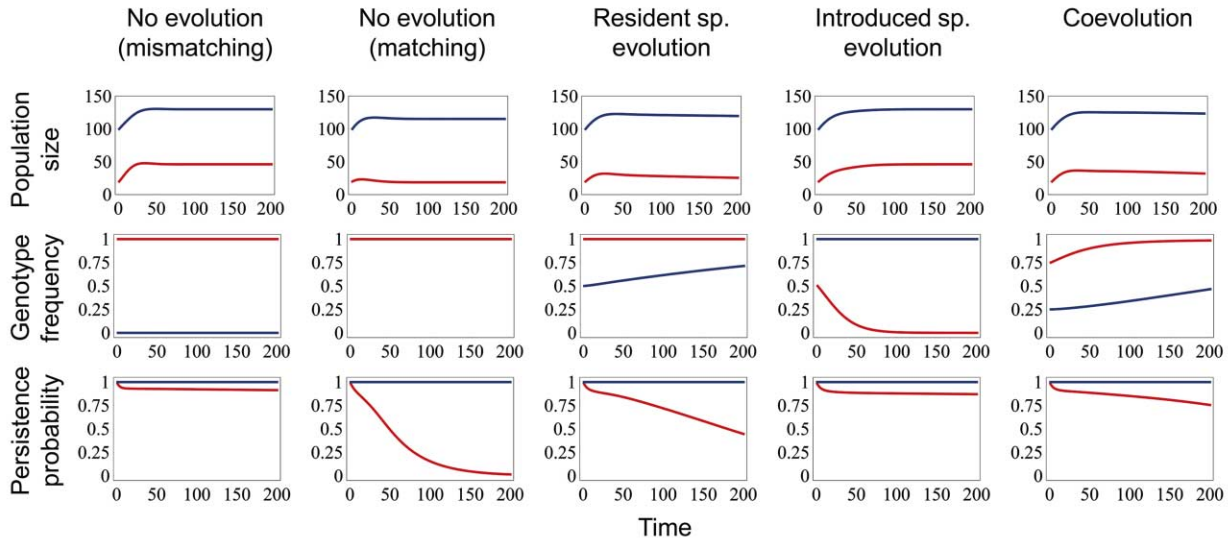
**Population and Genotype Frequency Dynamics and the Probability of Establishment**

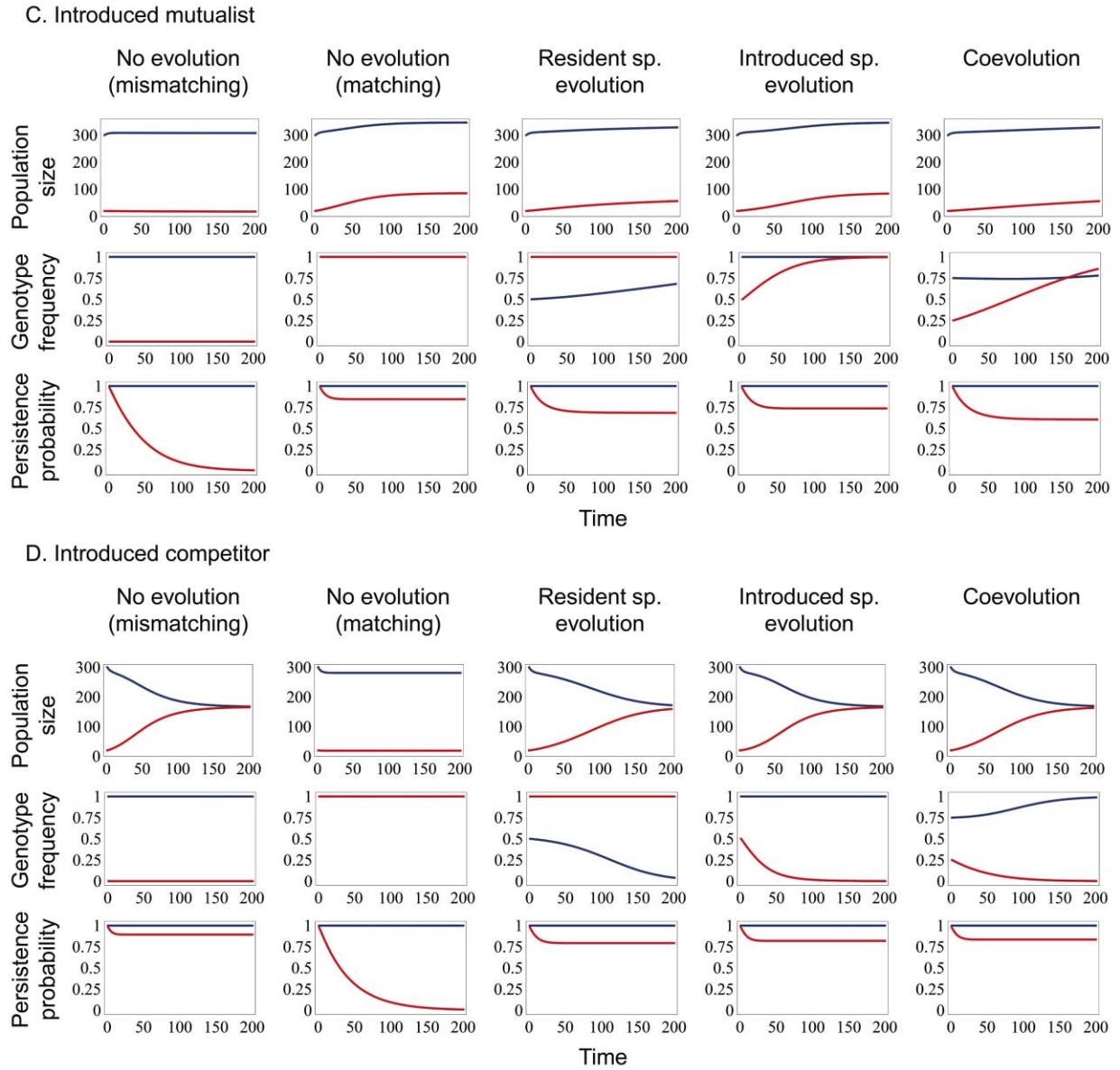
As described in “Methods,” equations (2)–(4) were evaluated numerically over time for different initial combinations of genotype frequencies in the resident and introduced species. Figures B1 and B2 show samples of the population and trait dynamics, along with the probability of species persistence over time after the initial introduction event. Figures B3 and B4 show details of how the probability of persistence of the introduced species depends on which species evolves.

A. Introduced predator



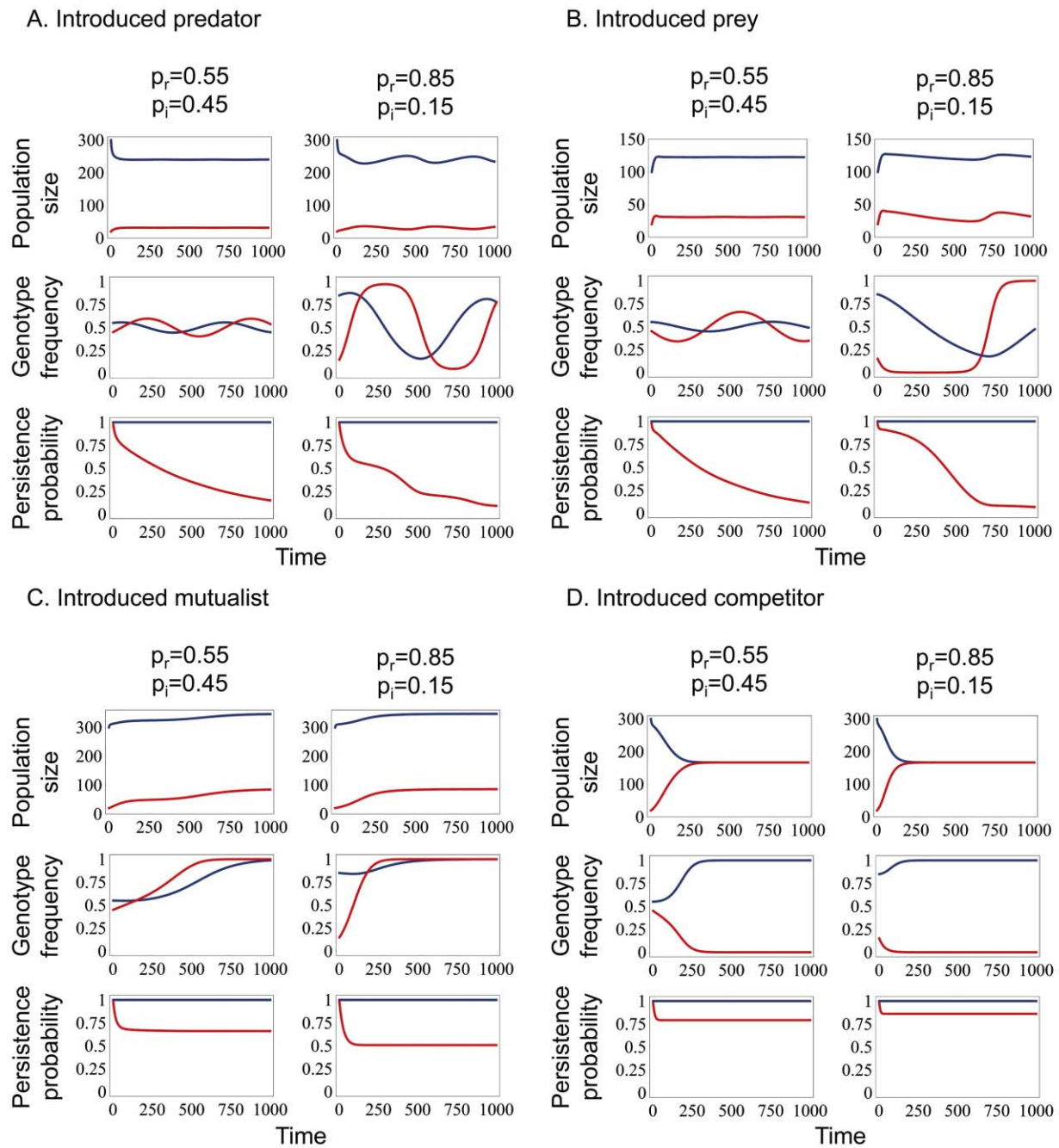
B. Introduced prey



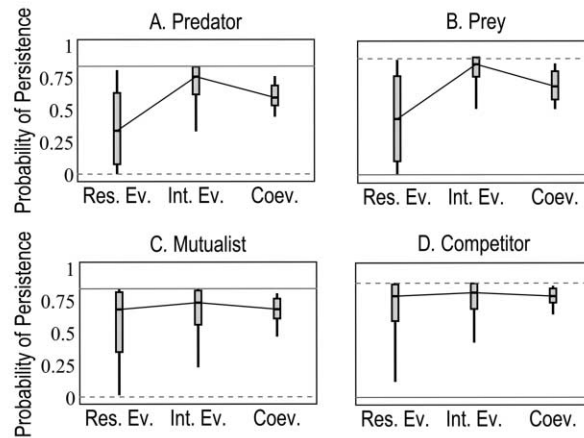


**Figure B1:** Dynamics of the resident (blue) and introduced (red) species over time after the initial introduction (at  $T = 0$ ) for each of the four introduction scenarios: predator (A), prey (B), mutualist (C), and competitor (D). For each of these scenarios, the top row shows the population sizes, the middle row shows the genotype frequencies, and the bottom row shows the probabilities of the species persisting over time. The columns give the dynamics for different combinations of initial genotype frequencies  $p_r$  in the resident and  $p_i$  in the introduced species. The initial genotype frequencies are  $p_r = 1$  and  $p_i = 0$  for “No evolution (mismatching),”  $p_r = 1$  and  $p_i = 1$  for “No evolution (matching),”  $p_r = 0.5$  and  $p_i = 1$  for “Resident sp. evolution,”  $p_r = 1$  and  $p_i = 0.5$  for “Introduced sp. evolution,” and  $p_r = 0.75$  and  $p_i = 0.25$  for “Coevolution.” When the initial genotype frequency is 0 or 1, the frequency is fixed over time because of the assumption that mutations are negligible over the time period modeled. Parameters:  $T = 200$ ,  $h = 1$ ,  $c = 0.2$ ,  $s = 1.25$ ,  $K = 300$ ,  $r = 0.25$ ; predator introduction (A):  $\gamma = -0.15$ ,  $\kappa = 0$ ,  $\theta = 0.4$ ,  $\beta = 0.52$ ; prey introduction (B):  $\gamma = 0.1$ ,  $\kappa = 3$ ,  $\theta = 0.4$ ,  $\beta = 0.61$ ; mutualist introduction (C):  $\gamma = -0.1$ ,  $\kappa = -2$ ,  $\theta = 0.2$ ,  $\beta = 0.68$ ; competitor introduction (D):  $\beta = 1$ .

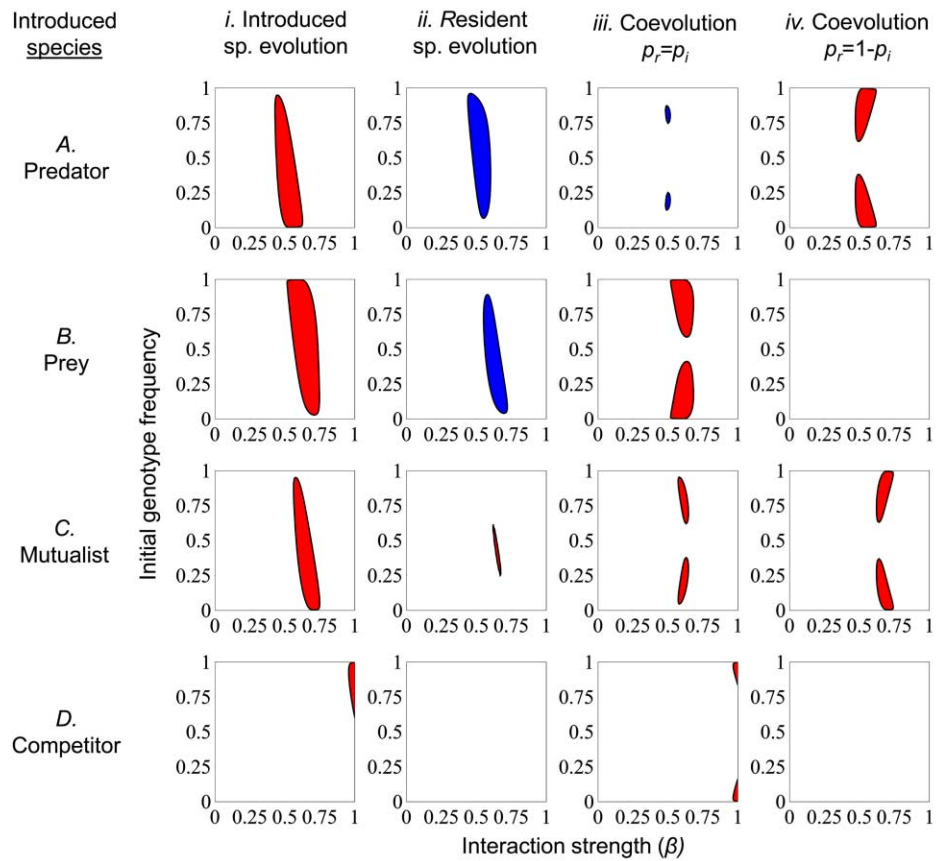




**Figure B2:** Role of different initial genotype frequency combinations in the coevolutionary dynamics of the resident (blue) and introduced (red) species over time for each of the four introduction scenarios: predator (A), prey (B), mutualist (C), and competitor (D). The rows are as in figure B1. In the left column, the genotypes are initially at intermediate frequencies,  $p_r = 0.55$  and  $p_i = 0.45$ , while in the right column, the genotypes are initially at more extreme frequencies,  $p_r = 0.85$  and  $p_i = 0.15$ . The timescale is increased to  $T = 1,000$  (100–250 generations; see “Methods”) to show the effect of predator-prey coevolutionary cycles on the probability of persistence. Other parameter values as in figure B1.



**Figure B3:** Probability of persistence for the introduced species (median, interquartile range, and 5%–95% interquartile range over all initial genotype frequencies; see “Methods”) when genetic variation was initially present in only the resident (Res. Ev.), only the introduced species (Int. Ev.), or both the resident and the introduced species (Coev.). The horizontal lines show the probability of persistence in the absence of genetic variation, at either fixed matching ( $i = j$ ; solid line) or fixed mismatching ( $i \neq j$ ; dashed line). In the top row, the net demographic effect of the interaction for the introduced species is positive; in the bottom row, the demographic effect of the interaction for the introduced species is negative. Parameter values are as in figure B1. Values of  $\beta$  for each interaction are those that give the maximum effect of genetic variation. Predator introduction (A):  $\beta = 0.52$ ; prey introduction (B):  $\beta = 0.61$ ; mutualist introduction (C):  $\beta = 0.68$ ; competitor introduction (D):  $\beta = 1$ .



**Figure B4:** Effect of initial genotype frequencies on the difference in probability of establishment of the introduced species, given genetic diversity in at least one species, compared to that in genetically fixed populations with the same mean interaction strengths. Colored regions denote where there is at least a 5% increase (red) or decrease (blue) in the probability of establishment of the introduced species, given genetic diversity. Columns *i* and *ii* show the full range of possible initial genotype frequencies for introduced-only and resident-only evolution, respectively, when the non-evolving species is fixed at a genotype frequency of 1. Columns *iii* and *iv* show only a subset of the possible initial genotype frequency combinations for coevolution. In column *iii*, initial genotype frequencies are the same in the introduced and resident species ( $p_r = p_i$ ). In column *iv*, initial genotype frequencies are inverted in order between the introduced and resident species ( $p_r = 1 - p_i$ ). Parameter values as in figure B1.