Revisiting Darwin's conundrum reveals a twist on the relationship between phylogenetic distance and invasibility

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A key goal of invasion biology is to identify the factors that favor species invasions. One potential indicator of invasiveness is the phylogenetic distance between a nonnative species and species in the recipient community. However, predicting invasiveness using phylogenetic information relies on an untested assumption: that both biotic resistance and facilitation weaken with increasing phylogenetic distance. We test the validity of this key assumption using a mathematical model in which a novel species is introduced into communities with varying ecological and phylogenetic relationships. Contrary to what is generally assumed, we find that biotic resistance and facilitation can either weaken or intensify with phylogenetic distance, depending on the mode of interspecific interactions (phenotype matching or phenotype differences) and the resulting evolutionary trajectory of the recipient community. Thus, we demonstrate that considering the mechanisms that drive phenotypic divergence between native and nonnative species can provide critical insight into the relationship between phylogenetic distance and invasibility.

coevolution | competition | consumer–resource | ecophylogenetics | mutualism

Invasive species are a major cause of concern due to their large ecological, social, and economic consequences (1–3). In principle, future invasions could be avoided by preventing introductions of potential invaders into susceptible communities. Thus, research has focused on identifying the characteristics that predispose species to becoming invasive (4–7) and the properties that make communities susceptible to invasion (8, 9). Although generalities have been elusive, one approach that has recently been gaining interest is using phylogenetic distance (time since cladogenesis) between nonnative species and species in the recipient community as an indicator of invasion potential.

Darwin was the first to suggest that the probability of establishment by introduced species depends on their relatedness to native species (10). However, as Darwin noted, the ecological similarity of related species can have opposing effects on their potential for coexistence ("Darwin's naturalization conundrum"). On the one hand, establishment in regions with close relatives should be facilitated by favorable abiotic conditions and the presence of suitable prey, hosts, and mutualists (Fig. 1*A*). On the other hand, establishment in these regions should be inhibited by competition with the relatives themselves and exploitation by shared natural enemies (Fig. 1*B*). Citing observations by Alphonse de Candolle and Asa Gray that naturalized species are more frequently from nonnative genera, Darwin concluded that competition was the dominant factor and relatedness to native species should reduce establishment success ("Darwin's naturalization hypothesis").

However, recent studies using statistical models, molecular phylogenetics, and experimental community assembly have revealed that the correlation between relatedness and establishment probability can be positive, negative, or zero (Table 1). These findings call into question the paramountcy of competition and have led to reconsideration of other biotic and abiotic factors (11). More fundamentally, doubt has been cast on the key assumption underlying both Darwin's intuitive arguments and contemporary research: that the effects of native species are strongest when phylogenetic distance to the nonnative species is low (Fig. 1) (12). Although this assumption is supported by studies showing that the presence of closely related species in a community increases competition (13), attack by natural enemies (14–18), and visitation by mutualists (19), a number of recent studies demonstrate the opposite, i.e., that distantly related species can experience more intense competition (12, 20) and herbivory (21).

Insight into the causes of these anomalous results can be found by focusing on the two key assumptions made by Darwin: (*i*) introduced species experience progressively weaker interactions as their phenotypic distance to resident species increases, and (*ii*) phenotypic distance is positively correlated with phylogenetic distance. Violation of either of these underlying assumptions could alter the predicted relationship between phylogenetic distance and biotic resistance and facilitation.

We suggest that both of these assumptions are sensitive to the mode of interaction between species. The interaction mode governs how the phenotypes of individuals affect the outcome of an interaction between them, and different interaction modes can lead to dissimilar evolutionary patterns (e.g., ref. 22). Two general interaction modes have been well documented: phenotype matching and phenotype differences. Phenotype matching yields interactions that are strongest when phenotypes are identical (Fig. S1); this interaction mode applies to traits such as those involved in exploitative competition mediated by shared resource

Significance

The application of phylogenetics is rapidly growing in many areas of biology. In invasion biology, phylogenetic information is now being used in an attempt to understand and predict species invasions. However, there is only a weak foundation for the prevalent predictions of how the phylogenetic distance between native and nonnative species should be related to the invasion success of the nonnative species. In this paper, a mechanistic model of species interactions and evolution is used to generate a unique set of predictions. These predictions deviate significantly from those assumed previously, suggesting that current explanations of phylogenetic distance–invasion relationships must be reevaluated. More generally, the results highlight the importance of considering the details of community processes when interpreting phylogenetic patterns.

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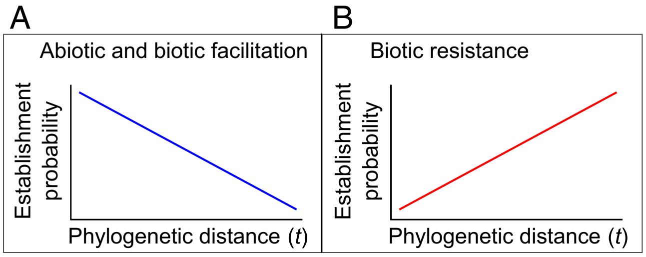

Fig. 1. Conventional predictions for the relationship between phylogenetic distance and establishment probability. (*A*) Abiotic conditions, mutualists, and resource species (e.g., prey and hosts) are expected to favor establishment of related species. As time *t* since cladogenesis increases, these favorable effects decline, leading to reduced probability of establishment. (*B*) Competitors and natural enemies are expected to disfavor establishment of related species. As time since cladogenesis increases, these unfavorable effects decline, leading to increased probability of establishment.

use, cooperative aspects of mutualism, victim preference, and the targeting of defenses against enemies (23) (Table S1). In contrast, phenotype differences yield interactions that favor the individual with a more extreme (generally, a larger) phenotype (Fig. S1); this interaction mode is more applicable to traits involved in interference competition mediated by competitive ability, conflict between mutualist partners, the magnitude of defenses against enemies, and the surmounting of those defenses by enemies (24) (Table S1).

Here, to investigate the relationships among phenotypic distance, interaction strength, phylogenetic distance, and establishment success, we develop a mathematical model and then analyze the model under different ecological and evolutionary scenarios. Specifically, we consider the roles of the recipient community type (competitive, mutualistic, or consumer–resource) and of the interaction mode (phenotype matching or phenotype differences).

Our mathematical analyses demonstrate that, as phylogenetic distance increases, the strength of biotic resistance and facilitation by the recipient community can decrease (as has been generally assumed), but may also increase. We find that this deviation from the expected outcome generally occurs because the component assumption (*i*) above is not universally valid. Specifically, introduced species can experience weaker or stronger interactions as their phenotypic distance to resident species increases, depending on the details of the interactions. These findings have significant implications for the interpretation of observed relationships between phylogenetic distance and establishment success, as well as for the use of phylogenetic information to understand invasion potential and community assembly.

Model and Analysis

To investigate the relationship between phylogenetic distance and establishment success, we calculate the probability that an introduced species, $\tilde{B}$, becomes established in a community containing its sister species, B, and an unrelated resident species, A (Fig. 2). We assume B and $\tilde{B}$ are sufficiently closely related that they share a niche and thus are competitors. In contrast, the unrelated resident species, A, may be a competitor, mutualist, consumer, or resource of both B and $\tilde{B}$. We further assume that these interspecific interactions among A, B, and $\tilde{B}$ are governed by a single quantitative trait in each species (z_A, z_B, and $z_{\tilde{B}}$, respectively). Encounters between individuals of different species have fitness consequences that depend on either the absolute (phenotype matching) or signed (phenotype differences) distance between their trait values (22–24).

Once species $\tilde{B}$ is introduced into the A–B community, its initial growth rate and, consequently, its probability of establishment are determined by interactions with the resident species. The outcomes of these interactions depend on the phenotypes of the residents A and B and of the introduced species $\tilde{B}$ itself at the time of introduction. Below, we develop an evolutionary model to find the distributions of phenotypes of species A, B, and $\tilde{B}$ at the time of introduction and then analyze how the establishment probability of $\tilde{B}$ changes with its phylogenetic distance from species B.

Let t represent the time since speciation between B and $\tilde{B}$ (Fig. 2*A*); therefore, t is also a measure of the phylogenetic distance between B and $\tilde{B}$. At $t = T_1$, species A and B begin to interact (Fig. 2*B*), and, at $t = T_2$, species $\tilde{B}$ is introduced into the A–B community (Fig. 2*C*). Note that $0 \leq T_1 \leq T_2$. We assume that the mean phenotypes of B and $\tilde{B}$ ($\bar{z}_B$ and $\bar{z}_{\tilde{B}}$, respectively) evolve independently without trend [e.g., by independent random genetic drift processes (25)] from a common ancestral value, $\bar{\zeta}$, until time $t = T_1$, after which the evolution of $\bar{z}_B$ in species B is driven primarily by interactions with A (detailed in the next section). The mean phenotype $\bar{z}_{\tilde{B}}$, meanwhile, continues evolving with no consistent direction up until the time species $\tilde{B}$ is introduced into the A–B community.

Evolution in the Recipient Community. We used a quantitative genetic framework (25) to model the evolution of resident species A and B from time T_1 until T_2, the time that species $\tilde{B}$ is first introduced into the community. For brevity, we describe the evolutionary recursions for species A; the equations for species B can be derived following the same logic.

Table 1. The effect of phylogenetic relatedness on the probability of establishment by nonnative species

Study	Taxon	Location	Effect of relatives
Mack et al., 1996 (32)	Plants	United States	–
Rejmanek, 1996 (33)	Plants	California	–
Daehler, 2001 (38)	Plants	Hawaii	+
Duncan and Williams, 2002 (39)	Plants	New Zealand	+
Diez et al., 2008 (40)			
Lambdon and Hulme, 2006 (47)	Plants	Mediterranean islands	0
Ricciardi and Mottiar, 2006 (48)	Fish	Global	0
Diez et al., 2009 (41)	Plants	Australia, New Zealand	+
Jiang et al., 2010 (34)	Bacteria	Experimental	–
Tan et al., 2012 (37)			
Davies et al., 2011 (35)	Plants	California (Serpentine)	–
Tingley et al., 2011 (42)	Amphibians	Global	+
van Wilgen and Richardson, 2011 (36)	Reptiles	California, Florida	–
Violle et al., 2011 (30)	Protists	Experimental	–
Ferreira et al., 2012 (43)	Reptiles	Global	+
Peay et al., 2012 (31)	Nectar yeast	Experimental	–
Maitner et al., 2012 (44)	Birds	Florida, Hawaii, New Zealand	+

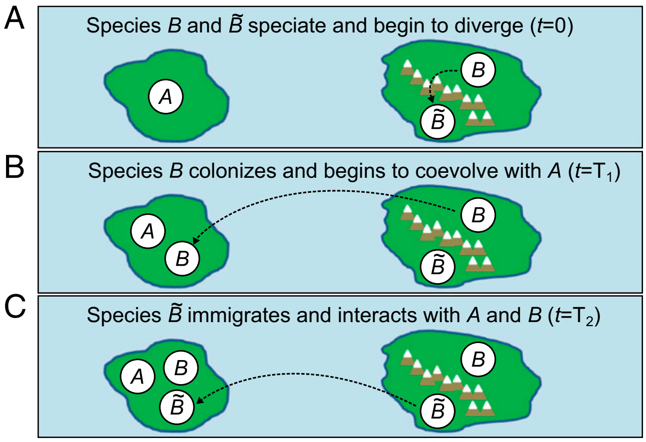

Fig. 2. A hypothetical species introduction scenario. (*A*) At time $t = 0$, two populations B and $\tilde{B}$ speciate as a result of geographic isolation and begin to diverge phenotypically (e.g., due to drift). (*B*) At time $t = T_1$, individuals of species B colonize the second island and begin to interact and coevolve with a resident species A. (*C*) At time $t = T_2$, individuals of species $\tilde{B}$ arrive on the second island. Whether species $\tilde{B}$ becomes established depends on its interactions with both species A and B.

We start by defining the fitness of an individual of species A in the absence of biotic interactions as k_A. We then assume that individuals of species A and B encounter one another at random. The fitness outcome of an encounter depends on both individuals' phenotypes, z_A and z_B, through an interaction function, $X_{AB}(z_A, z_B)$. Depending on the ecological interaction type (consumer–resource, competition, or mutualism) and the outcome of the encounter (favorable or unfavorable) for the focal individual, its fitness can be increased, decreased, or left unchanged by the interaction function. Thus, given an interspecific encounter, the fitness of an individual of species A becomes the following:

$$W_A(z_A, z_B) = k_A + X_{AB}(z_A, z_B). \quad \textbf{[1]}$$

In *Methods S1* of *SI Text*, we describe in detail two forms of the interaction function $X_{AB}(z_A, z_B)$ that correspond to phenotype differences and phenotype matching. Here, we outline the general modeling approach for both interaction modes.

Because phenotypes z_A and z_B can jointly affect fitness in species A and B, these traits may coevolve. Evolution of the mean phenotype of species A, $\bar{z}_A$, over one generation is described by the deterministic recursion (25, 26):

$$\Delta\bar{z}_A(t) = \frac{G_A}{\overline{W}_A(t)} \frac{\partial \overline{W}_A(t)}{\partial \bar{z}_A}, \quad \textbf{[2]}$$

where G_A is the additive genetic variance for phenotype z_A and

$$\overline{W}_A(t) = \iint W_A(z_A, z_B)\rho_{A,t}(z_A)\rho_{B,t}(z_B)\, dz_A dz_B \quad \textbf{[3]}$$

is the mean fitness of species A given phenotype distributions $\rho_{A,t}(z_A)$ and $\rho_{B,t}(z_B)$, which we assume remain Gaussian at all times t. Iterating Eq. **2**, the mean phenotype in species A at the time that species $\tilde{B}$ is introduced ($t = T_2$) is as follows:

$$\bar{z}_A(T_2) = \bar{z}_A(T_1) + \sum_{i=T_1}^{T_2-1} \Delta\bar{z}_A(i), \quad \textbf{[4a]}$$

in which $\bar{z}_A(T_1)$ is the mean phenotype of A when it first interacts with B. Similarly, at $t = T_2$, the mean phenotype in species B is as follows:

$$\bar{z}_B(T_2) = \bar{z}_B(T_1) + \sum_{i=T_1}^{T_2-1} \Delta\bar{z}_B(i). \quad \textbf{[4b]}$$

Eqs. **4** assume that only the means of the phenotype distributions change over time and that additive genetic variances G_A and G_B are constant (25, 27).

Probability of Establishment. We are interested in studying how establishment of the introduced species, $\tilde{B}$, depends on its phylogenetic distance (i.e., time since speciation, t) from its resident relative, B. Meanwhile, phenotypic divergence of B and $\tilde{B}$ is initially driven by stochastic processes ($0 < t \leq T_1$; Fig. 2*A*), then primarily by B's interactions with A ($t > T_1$; Fig. 2*B*; *Methods S1*). To test the effect of phylogenetic distance, we compare the probability of establishment of species $\tilde{B}$ at time $t > T_1$ to its probability of establishment at $t = T_1$, i.e., before any phenotypic divergence between B and $\tilde{B}$ driven by evolution in the A–B community.

Once $\tilde{B}$ is introduced into the A–B community at $t = T_2$, we assume that its probability of becoming established is directly related to its mean fitness, which determines its initial rate of population growth. The mean fitness of $\tilde{B}$ depends on interactions with the resident species; for simplicity, we assume that individuals of species $\tilde{B}$ are equally likely to encounter individuals of either resident species (this assumption is relaxed in the simulations described in *Methods S2* of *SI Text*). Thus, the mean fitness of species $\tilde{B}$ introduced at $t = T_2$ is as follows:

$$\begin{aligned}\overline{W}_{\tilde{B}}(T_2) = &\frac{1}{2}\iint W_{\tilde{B}}(z_{\tilde{B}}, z_A)\rho_{\tilde{B}}(z_{\tilde{B}})\rho_{A,T_2}(z_A) dz_{\tilde{B}}\, dz_A \\ &+ \frac{1}{2}\iint W_{\tilde{B}}(z_{\tilde{B}}, z_B)\rho_{\tilde{B}}(z_{\tilde{B}})\rho_{A,T_2}(z_B) dz_{\tilde{B}}\, dz_B,\end{aligned} \quad \textbf{[5]}$$

where $\rho_{\tilde{B}}(z_{\tilde{B}})$ is the phenotype distribution of $\tilde{B}$. The first term of Eq. **5** is the contribution to population mean fitness from those individuals that encounter species A, and the second term represents the contribution from those individuals that encounter species B.

Although Eq. **5** is sufficient to predict the short-term deterministic growth or decline of newly introduced species $\tilde{B}$, it ignores stochastic demographic effects that are particularly important in small populations (28). We accounted for demographic stochasticity implicitly using the following approach. Given initial population size N, the probability that $\tilde{B}$ goes extinct locally is approximately $e^{-N\overline{W}_{\tilde{B}}(T_2)}$, such that initial populations with slow growth are more likely to go extinct (see ref. 29 for an analogous approach). Consequently, we calculate the probability that $\tilde{B}$ becomes established (i.e., avoids immediate extinction) as follows:

$$P(T_2) = 1 - e^{-N\overline{W}_{\tilde{B}}(T_2)}, \quad \textbf{[6]}$$

where $\overline{W}_{\tilde{B}}(T_2)$ is its expected mean fitness when introduced at $t = T_2$ (Eq. **5**).

In *Methods S1*, we show that Eqs. **5** and **6** provide good approximations for the expected fitness and establishment probability of species $\tilde{B}$ even when allowing for weak, nondirectional phenotypic divergence between species B and $\tilde{B}$.

Results

What Is the Relationship Between Phylogenetic Distance and Establishment Probability? We derived analytic conditions for establishment probability of $\tilde{B}$ to increase with phylogenetic distance given that interactions are mediated by phenotype matching (*Methods S1*). These conditions are expressed in terms of the fitness effects of interactions, $\beta_{\tilde{B}A}$ (effect of A on $\tilde{B}$) and $\beta_{\tilde{B}B}$ (effect of B on $\tilde{B}$), and the directional, relative evolutionary rate coefficients of the resident species, $\varphi_A = -\frac{\alpha_M \beta_{AB} G_A}{2(k_A + \beta_{AB})}$

and $\varphi_B = -\frac{\alpha_M \beta_{BA} G_B}{2(k_B + \beta_{BA})}$, in which α_M is the sensitivity of the interaction function to the match between the individuals' phenotypes and β_{AB} and β_{BA} measure the fitness effects of interactions between A and B (see also *Methods S1* and Table S2). Note that φ_B determines the rate and direction that species B diverges phenotypically from its relative $\tilde{B}$.

The establishment probability of $\tilde{B}$ at $t = T_2$ will have increased compared with its value at $t = T_1$ if there has been a net decrease of resistance or a net increase of facilitation as a result of resident evolution. These favorable changes will occur after a single generation ($T_2 = T_1 + 1$) if

$$\beta_{\tilde{B}A}\varphi_A(2+\varphi_A) + \beta_{\tilde{B}B}\varphi_B^2 < 0. \qquad [7]$$

Communities in which residents A and B are competitors or mutualists satisfy Eq. **7** for all parameter combinations, but consumer–resource communities generally can only meet this condition if the fitness of $\tilde{B}$ is affected more by interactions with its sister species B than with A and if B evolves more rapidly than A. However, even if the establishment probability of $\tilde{B}$ initially decreases in consumer–resource communities, it will increase as $(T_2 - T_1) \rightarrow \infty$ if

$$-\beta_{\tilde{B}A}\varphi_A(2\varphi_B + \varphi_A) + \beta_{\tilde{B}B}\varphi_B^2 < 0, \qquad [8a]$$

when $\varphi_A + \varphi_B < 0$, and if

$$\beta_{\tilde{B}A}\varphi_A^2 + \beta_{\tilde{B}B}\varphi_B^2 < 0, \qquad [8b]$$

when $\varphi_A + \varphi_B > 0$. Thus, establishment probability in consumer–resource communities will eventually increase over a wide range of parameter values, especially if the dominant interactions $\tilde{B}$ faces are with a rapidly evolving sister species, B (Fig. 3).

For the phenotype differences model of interspecific interactions, we find that the establishment probability of $\tilde{B}$ will decrease with phylogenetic distance regardless of the recipient community type (*Methods S1*). The contrast between this result and those derived for phenotype matching suggests that the mode of interaction, rather than facilitation vs. resistance, is critical for understanding how the probability of establishment changes with phylogenetic distance.

We examined the robustness of our analytic results by developing complementary, individual-based simulations of diploid, sexual species with phenotypes determined by additive, unlinked loci (*Methods S2*). These simulations relax key assumptions of our analytical model including weak selection, Gaussian phenotype distributions, and fixed additive genetic variance. In accord with the deterministic model, the simulations show that, when fitness consequences of interspecific encounters depend on phenotype matching, the probability of establishment tends to increase with phylogenetic distance (Fig. 4, *Left*), and when these consequences depend on phenotype differences, the probability of establishment decreases as phylogenetic distance increases (Fig. 4, *Right*).

Both the analytical and simulation results show that establishment probability changes as an asymptoting function of phylogenetic distance. The timescale required to approach the asymptote (which exists, in part, because establishment probabilities are bounded by zero and 1) depends strongly on model parameters. For instance, if additive genetic variance is small, changes in establishment probability may continue to accrue over thousands to tens of thousands of generations. In contrast, if additive genetic variance is large, changes in establishment probability may occur over only a small number of generations before an asymptote is reached (Fig. S2).

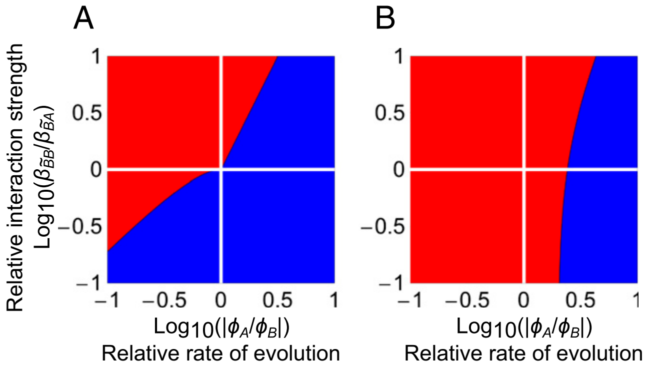

Fig. 3. The effect of resident, consumer–resource coevolution on establishment probability. When the probability of interactions is determined by phenotype matching and A and B are (*A*) resource and consumer or (*B*) consumer and resource, respectively, their coevolution can either increase (red) or decrease (blue) establishment probability of the introduced species, $\tilde{B}$. The change in establishment probability over time depends on the relative rate of evolution of A vs. B (φ_A/φ_B) and on the relative effects of interactions with the residents on the fitness of $\tilde{B}$ ($\beta_{\tilde{B}A}/\beta_{\tilde{B}B}$). Parameters: $\overline{z}_B(T_1) = \overline{z}_{\tilde{B}}(T_2) = 0$.

Our findings demonstrate that the conventional wisdom, i.e., that both biotic resistance and facilitation weaken with phylogenetic distance (Fig. 1), is not generally valid. Below, we examine in greater detail how the evolution of the recipient community shapes the relationship between phylogenetic distance and the establishment of introduced species.

How Does Biotic Facilitation Change as the Recipient Community Evolves? The establishment of introduced species is facilitated by interactions with resident resource species and mutualists. Traditionally, this biotic facilitation has been expected to weaken with increasing phenotypic distance, and thus also with increasing phylogenetic distance (Fig. 1*A*). As described below, we always found that increasing phenotypic distance led to weaker biotic facilitation. Furthermore, we found that phenotypic and phylogenetic distance increased together whenever interactions are governed by phenotype differences and when consumer–resource interactions are governed by phenotype matching. When interactions are governed by phenotype differences, resident phenotypes escalate in "arms races" that give the residents an ever-increasing advantage over a freshly introduced species (Fig. S3). Meanwhile, when consumer–resource interactions are governed by phenotype matching, the resident resource species evolves to reduce phenotypic overlap with its consumer during a "coevolutionary chase" that has the consequence of also decreasing phenotypic overlap with and facilitation of the introduced consumer (Fig. S4*C*).

The only deviation from the conventional prediction for facilitation occurs under phenotype matching when the introduced species $\tilde{B}$ is a mutualist of A. By "converging" to match its resident mutualist partner B, species A also decreases its phenotypic distance to the introduced species. This closer match increases the benefit of the mutualism for the two partners, resulting in increased facilitation of species $\tilde{B}$ (Fig. S4*B*).

How Does Biotic Resistance Change as the Recipient Community Evolves? The establishment of introduced species is resisted by interactions with resident competitors and consumers. Like facilitation, biotic resistance has been expected to weaken with increasing phenotypic and phylogenetic distance (Fig. 1*B*). Indeed, in scenarios of biotic resistance, we found that phenotypic distance does tend to increase with phylogenetic distance (although sometimes only after a transient decrease in phenotypic distance). We further found that increasing phenotypic distance leads to weaker biotic resistance whenever interactions are governed by phenotype matching. Evolution of resident B driven by phenotype matching with A always increases the phenotypic distance between species B and $\tilde{B}$, thereby shrinking niche overlap and weakening biotic resistance due to competition (Fig. S4 *A–D*). In the same way, "character displacement" of A

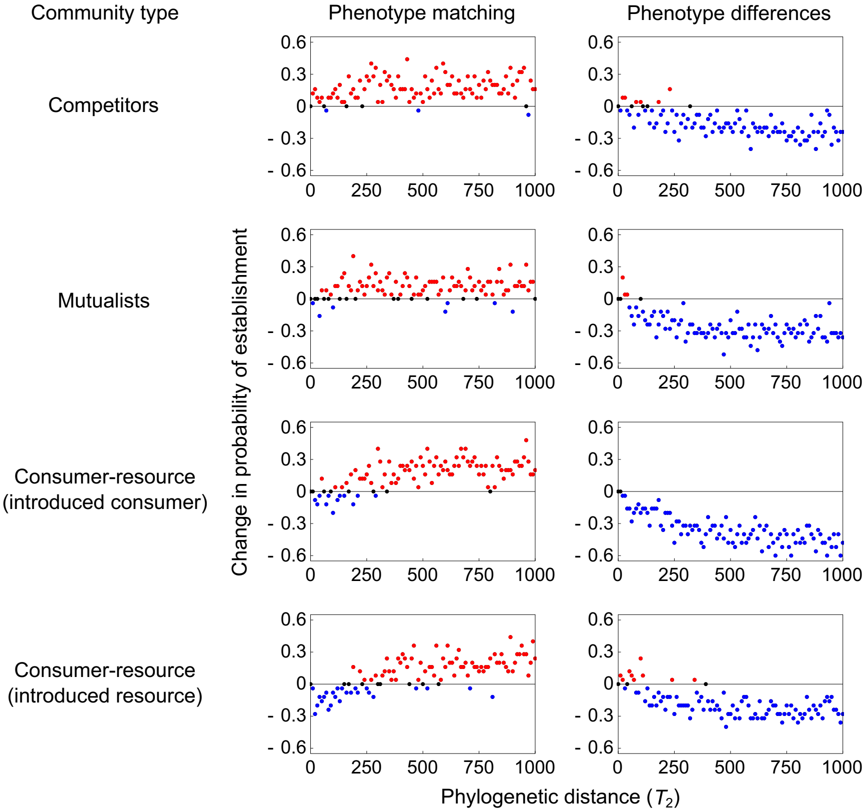

Fig. 4. The effect of phylogenetic distance on the probability of establishment. The change in establishment probability at $t = T_2$ is given relative to the establishment probability at $t = T_1 = 0$. Points are the mean of 25 simulation runs with randomly drawn initial genotypes and interaction fitness effects. The color of points represent whether the establishment probability increased (red), decreased (blue), or was unchanged (black). The direction of change in establishment probability depends on whether interactions were mediated by phenotype matching (*Left*) or phenotype differences (*Right*). Simulation parameters are given in *Methods S2*.

when it is a competitor of B yields weaker biotic resistance against $\tilde{B}$ (Fig. S4*A*). Evolution of a resident consumer A engaged in a coevolutionary chase mediated by phenotype matching also tends to increase the phenotypic distance between species A and its introduced resource species $\tilde{B}$, thus making species $\tilde{B}$ less vulnerable to exploitation (after a transient increase, Fig. S4*D*; but see Fig. 3).

Importantly, interactions mediated by phenotype differences never lead to the conventionally predicted decrease in resistance. This exception occurs despite the positive relationship between phenotypic and phylogenetic distance that is generated by arms races between the residents (Fig. S3). By the definition of phenotype differences, increasing phenotype distance intensifies an antagonistic interaction for the species with the less extreme phenotype (Fig. S1). Therefore, as it is the introduced species $\tilde{B}$ that is left behind by the arms race (Fig. S3), biotic resistance against $\tilde{B}$ increases with phylogenetic distance.

Discussion

In the search for indicators of invasion potential, the phylogenetic distance between native and introduced species has emerged as an attractive candidate. However, the use of phylogenetic information is complicated by the fact that different relationships between phylogenetic distance and invasion potential have been expected depending on whether resistance (e.g., from competitors and natural enemies) or facilitation (e.g., from prey, mutualists, and the abiotic environment) is more significant (10, 11). Here, we have shown that the reality is even more complex; the relationship between phylogenetic distance and the strength of biotic resistance or facilitation depends on the mechanisms that underlie interspecific interactions and evolution within the recipient community.

Considering the effects of the recipient community as a whole, we show that establishment probability generally increases with phylogenetic distance when the outcomes of resident interactions are determined by phenotypic matching, as for competitors undergoing character displacement, converging mutualists, or consumer–resource pairs involved in a coevolutionary chase. In contrast, we show that establishment probability declines with phylogenetic distance when the outcomes of resident interactions are determined by phenotypic differences, as for any community type locked in a coevolutionary arms race. Consequently, our results do not support interpretations that are generally offered for empirically observed patterns, i.e., that positive relationships between phylogenetic distance and nonnative establishment (as in Fig. 1*B*) are due to biotic resistance from related competitors and their natural enemies (30–37), and that negative relationships (as in Fig. 1*A*) are due to environmental filtering (38–44).

Our model makes empirically testable predictions that run counter to conventional wisdom in three cases. First, when competitive interactions are mediated by phenotype differences, we predict that the evolution of increased competitive ability by native species should cause the establishment probability of nonnative species to decline with increasing phylogenetic distance. This prediction is consistent with observations from experimental tests of plant competitive ability (20, 45). Second, we predict that, when consumer–resource interactions are mediated by phenotype differences, evolutionary escalation of defense and attack traits in the native species should cause the establishment probability of nonnative species to decrease with phylogenetic distance. Such escalation between native species may explain why native herbivore damage to nonnative plants has been found to increase with these plants' phylogenetic distance to native plants in one study (21). Third, we predict that evolution of phenotype matching between native mutualists should also increase the match to related, newly introduced species, thereby increasing facilitation and establishment probability with phylogenetic distance. This added benefit could be offset in nature, however, by strong competition for shared mutualists (46).

In all cases, our results show that establishment probability ultimately reaches an asymptotic value, such that further increases in phylogenetic distance have no additional influence. Because the rate at which this asymptote is reached depends upon model parameters and thus will likely vary among groups of organisms, it will generally be impossible to predict, a priori, over which timescales comparative studies should be conducted to maximize their power to detect an impact of phylogenetic distance. However, our results do allow us to make one concrete recommendation, namely, that comparative studies will be most powerful when they include at least some pairs of resident and introduced species that have speciated only recently.

Here, we chose to focus on a simplified recipient community to test the logic of the assumptions underlying Darwin's naturalization conundrum. This focus enabled us to identify a fundamental flaw in the logic; in contrast to what has been assumed, we find that the strength of interactions experienced by the introduced species can increase with phenotypic distance to a related, resident species. We expect this general finding also applies to more complex communities and therefore argue that more complex models developed for specific systems will have to consider the mechanisms underlying interspecific interactions to generate useful predictions.

Our study shows that a community's evolutionary history, i.e., how much and in what direction it has diverged phenotypically from the source communities of potential invaders, is a key predictor of its susceptibility to colonization by nonnative species. Whether a nonnative species is likely to encounter strong or weak interactions is critical for its probability of establishment (29). Here, we have shown that the strength of the interactions an introduced species faces depends not only on its relatedness to native species, as had been assumed previously, but also on how native species have evolved to interact with each other. Evolution in the native community is qualitatively different depending on the interaction mode—phenotype matching or phenotype differences—and both modes are prominent in a variety of community types (22). Greater consideration of these mechanisms underlying biotic interactions will provide better insight into the probability of successful establishment by introduced species, as well as into community assembly more generally (e.g., ref. 45).

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1. Mack RN, et al. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol Appl* 10(3):689–710.
2. Reaser JK, et al. (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environ Conserv* 34(2):98–111.
3. Simberloff D (2011) How common are invasion-induced ecosystem impacts? *Biol Invasions* 13(5):1255–1268.
4. Kolar CS, Lodge DM (2001) Progress in invasion biology: Predicting invaders. *Trends Ecol Evol* 16(4):199–204.
5. Küster EC, Kuhn I, Bruelheide H, Klotz S (2008) Trait interactions help explain plant invasion success in the German flora. *J Ecol* 96(5):860–868.
6. Moles AT, Gruber MAM, Bonser SP (2008) A new framework for predicting invasive plant species. *J Ecol* 96(1):13–17.
7. Küster EC, Durka W, Kuhn I, Klotz S (2010) Differences in the trait compositions of non-indigenous and native plants across Germany. *Biol Invasions* 12(7):2001–2012.
8. Kennedy TA, et al. (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417(6889):636–638.
9. Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7(10):975–989.
10. Darwin C (1859) *The Origin of Species* (J. Murray, London).
11. Mitchell CE, et al. (2006) Biotic interactions and plant invasions. *Ecol Lett* 9(6): 726–740.
12. Mayfield MM, Levine JM (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol Lett* 13(9):1085–1093.
13. Burns JH, Strauss SY (2011) More closely related species are more ecologically similar in an experimental test. *Proc Natl Acad Sci USA* 108(13):5302–5307.
14. Connor EF, Faeth SH, Simberloff D, Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects—a comparison of introduced and native trees. *Ecol Entomol* 5(3):205–211.
15. Agrawal AA, et al. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86(11):2979–2989.
16. Gilbert GS, Webb CO (2007) Phylogenetic signal in plant pathogen-host range. *Proc Natl Acad Sci USA* 104(12):4979–4983.
17. Hill SB, Kotanen PM (2009) Evidence that phylogenetically novel non-indigenous plants experience less herbivory. *Oecologia* 161(3):581–590.
18. Ness JH, Rollinson EJ, Whitney KD (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120(9):1327–1334.
19. Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. *Biol Rev Camb Philos Soc* 75(1):65–93.
20. Cahill JF, Kembel SW, Lamb EG, Keddy PA (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspect Plant Ecol Evol Syst* 10(1):41–50.
21. Parker JD, Burkepile DE, Lajeunesse MJ, Lind EM (2012) Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores. *Divers Distrib* 18(1):1–9.
22. Yoder JB, Nuismer SL (2010) When does coevolution promote diversification? *Am Nat* 176(6):802–817.
23. Nuismer SL, Doebeli M, Browning D (2005) The coevolutionary dynamics of antagonistic interactions mediated by quantitative traits with evolving variances. *Evolution* 59(10):2073–2082.
24. Nuismer SL, Ridenhour BJ, Oswald BP (2007) Antagonistic coevolution mediated by phenotypic differences between quantitative traits. *Evolution* 61(8):1823–1834.
25. Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30(2):314–334.
26. Abrams PA, Harada Y, Matsuda H (1993) On the relationship between quantitative genetic and ESS models. *Evolution* 47(3):982–985.
27. Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. *Biotic Interactions and Global Change*, eds Kareiva P, Kingsolver JG, Huey R (Sinauer Associates, Sunderland, MA), pp 234–250.
28. Sax DF, Brown JH (2000) The paradox of invasion. *Glob Ecol Biogeogr* 9(5):363–371.
29. Jones EI, Gomulkiewicz R (2012) Biotic interactions, rapid evolution, and the establishment of introduced species. *Am Nat* 179(2):E28–E36.
30. Violle C, Nemergut DR, Pu ZC, Jiang L (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecol Lett* 14(8):782–787.
31. Peay KG, Belisle M, Fukami T (2012) Phylogenetic relatedness predicts priority effects in nectar yeast communities. *Proc R Soc B Biol Sci* 279(1729):749–758.
32. Mack RN, Moran VC, Hoffmann JH, eds (1996) Biotic barriers to plant naturalization. *Proceedings of the Ninth International Symposium on Biological Control of Weeds*, eds Moran VC, Hoffmann JH (University of Cape Town, Stellenbosch, South Africa), pp 39–46.
33. Rejmanek M (1996) A theory of seed plant invasiveness: The first sketch. *Biol Conserv* 78(1-2):171–181.
34. Jiang L, Tan JQ, Pu ZC (2010) An experimental test of Darwin's naturalization hypothesis. *Am Nat* 175(4):415–423.
35. Davies KF, Cavender-Bares J, Deacon N (2011) Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. *Divers Distrib* 17(1):35–42.
36. van Wilgen NJ, Richardson DM (2011) Is phylogenetic relatedness to native species important for the establishment of reptiles introduced to California and Florida? *Divers Distrib* 17(1):172–181.
37. Tan JQ, Pu ZC, Ryberg WA, Jiang L (2012) Species phylogenetic relatedness, priority effects, and ecosystem functioning. *Ecology* 93(5):1164–1172.
38. Daehler CC (2001) Darwin's naturalization hypothesis revisited. *Am Nat* 158(3):324–330.
39. Duncan RP, Williams PA (2002) Ecology: Darwin's naturalization hypothesis challenged. *Nature* 417(6889):608–609.
40. Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecol Lett* 11(7):674–681.
41. Diez JM, et al. (2009) Learning from failures: Testing broad taxonomic hypotheses about plant naturalization. *Ecol Lett* 12(11):1174–1183.
42. Tingley R, Phillips BL, Shine R (2011) Establishment success of introduced amphibians increases in the presence of congeneric species. *Am Nat* 177(3):382–388.
43. Ferreira RB, Beard KH, Peterson SL, Poessel SA, Callahan CM (2012) Establishment of introduced reptiles increases with the presence and richness of native congeners. *Amphib-Reptil* 33(3-4):387–392.
44. Maitner BS, Rudgers JA, Dunham AE, Whitney KD (2012) Patterns of bird invasion are consistent with environmental filtering. *Ecography* 35(7):614–623.
45. Kunstler G, et al. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecol Lett* 15(8):831–840.
46. Burns JH, Ashman TL, Steets JA, Harmon-Threatt A, Knight TM (2011) A phylogenetically controlled analysis of the roles of reproductive traits in plant invasions. *Oecologia* 166(4): 1009–1017.
47. Lambdon PW, Hulme PE (2006) How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. *J Biogeogr* 33(6):1116–1125.
48. Ricciardi A, Mottiar M (2006) Does Darwin's naturalization hypothesis explain fish invasions? *Biol Invasions* 8(6):1403–1407.

Supporting Information

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SI Text

Methods S1

Phenotype Differences Model. In this model, the outcome of an interspecific encounter is determined by the signed distance between phenotypes (Fig. S1; for examples, see Table S1).

For any type of species interaction, each individual has the potential to receive either a relatively favorable (x_F) or a relatively unfavorable (x_U) outcome. For example, when an individual of predator species A encounters an individual of prey species B, the favorable outcome for the predator is to consume the prey (this is the unfavorable outcome for the prey) and the unfavorable outcome for the predator is for the prey to escape (this is the favorable outcome for the prey). For individuals of species A encountering individuals of species B, we represent the contribution of these alternate outcomes to fitness as $\beta(x_F)=\beta^F_{AB}$ and $\beta(x_U)=\beta^U_{AB}$, for the favorable and unfavorable outcomes, respectively. The specific outcomes that we use for each type of interspecific interaction are given in Table S2.

The probability that an individual receives the favorable outcome depends on the signed distance between phenotypes. Here, we assume that the probability an individual receives the favorable outcome increases nonlinearly with the amount that its phenotype exceeds that of the encountered individual. For an individual of species A encountering an individual of species B, this probability is $p(x_F)=\frac{1}{1+e^{-\alpha_D(z_A-z_B)}}$, in which $\alpha_D > 0$ measures how sensitive the outcome is to the phenotypes of the individuals (1). Meanwhile, the probability that the individual of species A receives the unfavorable outcome is $p(x_U)=1-p(x_F)=\frac{1}{1+e^{-\alpha_D(z_B-z_A)}}$.

The predicted outcome of an encounter depends jointly on the probabilities of the favorable and unfavorable outcomes and the fitness effects of these alternate outcomes. Thus, the expected outcome for an individual of species A with phenotype z_A encountering an individual of species B with phenotype z_B is as follows:

$$X_{AB}(z_A,z_B)=\frac{\beta^F_{AB}}{1+e^{-\alpha_D(z_A-z_B)}}+\frac{\beta^U_{AB}}{1+e^{-\alpha_D(z_B-z_A)}}. \qquad \textbf{[S1]}$$

For an illustration of this function, see Fig. S1 *A–C*. From Eq. **1**, the fitness of this individual of species A is as follows:

$$W_A(z_A,z_B)=k_A+\frac{\beta^F_{AB}}{1+e^{-\alpha_D(z_A-z_B)}}+\frac{\beta^U_{AB}}{1+e^{-\alpha_D(z_B-z_A)}}. \qquad \textbf{[S2]}$$

Although we can numerically evaluate the population mean fitness of species A and the evolution of mean phenotype, $\bar{z}_A$, using Eq. **S2** with Eqs. **2–4**, it is not possible to write out exact, closed-form expressions. However, Eq. **S2** can be well approximated using a first-order Taylor series in $\varepsilon \ll 1$, assuming $\alpha_D \sim O(\varepsilon)$ (1). Using this approximation, the mean fitness of species A at $t \geq T_1$ is as follows:

$$\overline{W}_A(t)\approx k_A+\frac{1}{2}\left(\beta^F_{AB}+\beta^U_{AB}\right)+\frac{1}{4}\alpha_D\left(\beta^F_{AB}-\beta^U_{AB}\right)\left(\bar{z}_A(t)-\bar{z}_B(t)\right). \qquad \textbf{[S3]}$$

This approximation is accurate as long as the fitness outcomes of interactions are not too sensitive to the phenotype distance ($z_A - z_B$), and thus implies that selection must be weak. We can approximate evolution of the mean phenotype in species A over one generation using Eq. **2** and Eq. **S3** as follows:

$$\Delta\bar{z}_A(t)\approx\frac{\alpha_D\left(\beta^F_{AB}-\beta^U_{AB}\right)G_A}{4k_A+2\left(\beta^F_{AB}+\beta^U_{AB}\right)+\alpha_D\left(\beta^F_{AB}-\beta^U_{AB}\right)\left(\bar{z}_A(t)-\bar{z}_B(t)\right)}. \qquad \textbf{[S4]}$$

Given the definitions in Table S2 (i.e., $\beta^F_{ij}-\beta^U_{ij}>0$ and $|\beta^F_{ij}+\beta^U_{ij}|\leq k_i$ for any pair of species i and j), Eq. **S4** and the corresponding equation for the evolution of species B always lead to phenotypic escalation (i.e., an "arms race"; Fig. S3). Thus, for all $t > T_1$, we find $\bar{z}_A(t)>\bar{z}_A(T_1)$ and $\bar{z}_B(t)>\bar{z}_B(T_1)$.

Finally, we can approximate the mean fitness of species $\tilde{B}$ at the time of introduction, $t = T_2$, using Eq. **5** and Eq. **S3**,

$$\begin{aligned}\overline{W}_{\tilde{B}}(T_2)\approx{}& k_{\tilde{B}}+\frac{1}{2}\left(\beta^F_{\tilde{B}A}+\beta^U_{\tilde{B}A}\right)+\frac{1}{4}\alpha_D\left(\beta^F_{\tilde{B}A}-\beta^U_{\tilde{B}A}\right)\left(\bar{z}_{\tilde{B}}(T_2)-\bar{z}_A(T_2)\right)\\&+\frac{1}{2}\left(\beta^F_{\tilde{B}B}+\beta^U_{\tilde{B}B}\right)+\frac{1}{4}\alpha_D\left(\beta^F_{\tilde{B}B}-\beta^U_{\tilde{B}B}\right)\left(\bar{z}_{\tilde{B}}(T_2)-\bar{z}_B(T_2)\right).\end{aligned} \qquad \textbf{[S5]}$$

Because $\bar{z}_A(t)>\bar{z}_A(T_1)$ and $\bar{z}_B(t)>\bar{z}_B(T_1)$ for all $t > T_1$, we can see from Eq. **S5** and the definitions in Table S2 that $\overline{W}_{\tilde{B}}(T_2)<\overline{W}_{\tilde{B}}(T_1)$ for all $T_2 > T_1$. Consequently, the establishment probability of species $\tilde{B}$ calculated in Eq. **6** also must always decrease with increasing phylogenetic distance (Fig. S3). Establishment probability does not decrease indefinitely, however. Establishment probability will either decline to zero or reach an asymptote (e.g., Fig. S2*A*) once the phenotypic distance between the residents and the introduced species has already become so large that further evolution of the residents does not affect their interaction with the introduced species (Fig. S1 *A–C*).

Phenotype Matching Model. In this model, the outcome of a random interspecific encounter depends on the absolute distance between phenotypes (Fig. S1; for examples, see Table S1).

As in the phenotype differences model described above, random encounters are assumed to have two possible outcomes. In this case, the outcomes are an interaction that changes the fitness of both individuals (x_I), or an encounter that ends without an interaction (x_{NI}). The probability of an interaction following an encounter between an individual of species A and an individual of species B is assumed to increase nonlinearly with the similarity of their phenotypes, z_A and z_B, and is expressed $p(x_I)=e^{-\frac{\alpha_M}{2}(z_A-z_B)^2}$, in which $\alpha_M > 0$ measures how sensitive the probability of interaction is to the phenotypes of the individuals (2). The probability that the encounter ends without an interaction is $p(x_{NI})=1-p(x_I)$.

If an interaction occurs, the fitness of individual A is changed by an amount $\beta(x_I)=\beta_{AB}$. The fitness effects of an interaction can be positive or negative depending on the type of interspecific interaction (e.g., positive for mutualists and consumers, negative for competitors and resource species; see also Table S2). If an interaction does not occur, the fitness effect is simply $\beta(x_{NI})=0$.

The expected outcome for an individual of species A with phenotype z_A encountering an individual of species B with phenotype z_B is as follows:

$$X_{AB}(z_A, z_B) = \beta_{AB} e^{-\frac{\alpha_M}{2}(z_A - z_B)^2}. \qquad \textbf{[S6]}$$

For an illustration of this function, see Fig. S1 *D–F*. From Eq. **1**, the fitness of this individual of species A is as follows:

$$W_A(z_A, z_B) = k_A + \beta_{AB} e^{-\frac{\alpha_M}{2}(z_A - z_B)^2}. \qquad \textbf{[S7]}$$

We can approximate the mean fitness of species A using Eq. **3** and Eq. **S7** and assuming that the phenotype distributions $\rho_{A,t}(z_A)$ and $\rho_{B,t}(z_B)$ are Gaussian with means $\bar{z}_A(t)$ and $\bar{z}_B(t)$ and phenotypic variances P_A and P_B, respectively. According to this method, the mean fitness of species A at $t \geq T_1$ is as follows:

$$\overline{W}_A(t) = k_A + \beta_{AB}\gamma_{AB} e^{-\frac{\alpha_M \gamma_{AB}^2}{2}(\bar{z}_A(t) - \bar{z}_B(t))^2}, \qquad \textbf{[S8]}$$

in which $\gamma_{AB} = \frac{1}{\sqrt{1 + \alpha_M(P_A + P_B)}}$.

From Eq. **2** and Eq. **S8**, the change in the mean phenotype of species A over one generation is as follows:

$$\Delta\bar{z}_A(t) = -\alpha_M \beta_{AB} G_A(\bar{z}_A(t) - \bar{z}_B(t)) \frac{\gamma_{AB}^2}{\beta_{AB} + \frac{k_A}{\gamma_{AB}} e^{-\frac{\alpha_M \gamma_{AB}^2}{2}(\bar{z}_A(t) - \bar{z}_B(t))^2}}, \qquad \textbf{[S9]}$$

in which the additive genetic variance G_A is less than or equal to the phenotypic variance, P_A. Although we cannot write analytical solutions for the mean phenotypes of species A and B as functions of time t, we can follow the coevolution of species A and B numerically using Eq. **S9** and the recursion Eqs. **4** (Fig. S4).

We can then use these numerical solutions for $\bar{z}_A(t)$ and $\bar{z}_B(t)$ to evaluate the mean fitness of species $\tilde{B}$ introduced at $t = T_2$, which from Eq. **5** and Eq. **S8** is as follows:

$$\begin{aligned}\overline{W}_{\tilde{B}}(T_2) = k_{\tilde{B}} &+ \frac{1}{2}\beta_{\tilde{B}A}\gamma_{\tilde{B}A} e^{-\frac{\alpha_M \gamma_{\tilde{B}A}^2}{2}\left(\bar{z}_{\tilde{B}}(T_2) - \bar{z}_A(T_2)\right)^2} \\ &+ \frac{1}{2}\beta_{\tilde{B}B}\gamma_{\tilde{B}B} e^{-\frac{\alpha_M \gamma_{\tilde{B}B}^2}{2}\left(\bar{z}_{\tilde{B}}(T_2) - \bar{z}_B(T_2)\right)^2}. \qquad \textbf{[S10]}\end{aligned}$$

Furthermore, we can use the numerical solution to Eq. **S10** to evaluate Eq. **6**, the establishment probability of species $\tilde{B}$ introduced at time T_2 (Fig. S4). Unlike in the phenotype differences model, here the mean fitness of $\tilde{B}$, and consequently the establishment probability of $\tilde{B}$, can either increase or decrease over time. Once again, these changes in establishment probability cannot continue indefinitely with increasing phylogenetic distance, as establishment probability is bound between zero and 1. Additionally, the change in establishment probability will reach an asymptote (e.g., Fig. S2*B*) if residents reach an evolutionary equilibrium (further increases in phylogenetic distance are not associated with additional phenotypic change) or if the phenotypic distance between the residents and the introduced species becomes so large that further increases in phenotypic distance do not change the interaction with the introduced species (Fig. S1 *D–F*).

Unfortunately, it is not obvious from Eq. **S10** how the fitness of species $\tilde{B}$ changes with the time of introduction. Therefore, in the next section, we derive a weak selection approximation of the phenotype matching model that allows us write general conditions for the change in establishment probability of $\tilde{B}$ over time.

Weak Selection Approximation of the Phenotype Matching Model. To approximate the phenotype matching model above, we use a first-order Taylor series expansion of Eq. **S9** in $\varepsilon \ll 1$, assuming $\alpha_M \sim O(\varepsilon)$, as in the phenotype differences model described above. Using the Taylor series approximation of Eq. **3** with Eq. **S7** and given phenotype distributions $\rho_{A,t}(z_A)$ and $\rho_{B,t}(z_B)$ with means $\bar{z}_A(t)$ and $\bar{z}_B(t)$ and phenotypic variances P_A and P_B, respectively, the mean fitness of species A at $t \geq T_1$ is approximately as follows:

$$\overline{W}_A(t) \approx k_A + \beta_{AB} - \frac{\alpha_M}{2}\beta_{AB}\left((\bar{z}_A(t) - \bar{z}_B(t))^2 + P_A + P_B\right). \qquad \textbf{[S11]}$$

The change of the mean phenotype of species A in one generation, from Eq. **2**, can now be approximated as follows:

$$\Delta\bar{z}_A(t) \approx \varphi_A(\bar{z}_A(t) - \bar{z}_B(t)), \qquad \textbf{[S12]}$$

where $\varphi_A = -\frac{\alpha_M \beta_{AB} G_A}{2(k_A + \beta_{AB})}$ and $G_A \leq P_A$. To follow the coevolution of mean phenotypes $\bar{z}_A(t)$ and $\bar{z}_B(t)$, we use the recursion

$$\begin{bmatrix}\bar{z}_A(t+1)\\ \bar{z}_B(t+1)\end{bmatrix} = M\begin{bmatrix}\bar{z}_A(t)\\ \bar{z}_B(t)\end{bmatrix}, \qquad \textbf{[S13]}$$

in which $M = \begin{bmatrix}\varphi_A + 1 & -\varphi_A\\ -\varphi_B & \varphi_B + 1\end{bmatrix}$. The matrix M has eigenvalues $\lambda_1 = 1$ and $\lambda_2 = 1 + \varphi_A + \varphi_B$ and eigenvectors $\vec{u}_1 = [1 \quad 1]$ and $\vec{u}_2 = [-\varphi_A \quad \varphi_B]$. Solving for the coevolved mean phenotypes of species A and B at $t \geq T_1$,

$$\begin{aligned}\begin{bmatrix}\bar{z}_A(t)\\ \bar{z}_B(t)\end{bmatrix} &= \begin{bmatrix}u_{11} & u_{21}\\ u_{12} & u_{22}\end{bmatrix}\begin{bmatrix}\lambda_1 & 0\\ 0 & \lambda_2\end{bmatrix}^{t-T_1}\begin{bmatrix}u_{11} & u_{21}\\ u_{12} & u_{22}\end{bmatrix}^{-1}\begin{bmatrix}\bar{z}_A(T_1)\\ \bar{z}_B(T_1)\end{bmatrix} \\ &= \begin{bmatrix}1 & -\varphi_A\\ 1 & \varphi_B\end{bmatrix}\begin{bmatrix}1 & 0\\ 0 & (1 + \varphi_A + \varphi_B)^t\end{bmatrix}\begin{bmatrix}1 & -\varphi_A\\ 1 & \varphi_B\end{bmatrix}^{-1}\begin{bmatrix}\bar{z}_A(0)\\ \bar{z}_B(0)\end{bmatrix}, \qquad \textbf{[S14]}\end{aligned}$$

gives the solutions:

$$\bar{z}_A(t) = \bar{z}_A(T_1) - \frac{\varphi_A}{\varphi_A + \varphi_B}\left(1 - (1 + \varphi_A + \varphi_B)^{t-T_1}\right)(\bar{z}_A(0) - \bar{z}_B(0)), \qquad \textbf{[S15a]}$$

$$\bar{z}_B(t) = \bar{z}_B(T_1) - \frac{\varphi_B}{\varphi_A + \varphi_B}\left(1 - (1 + \varphi_A + \varphi_B)^{t-T_1}\right)(\bar{z}_B(0) - \bar{z}_A(0)). \qquad \textbf{[S15b]}$$

Then, from Eq. **5** and Eq. **S11**, the mean fitness of species $\tilde{B}$ introduced at time $T_2 \geq T_1$ is as follows:

$$\begin{aligned}\overline{W}_{\tilde{B}}(T_2) = k_{\tilde{B}} &+ \frac{1}{2}\beta_{\tilde{B}A} - \frac{\alpha_M}{4}\beta_{\tilde{B}A}\left(\left(\bar{z}_{\tilde{B}}(T_2) - \bar{z}_A(T_2)\right)^2 + P_A + P_{\tilde{B}}\right) \\ &+ \frac{1}{2}\beta_{\tilde{B}B} - \frac{\alpha_M}{4}\beta_{\tilde{B}B}\left(\left(\bar{z}_{\tilde{B}}(T_2) - \bar{z}_B(T_2)\right)^2 + P_B + P_{\tilde{B}}\right). \qquad \textbf{[S16]}\end{aligned}$$

Using the solutions in Eqs. **S15** with Eq. **S16**, we can find the parameter conditions that yield $\overline{W}_{\tilde{B}}(T_2) > \overline{W}_{\tilde{B}}(T_1)$. Given the relationship between mean fitness and establishment probability in Eq. **6**, parameter conditions that increase mean fitness of $\tilde{B}$ will also increase the establishment probability of $\tilde{B}$. We consider two cases, described in *Results* of the main text. First, we consider whether A–B coevolution immediately ($T_2 = T_1 + 1$) increases establishment probability (Eq. **7**). Second, we consider whether A–B coevolution asymptotically ($(T_2 - T_1) \to \infty$) increases establishment probability (Eqs. **8** and Fig. 3).

Accounting for Phenotypic Divergence Between Sister Species Before Colonization. Let $t = T_1$ designate the phylogenetic distance between sister species B and $\tilde{B}$ when coevolution between the nonsister species A and B begins. The mean fitness of species $\tilde{B}$ at introduction time $T_2 \geq T_1$ is a function of $d_A = \bar{z}_{\tilde{B}}(T_2) - \bar{z}_A(T_2)$ and $d_B = \bar{z}_{\tilde{B}}(T_2) - \bar{z}_B(T_2)$ for phenotypic differences (Eq. **S5**) and of d_A^2 and d_B^2 for phenotypic matching (Eq. **S16**).

Suppose the ancestral mean phenotype at the time the sister species B and $\tilde{B}$ formed is $\bar{\zeta}$. Under many biological scenarios (e.g., random genetic drift or nondirectional fluctuating selection), it is reasonable to assume that

$$E\left[\bar{z}_B(T_1)\right] = \bar{\zeta} \qquad \textbf{[S17a]}$$

and

$$E\left[\bar{z}_{\tilde{B}}(t)\right] = \bar{\zeta} \text{ for all } t \geq 0, \text{ including } t = T_2. \qquad \textbf{[S17b]}$$

If phenotypic divergence of the sister species before $t = T_1$ is not too extensive and if coevolution is the dominant source of evolution in A and B after their community formed, then for $t \geq T_1$:

$$E[\bar{z}_A(t)] \approx \widehat{\bar{z}}_A(t), \qquad \textbf{[S18a]}$$

$$E[\bar{z}_B(t)] \approx \widehat{\bar{z}}_B(t), \qquad \textbf{[S18b]}$$

where $\widehat{\bar{z}}_A(t)$ and $\widehat{\bar{z}}_B(t)$ are solutions of Eqs. **4** with initial condition $\bar{z}_B(T_1) = \bar{\zeta}$. [Approximations (**S18**) can be justified using Taylor series of $\bar{z}_A(t)$ and $\bar{z}_B(t)$ (see, e.g., ref. 3, pp. 328–329).] The expected values of d_A and d_B over the various preintroduction histories are as follows:

$$E(d_A) = E\left[\bar{z}_{\tilde{B}}(T_2)\right] - E[\bar{z}_A(T_2)] \approx \bar{\zeta} - \widehat{\bar{z}}_A(T_2), \qquad \textbf{[S19a]}$$

$$E(d_B) = E\left[\bar{z}_{\tilde{B}}(T_2)\right] - E[\bar{z}_B(T_2)] \approx \bar{\zeta} - \widehat{\bar{z}}_B(T_2). \qquad \textbf{[S19b]}$$

Using Eqs. **S19** for the expectations of d_A and d_B shows the expected mean fitness of species $\tilde{B}$ upon introduction into the A–B community is equivalent to formula **S5** for phenotypic differences with the substitutions $\bar{z}_{\tilde{B}}(T_2) = \bar{\zeta}$, $\bar{z}_B(T_2) = \widehat{\bar{z}}_B(T_2)$, and $\bar{z}_A(T_2) = \widehat{\bar{z}}_A(T_2)$.

For phenotypic matching, the expected mean fitness of $\tilde{B}$ upon introduction (Eq. **S16**) involves $E(d_A^2)$ and $E(d_B^2)$. Note that

$$E\left(d_A^2\right) = E\left[\bar{z}_{\tilde{B}}^2(T_2)\right] - 2E\left[\bar{z}_{\tilde{B}}(T_2)\bar{z}_A(T_2)\right] + E\left[\bar{z}_A^2(T_2)\right], \qquad \textbf{[S20a]}$$

$$E\left(d_B^2\right) = E\left[\bar{z}_{\tilde{B}}^2(T_2)\right] - 2E\left[\bar{z}_{\tilde{B}}(T_2)\bar{z}_B(T_2)\right] + E\left[\bar{z}_B^2(T_2)\right]. \qquad \textbf{[S20b]}$$

Because $\tilde{B}$ evolves independently of A and B before it is introduced,

$$E\left[\bar{z}_{\tilde{B}}(T_2)\bar{z}_A(T_2)\right] = E\left[\bar{z}_{\tilde{B}}(T_2)\right]E\left[\bar{z}_A(T_2)\right] \approx \bar{\zeta}\,\widehat{\bar{z}}_A(T_2), \qquad \textbf{[S21a]}$$

$$E\left[\bar{z}_{\tilde{B}}(T_2)\bar{z}_B(T_2)\right] = E\left[\bar{z}_{\tilde{B}}(T_2)\right]E\left[\bar{z}_B(T_2)\right] \approx \bar{\zeta}\,\widehat{\bar{z}}_B(T_2). \qquad \textbf{[S21b]}$$

To justify Eq. **S21b**, write $\bar{z}_B(T_2) = \bar{\zeta} + \Delta_B + \delta_B$ and $\bar{z}_{\tilde{B}}(T_2) = \bar{\zeta} + \Delta_{\tilde{B}} + \delta_{\tilde{B}}$, where the Δs are the changes in mean phenotype from speciation ($t = 0$) to the beginning of A–B coevolution ($t = T_1$) and the δs are the changes from T_1 to T_2. We have

$$E(\Delta_B) = E\left(\Delta_{\tilde{B}}\right) = E\left(\delta_{\tilde{B}}\right) = 0 \qquad \textbf{[S22a]}$$

and

$$E(\delta_B) = E[\bar{z}_B(T_2) - \bar{z}_B(T_1)] = E[\bar{z}_B(T_2)] - E[\bar{z}_B(T_1)] \approx \widehat{\bar{z}}_B(T_2) - \bar{\zeta}. \qquad \textbf{[S22b]}$$

The product $\bar{z}_{\tilde{B}}(T_2)\bar{z}_B(T_2) = \bar{\zeta}^2 + \bar{\zeta}(\Delta_{\tilde{B}} + \delta_{\tilde{B}} + \Delta_B + \delta_B) + \Delta_{\tilde{B}}\Delta_B + \Delta_{\tilde{B}}\delta_B + \delta_{\tilde{B}}\Delta_B + \delta_{\tilde{B}}\delta_B$. Taking expectations and using Eqs. **S22** gives the following:

$$E\left[\bar{z}_{\tilde{B}}(T_2)\bar{z}_B(T_2)\right] \approx \bar{\zeta}\,\widehat{\bar{z}}_B(T_2) + E\left(\Delta_{\tilde{B}}\Delta_B\right) + E\left(\Delta_{\tilde{B}}\delta_B\right) + E\left(\delta_{\tilde{B}}\Delta_B\right) + E\left(\delta_{\tilde{B}}\delta_B\right). \qquad \textbf{[S23]}$$

Because evolutionary changes in the two species are mutually independent, each expected product in Eq. **S23** is the product of expectations, which, using Eq. **S22a**, shows that Eq. **S23** reduces to Eq. **S21b**. A similar argument justifies Eq. **S21a**.

Finally, let $\sigma_B^2 = \text{var}[\bar{z}_B(T_1)]$ and $\sigma_{\tilde{B}}^2 = \text{var}[\bar{z}_{\tilde{B}}(T_2)]$. Because both $\bar{z}_A(T_2)$ and $\bar{z}_B(T_2)$ are functions of $\bar{z}_B(T_1)$, using Taylor series approximations (e.g., ref. 3, pp. 328–329), we also have

$$\text{var}[\bar{z}_A(T_2)] \approx c_A\sigma_B^2, \qquad \textbf{[S24a]}$$

$$\text{var}[\bar{z}_B(T_2)] \approx c_B\sigma_B^2, \qquad \textbf{[S24b]}$$

for some positive constants c_A and c_B. Thus, Eqs. **S20** are

$$E\left(d_A^2\right) \approx \left(\bar{\zeta}^2 - \sigma_{\tilde{B}}^2\right) - 2\bar{\zeta}\,\widehat{\bar{z}}_A(T_2) + \left[\widehat{\bar{z}}_A^2(T_2) + c_A\sigma_B^2\right]$$

$$= \left[\bar{\zeta} - \widehat{\bar{z}}_A(T_2)\right]^2 + \sigma_{\tilde{B}}^2 + c_A\sigma_B^2, \qquad \textbf{[S25a]}$$

$$E\left(d_B^2\right) \approx \left(\bar{\zeta}^2 - \sigma_{\tilde{B}}^2\right) - 2\bar{\zeta}\,\widehat{\bar{z}}_B(T_2) + \left[\widehat{\bar{z}}_B^2(T_2) + c_B\sigma_B^2\right]$$

$$= \left[\bar{\zeta} - \widehat{\bar{z}}_B(T_2)\right]^2 + \sigma_{\tilde{B}}^2 + c_B\sigma_B^2. \qquad \textbf{[S25b]}$$

If the divergence variances σ_B^2 and $\sigma_{\tilde{B}}^2$ are both small compared with the phenotypic variances P_B and $P_{\tilde{B}}$ [as occurs, e.g., under random genetic drift in large populations (4)], then $E(d_A^2) \approx [\bar{\zeta} - \widehat{\bar{z}}_A(T_2)]^2$ and $E(d_B^2) \approx [\bar{\zeta} - \widehat{\bar{z}}_B(T_2)]^2$ to good approximation in the formula for the expected fitness of species $\tilde{B}$ at introduction given phenotypic matching, which is equivalent to Eq. **S16** with the substitutions $\bar{z}_{\tilde{B}}(T_2) = \bar{\zeta}$, $\bar{z}_B(T_2) = \widehat{\bar{z}}_B(T_2)$, and $\bar{z}_A(T_2) = \widehat{\bar{z}}_A(T_2)$.

Methods S2

Individual-based simulations were run for phenotype matching and phenotype differences models for all community types (competitors, mutualists, and consumer–resource). These simulations allowed us to relax the assumptions of density independence, fixed phenotypic variances, and weak selection and to incorporate explicitly the effects of demographic stochasticity.

Simulations followed populations of diploid, sexual species with phenotypes determined additively by integer alleles at five unlinked, diallelic loci. Individual fitness, from Eq. **1**, was modified for discrete, logistic population growth with population size *N*, carrying capacity *K*, and intrinsic growth rate *r*. Specifically, the fitness of an individual A in the absence of an interaction was defined as $k_A = 1 + r\left(1 - \frac{N_A}{K}\right)$. For all species, $r = 0.2$, which is too low to produce chaotic dynamics. Initial allele frequency distributions were chosen to allow equivalent evolutionary change in each community type. The alleles for each individual of species A were drawn from a random uniform integer distribution with limits [0,9]. Alleles for individuals of species B and $\tilde{B}$

were drawn from a random uniform integer distribution with limits [1,10] in all cases except mutualist communities with phenotype matching, where the limits were [4,13] to allow convergence (e.g., Fig. S4*B*). Because mutualism can lead to population sizes significantly larger than the carrying capacity even with intraspecific density dependence, the carrying capacity for mutualist species was 100; the carrying capacity for all other species was 500.

At the beginning of each run, $t = T_1$, the fitness effects, $\beta(x_n)$, of encounters between resident species A and B were chosen randomly from uniform distributions as shown in Table S2. Note that, because we found no effect on average of divergence during the time period $0 < t \leq T_1$, we set $T_1 = 0$ for simplicity. Because the introduced species $\tilde{B}$ is the sister species of B, it receives the same fitness effects from encounters with A, and competition with B has the same fitness effect as intraspecific competition ($-r$). The population sizes of species A and B were then initialized at their numerically calculated equilibria given the expected phenotype distributions before evolution. Alleles for each individual were then drawn at random from uniform distributions with the ranges given above.

At each time $t \geq T_1$, the populations interact and reproduce to form a new, nonoverlapping generation. The number of interspecific encounters between A and B per generation was set to the floor (greatest integer below) of the expected number, $\lfloor N_A N_B / K \rfloor$. For this number of encounters, individuals were drawn randomly (with replacement) from the pair of species. In both the phenotype differences and phenotype matching cases, encounters resulted in $n = 2$ different outcomes at their respective phenotype-dependent probabilities, $p(x_n)$, defined as in the preceding sections with $\alpha_D = 0.05$ and $\alpha_M = 0.002$. Outcome x_1, with fitness effect $\beta(x_1)$, was chosen if a randomly selected value from the uniform distribution $[0,1] \leq p(x_1)$; otherwise, outcome x_2, with corresponding fitness effect $\beta(x_2)$, was chosen.

Each diploid individual produced a number of haploid gametes drawn randomly from a Poisson distribution with 2× the individual's expected fitness as the mean. Gametes were produced with a randomly chosen parental chromosome as a template. Recombination between parental chromosomes occurred with a probability 0.5 (unlinked) between each locus and mutation either increased or decreased the integer value of an allele (+1 or −1) with probability 0.001. New diploid individuals were formed by randomly drawing pairs of gametes (without replacement) until either zero or one gamete was left.

If $t = T_2$ (the "introduction time"), an initial $\tilde{B}$ population of four individuals was randomly drawn as described above. Then, for every t until $t = T_2 + 20$ (i.e., 20 generations postintroduction), individuals of the $\tilde{B}$ population interacted and reproduced following the same rules as the residents. At $t = T_2 + 20$, the $\tilde{B}$ population was tested to determine whether it had grown from its initial size. If so, it was recorded as "established" in the community. For every community type and interaction mode considered, 25 independent simulations were run for each T_2, which were spaced every 10 generations up to $T_2 = 1{,}000$.

1. Nuismer SL, Ridenhour BJ, Oswald BP (2007) Antagonistic coevolution mediated by phenotypic differences between quantitative traits. *Evolution* 61(8):1823–1834.
2. Nuismer SL, Doebeli M, Browning D (2005) The coevolutionary dynamics of antagonistic interactions mediated by quantitative traits with evolving variances. *Evolution* 59(10): 2073–2082.
3. Casella G, Berger RL (1990) *Statistical Inference* (Duxbury Press, Belmont, CA).
4. Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30(2):314–334.

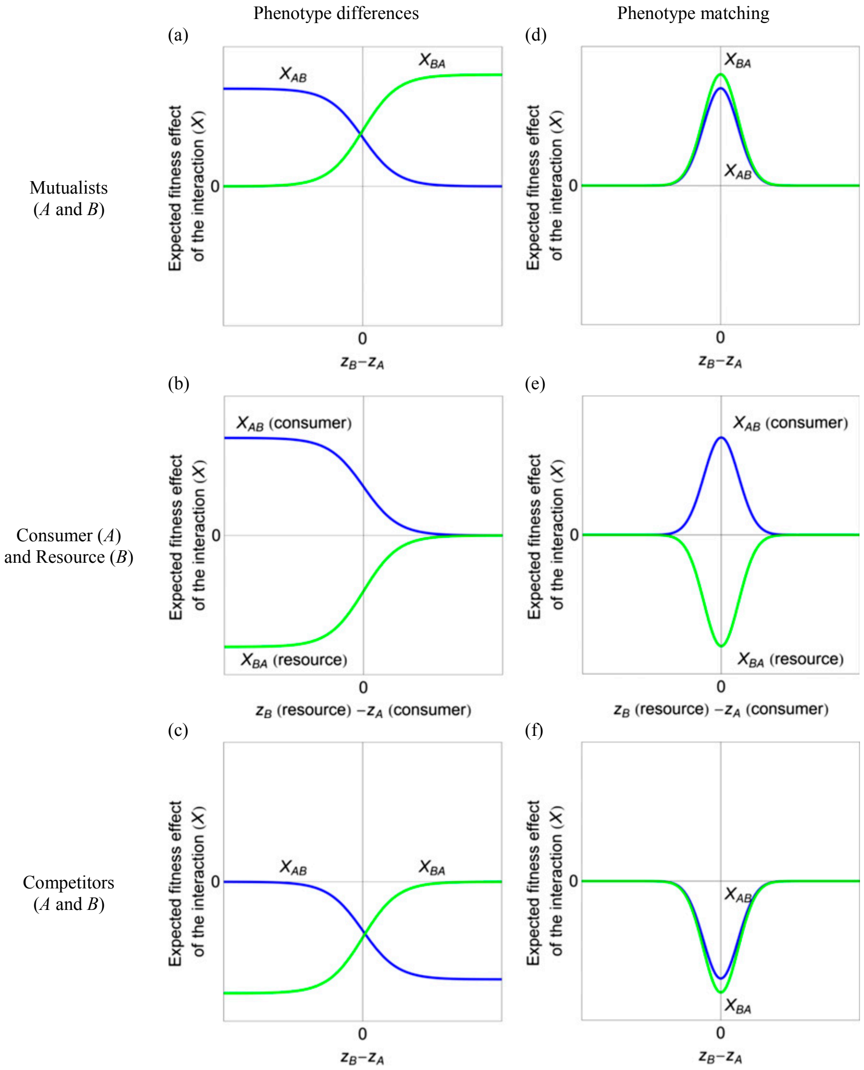

Fig. S1. Expected fitness consequences of mutualistic, consumer–resource, and competitive interactions when the outcome is determined by phenotype differences (*A*–*C*) or phenotype matching (*D*–*F*). Each panel depicts the effects of interspecific interactions on the fitness of individuals of species *A* and *B*, in which X_{AB} (blue line), the effect of an individual of species *B* on an individual of species *A*, is a function of the distance between the phenotypes of the two individuals, z_B and z_A, respectively. Similarly, X_{BA} (green line) is the effect of an individual of species *A* on an individual of species *B* and is also a function of the distance between the phenotypes z_B and z_A. A positive (negative) function value means the interaction increases (reduces) the fitness of the participant from that species.

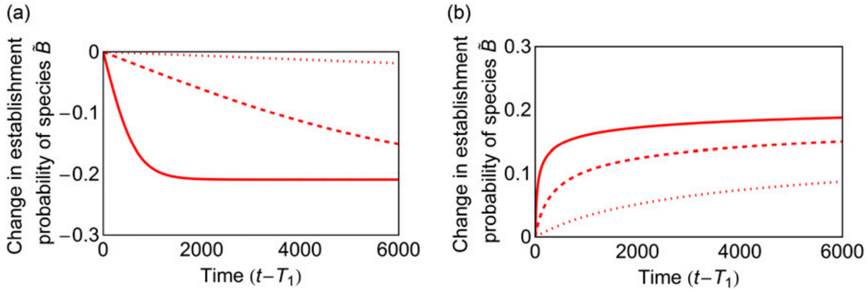

Fig. S2. The change in establishment probability of species $\tilde{B}$ if introduced into a competitive community at time $T_2 = t - T_1$ at different levels of additive genetic variance. Species $\tilde{B}$ is introduced into a community with interactions mediated by (*A*) phenotype differences ($\beta_{ij}^F = 0$ and $\beta_{ij}^U = -\beta$ for every pair of species *i* and *j*) or (*B*) phenotype matching ($\beta_{ij} = -\beta$ for every pair of species *i* and *j*). The lines show three levels of additive genetic variance: high (solid line, $G_A = G_B = G_{\tilde{B}} = 0.1$), intermediate ($G_A = G_B = G_{\tilde{B}} = 0.01$), and low ($G_A = G_B = G_{\tilde{B}} = 0.001$). Parameters: $\bar{z}_A(T_1) = 1$, $\bar{z}_{\tilde{B}} = \bar{z}_B(T_1) = 0$, $n = 1$, $k_A = k_B = k_{\tilde{B}} = 0.5$, $\alpha_D = \alpha_M = 0.25$, and $\beta = 0.3$.

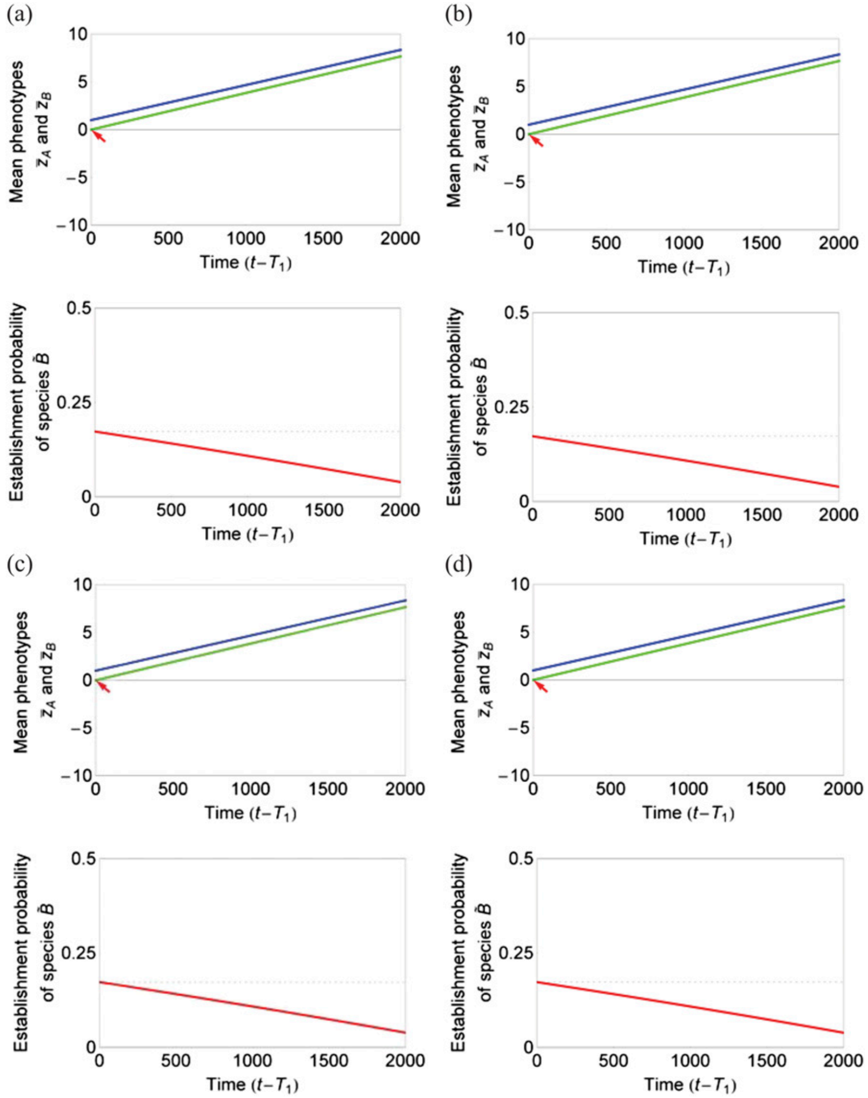

Fig. S3. Trajectories of coevolution in the resident community and the effect on establishment probability given interactions mediated by phenotype differences. The upper panels show the mean phenotype values of species *A* (blue) and *B* (green) over time. The red arrow shows the mean phenotype of the introduced species, $\tilde{B}$, which is fixed at $\bar{z}_{\tilde{B}} = \bar{z}_B(T_1) = 0$. The lower panels show the establishment probability of species $\tilde{B}$ if introduced into a community at time $T_2 = t - T_1$ (red) compared with the initial establishment probability (at $T_2 = T_1$; dotted gray). The residents are engaged in a coevolutionary arms race in all community types modeled (*A*) competitors, $k_A = k_B = k_{\tilde{B}} = 0.6$, (*B*) mutualists, $k_A = k_B = k_{\tilde{B}} = 0.2$, (*C*) resource (*A*) and consumer (*B*), $k_A = 0.4$, $k_B = k_{\tilde{B}} = 0.2$, and (*D*) consumer (*A*) and resource (*B*), $k_A = 0.2$, $k_B = k_{\tilde{B}} = 0.4$. Parameters: $\alpha_D = 0.1$, $G_A = G_B = G_{\tilde{B}} = 0.15$, $\bar{z}_A(T_1) = 1$, $n = 1$; β_{ij}^F and β_{ij}^U for each pair of species *i* and *j* are as defined in Table S2 with $\beta = 0.4$.

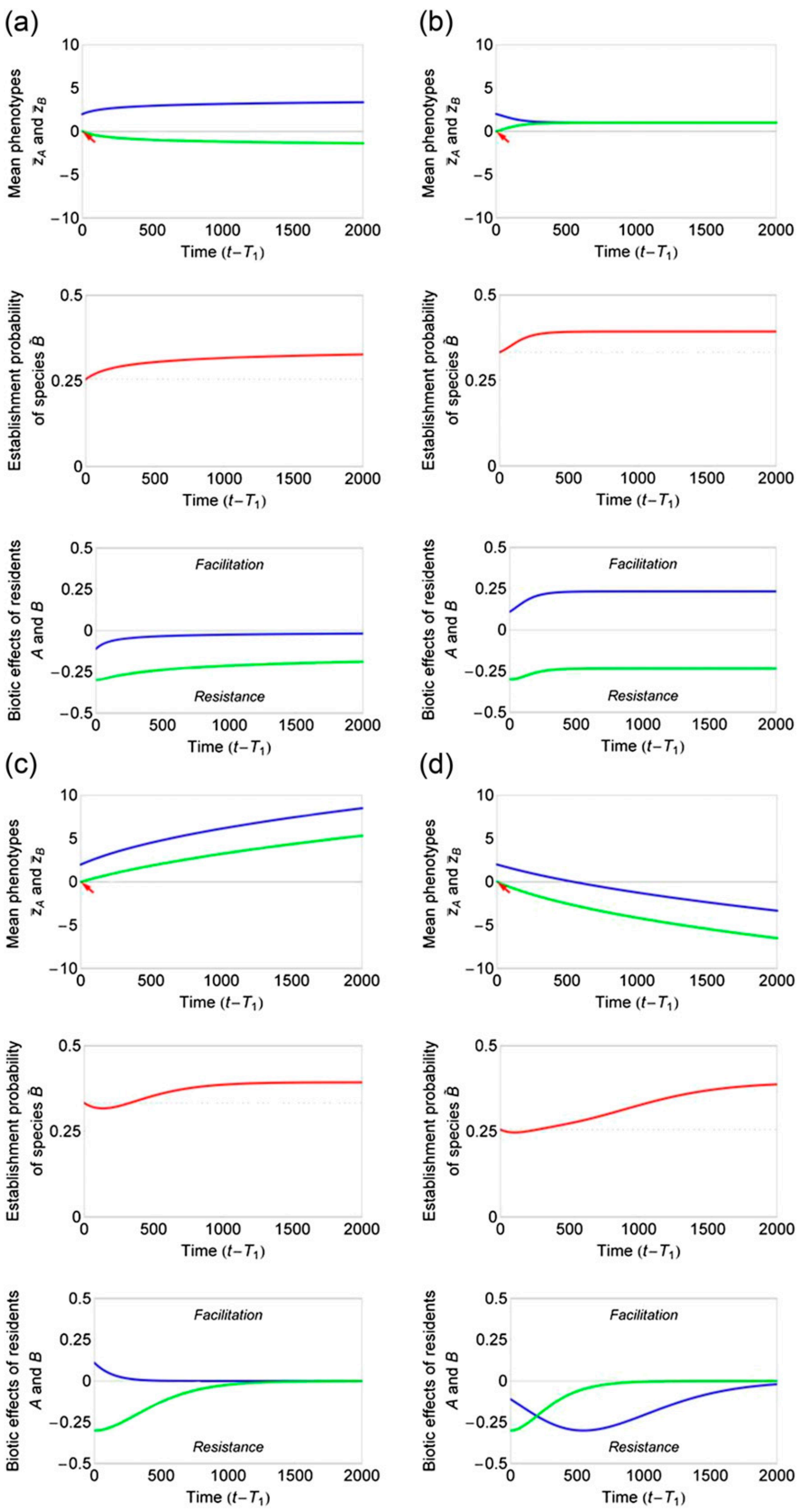

Fig. S4. Trajectories of coevolution in the resident community and the effect on establishment probability given interactions mediated by phenotype matching. The top panels show the mean phenotype values of species *A* (blue) and *B* (green) over time. The red arrow shows the mean phenotype of the introduced species, $\tilde{B}$, which is fixed at $\bar{z}_{\tilde{B}} = \bar{z}_B(T_1) = 0$. The middle panels show the establishment probability of species $\tilde{B}$ if introduced into a community at time $T_2 = t - T_1$ (red) compared with the initial establishment probability (at $T_2 = T_1$; dotted gray). The bottom panels show the contribution of species *A* (blue) and *B* (green) to the fitness of the introduced species, $\tilde{B}$. When this contribution is positive (negative), it facilitates (resists) growth of the introduced species. (*A*) The residents are competitors ($\beta_{AB} = -\beta$, $\beta_{BA} = -\beta$) and evolve character displacement. (*B*) The residents are mutualists ($\beta_{AB} = \beta$, $\beta_{BA} = \beta$) and evolve character matching. (*C*) The residents are resource (*A*; $\beta_{AB} = -\beta$) and consumer (*B*; $\beta_{BA} = \beta$) and evolve in a coevolutionary chase. (*D*) The residents are consumer (*A*; $\beta_{AB} = \beta$) and resource (*B*; $\beta_{BA} = -\beta$) and again evolve in a coevolutionary chase. Parameters: $k_A = k_B = k_{\tilde{B}} = 0.5$, $\alpha_M = 0.25$, $\beta = 0.3$, $\beta_{\tilde{B}A} = \beta_{BA}$, $\beta_{\tilde{B}B} = -\beta$, $G_A = G_B = G_{\tilde{B}} = 0.025$, $\bar{z}_A(T_1) = 2$, and $n = 1$.

Table S1. Illustrative examples of interactions that are mediated by phenotype differences or phenotype matching and their evolutionary outcomes

Ecological interaction type	Phenotype differences	Phenotype matching
Mutualism	Pollination of flowers by insects: increasing nectar spur length and proboscis length (“Darwin’s race”) (1)	Nutritional mutualism between legumes and rhizobia: matching of chemical signals and receptors (2)
Consumer–resource	Seed predation of camellias by weevils: increasing pericarp thickness and rostrum length (3)	Brood parasitism by cuckoos: mimicry of host eggs by cuckoos (4)
Competition	Interference competition among plants through allelopathy: increasing production of toxic chemicals and tolerance to toxins (5)	Exploitative competition among Darwin’s finches: character displacement of beak morphology (6)

1. Muchhala N, Thomson JD (2009) Going to great lengths: Selection for long corolla tubes in an extremely specialized bat-flower mutualism. *Proc R Soc B Biol Sci* 276(1665):2147–2152.
2. Heath KD, Tiffin P (2009) Stabilizing mechanisms in a legume-rhizobium mutualism. *Evolution* 63(3):652–662.
3. Toju H, Sota T (2006) Imbalance of predator and prey armament: Geographic clines in phenotypic interface and natural selection. *Am Nat* 167(1):105–117.
4. Soler JJ, Aviles JM, Soler M, Moller AP (2003) Evolution of host egg mimicry in a brood parasite, the great spotted cuckoo. *Biological Journal of the Linnean Society* 79(4):551–563.
5. Lankau RA (2012) Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proc Natl Acad Sci USA* 109(28):11240–11245.
6. Grant PR, Grant BR (2006) Evolution of character displacement in Darwin’s finches. *Science* 313(5784):224–226.

Table S2. Fitness consequences of species interactions in the phenotype differences and phenotype matching models

	Phenotype differences		
Species type	Favorable outcome	Unfavorable outcome	Phenotype matching
Competitor	0	$-\beta$	$-\beta$
Mutualist	β	0	β
Consumer	β	0	β
Resource	0	$-\beta$	$-\beta$

For all entries, the baseline effect $\beta > 0$ is given with the appropriate sign for the interaction type. The analytical models assume $0 < \beta < k$, such that the magnitude of the fitness effect of an interaction is less than fitness in the absence of an interaction. The simulations assume $0 \leq \beta \leq r$, such that the magnitude of the fitness effect of an interaction is equal or less than the intrinsic growth rate.