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Author(s): Rafael L. G. Raimundo, Jean P. Gibert, David H. Hembry, and Paulo R. Guimarães Jr.

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Conflicting Selection in the Course of Adaptive Diversification: The Interplay between Mutualism and Intraspecific Competition

Rafael L. G. Raimundo,¹ Jean P. Gibert,² David H. Hembry,^{3,*} and Paulo R. Guimarães Jr.^{1,†}

1. Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, no. 321, 05508-900 Sao Paulo SP, Brazil; 2. School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588; 3. Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720

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ABSTRACT: Adaptive speciation can occur when a population undergoes assortative mating and disruptive selection caused by frequency-dependent intraspecific competition. However, other interactions, such as mutualisms based on trait matching, may generate conflicting selective pressures that constrain species diversification. We used individual-based simulations to explore how different types of mutualism affect adaptive diversification. A magic trait was assumed to simultaneously mediate mate choice, intraspecific competition, and mutualisms. In scenarios of intimate, specialized mutualisms, individuals interact with one or few individual mutualistic partners, and diversification is constrained only if the mutualism is obligate. In other scenarios, increasing numbers of different partners per individual limit diversification by generating stabilizing selection. Stabilizing selection emerges from the greater likelihood of trait mismatches for rare, extreme phenotypes than for common intermediate phenotypes. Constraints on diversification imposed by increased numbers of partners decrease if the trait matching degree has smaller positive effects on fitness. These results hold after the relaxation of various assumptions. When trait matching matters, mutualism-generated stabilizing selection would thus often constrain diversification in obligate mutualisms, such as ant–myrmecophyte associations, and in low-intimacy mutualisms, including plant–seed disperser systems. Hence, different processes, such as trait convergence favoring the incorporation of nonrelated species, are needed to explain the higher richness of low-intimacy assemblages—shown here to be up to 1 order of magnitude richer than high-intimacy systems.

Keywords: assortative mating, disruptive selection, magic traits, trait complementarity, stabilizing selection.

* Current address: Center for Ecological Research, Kyoto University, 2-509-3 Hirano, Otsu, Shiga 520-2113, Japan.

† Corresponding author; e-mail: prguima@usp.br.

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Introduction

Frequency-dependent intraspecific competition can generate disruptive selection within a population, favoring rare extreme phenotypes and promoting sympatric speciation (Rosenzweig 1978). Speciation as a result of intraspecific competition for resources also depends on assortative mating (in which individuals mate preferentially with mates similar to themselves) within ecologically diverging subpopulations (Dieckmann et al. 2004). The notion that disruptive selection caused by frequency-dependent competition can lead to speciation if associated with nonrandom mating has been formalized under the theoretical framework of adaptive diversification (Doebeli 2011). Studies on wild populations support critical assumptions of adaptive diversification models, such as the commonness of disruptive selection (Kingsolver et al. 2001; Bolnick and Fitzpatrick 2007) and of traits that are under natural selection and that also affect mate choice (“magic traits”; Servedio et al. 2011). On the other hand, adaptive diversification can often be constrained by conflicting forces, such as stabilizing selection caused by biotic interactions (Thompson 2005). Investigating scenarios of conflicting selection is thus a further step to deepen our understanding of how different types of ecological interactions shape adaptive diversification (Doebeli and Dieckmann 2000).

Organisms participate in several different types of interspecific interactions. These interactions exert potentially conflicting selective pressures, and their joint impact may shape diversification (Siepielski and Benkman 2009). Indeed, opposing selective pressures on the same trait exerted by different types of ecological interactions may be a ubiquitous phenomenon shaping phenotypic evolution and diversification (Strauss and Irwin 2004). The development of integrative frameworks exploring the interplay between

intra- and interspecific ecological interactions is required to improve our understanding of how basic attributes of ecological interactions are connected with patterns of diversification at the community level (Fontaine et al. 2011; Jones et al. 2012). Mutualisms based on trait complementarity—that is, the functional matching between interacting species, such as the match between floral corolla depth and the length of hummingbird bills (Dalsgaard et al. 2008)—are examples of interspecific interactions that generate stabilizing selection and could counterweigh the diversifying effects imposed by intraspecific competition. Stabilizing selection emerges from trait complementarity because common intermediate phenotypes benefit more from mutualisms than do rare extreme phenotypes; the former are more likely to complement the most common local phenotypes of the other species (Thompson 2005). It is expected that this stabilizing effect will not be homogenous among different types of mutualisms because the wide variation in the natural history of mutualistic interactions should be associated with variable levels of dependence and species specificity (Bronstein 2009).

Indeed, different types of mutualisms vary in basic attributes that may affect diversification regimes. One of such attributes is the interaction intimacy, which is characterized by the degree of physiological integration and by the levels of physical and trophic dependence between the interacting species (Ollerton 2006; Fontaine et al. 2011). Symbiotic mutualisms are extreme cases of high-intimacy interactions in which individuals of one species (the symbiont) have an extensive physical and physiological integration with another species (the host), as exemplified by plant-*Rhizobium* associations (Bronstein 2009). As a consequence of a tight biological integration, individuals in high-intimacy systems tend to interact with few individuals of the other species during their lifetimes (Guimarães et al. 2007; Pires and Guimarães 2013). In contrast, seed dispersal systems illustrate low-intimacy mutualisms in which individuals of the interacting species have a low degree of biological integration and physical dependence (Ollerton 2006). Organisms involved in low-intimacy mutualisms may interact with many interspecific individuals during their lifetimes, as occur in interactions between plants with diverse seed dispersal strategies and generalist seed dispersers (Herrera 1995). Although interaction intimacy at the individual level is not necessarily correlated to specialization at the species level, there are well-known cases in which high interaction intimacy is correlated to high specialization, as occur in mutualisms between sea anemones and associated species of anemonefishes (Ricciardi et al. 2010). Conversely, low interaction intimacy at the individual level is often correlated to low specialization at the species level, as illustrated by generalized pollinators and generalist-pollinated plants (Waser 1996).

Another feature of mutualistic interactions that can affect diversification regimes is the extent to which trait matching affects fitness. In nature, the degree of the positive impact of trait matching on fitness is highly variable. For instance, in organisms involved in intimate associations, mismatched individuals that are unable to perform mutualistic interactions may even be excluded from the mating pool, as occurs in associations between ants and myrmecophytes (Fonseca and Ganade 1996; Fonseca 1999). Similarly, the fitness consequences of mutualistic interactions between self-incompatible plants and specialized pollinators may be highly dependent on trait complementarity (Anderson and Johnson 2008; Thompson et al. 2013). However, phenotype matching may be less important in low-intimacy interactions between species involved in interspecific cooperative hunting (Minta et al. 1992; Bshary et al. 2006).

Here, we used individual-based simulations to assess how the interplay between mutualistic interactions and intraspecific competition affects adaptive diversification. We focused on mutualisms in which trait complementarity between the interacting species plays a role in the fitness outcomes of the interaction (Bascompte and Jordano 2007). In nature, reciprocal fitness benefits commonly favors trait complementarity in various mutualistic systems, from pollination to plant protection by ants (Thompson 2005; Anderson and Johnson 2008; but see Anderson et al. 2010 for different mechanisms resulting in trait mismatches between mutualistic species). We thus incorporated mutualisms characterized by trait complementarity into a scenario of adaptive speciation. In doing so, we assumed that a magic trait mediates mate choice and intraspecific competition and also affects mutualistic interactions (Bhattacharyay and Drossel 2005). For example, body size works as a magic trait in various taxa (Servedio et al. 2011) and is often involved in mutualistic trait complementarity, as exemplified by fitness advantages to ant queens whose body sizes match the sizes of available domatias of myrmecophytes (Fonseca 1999). Furthermore, two or more genetically correlated traits, one involved in divergent selection and other in assortative mating, can work as a magic phenotype that also mediates mutualistic interactions. For example, in Darwin finches (*Geospiza* spp.), beak morphology (which affects song patterns) and body size are considered a magic phenotype (Servedio et al. 2011). The same traits may mediate mutualisms in at least seven sympatric *Geospiza* species that are known to act as effective seed dispersers (Guerrero and Tye 2009).

We designed two simulation experiments to investigate how different types of ecological interactions at the individual level affect the diversification patterns observed at the species level. These simulation experiments encompass distinct scenarios for the interplay between the di-

versifying effects generated by intraspecific competition and the stabilizing effects of mutualisms. In a first simulation experiment, we investigated species diversification in the case of an intimate, specialized association in which individuals have few mutualistic partners and the interaction has a high impact on fitness. Specifically, we explored the effects on diversification imposed by the fates of individuals that remain without any mutualistic partner. We contrasted simulations in which individuals unable to perform mutualistic interactions persist in the mating pool (as in nonobligate mutualisms) to simulations in which they are removed from the population and thus are unable to reproduce (as in obligate mutualisms). In a second simulation experiment, we explored the effects imposed by different types of mutualisms on diversification. To simulate different types of mutualisms, we varied two interaction attributes associated to the interaction intimacy: (i) the number of different individual partners with which individuals interact and (ii) the effect of the degree of phenotype matching on fitness.

The Model

We used individual-based models (IBMs) to simulate phenotypic evolution in a pair of free-living species, A and B , which are reciprocally involved in mutualistic interactions. Both species reproduce sexually in discrete, nonoverlapping generations. The individuals of each species are characterized by magic traits z_A and z_B , which mediate intra- and interspecific ecological interactions and influence mate choice. The initial values of z_A and z_B are assigned by sampling from Gaussian distributions with means \bar{z}_A and \bar{z}_B and standard deviations σ_A and σ_B , respectively. During a given time step, individuals (i) face environmental stabilizing selection (which excludes selective pressures imposed by competition and mutualism), (ii) experience intraspecific competition, (iii) engage in mutualistic interactions, (iv) reproduce, and die. We defined N_A as the number of individuals in species A or of all species derived from A and N_B as the number of individuals of species B or of all species derived from B . The same numbers of individuals $N_A = N_B$ are born at each time step. To simulate populations at the carrying capacity, N_A and N_B are constant over time, implying intraspecific competition is relevant to ecological dynamics. We later relax these assumptions. Further details are given below.

Stabilizing Selection

Stabilizing selection accounts for all selective pressures on traits z_A and z_B imposed by the environment, excluding those exerted by intraspecific competition and mutualism. Any given individual i of a species K (with K being A , B , or the

species originating from A or B) displaying the phenotype z_{K_i} has a survival probability $P_{\text{surv}}(z_{K_i})$, defined as

$$P_{\text{surv}}(z_{K_i}) = \exp[-\gamma(z_{K_i} - \theta_K)^2], \quad (1)$$

where θ_K is the phenotype of species K favored by stabilizing selection and γ is degree of sensitivity of that individual to stabilizing selection, which is equal for A and B . For a fixed value of z_{K_i} , as γ increases, $P_{\text{surv}}(z_{K_i})$ decreases from 1 (no selection) to approximately 0 (strong selection). To simulate environment-induced mortality, we randomly assign a number, $r_{z_{K_i}}$, sampled from a uniform distribution between 0 and 1, to each individual i . Individual i dies if $r_{z_{K_i}} > P_{\text{surv}}(z_{K_i})$ (Yoder and Nuismer 2010).

Intraspecific Competition

We assume that conspecific individuals with similar phenotypes ($z_{K_i} = z_{K_j}$) compete more intensively than do more dissimilar individuals. Consequently, competition among individuals for resources that are extrinsic to the mutualistic interaction results in frequency-dependent disruptive selection. The function describing the competition between two individuals of species K with phenotypes z_{K_i} and z_{K_j} is

$$\alpha(z_{K_i}, z_{K_j}) = \exp[-c(z_{K_i} - z_{K_j})^2], \quad (2)$$

such that higher c is associated with stronger competition (Bürger et al. 2006). The function P_{comp} describes the effect of frequency-dependent intraspecific competition on individuals' mating probabilities. We assume that competition linearly reduces P_{comp} . Furthermore, in our baseline model, we assumed that the fitness components arising from ecological interactions affect only females mating probabilities (see the section "Relaxation of Assumptions" below for the alternative scenario in which ecological interactions also affects the males mating probabilities). The effect of competition on a female i of a species K is defined by

$$P_{\text{comp}}(z_{K_i}) = \frac{1 - \bar{\alpha}(z_{K_i})}{\max_p (1 - \bar{\alpha}(z_{K_p}))}, \quad (3)$$

where $p = 1, 2, \dots, N_{K_f}$. Here, $\bar{\alpha}(z_{K_i})$ is the average intraspecific competition faced by an individual i with phenotype z_{K_i} with respect to all other individuals within the population. Term N_{K_f} is the number of females within the population of the species K . The denominator of equation (3) rescales the values of $P_{\text{comp}}(z_{K_i})$ to the largest degree of intraspecific competition endured by females in the population, thus providing a proxy for the relative female fitness component arising from intraspecific competition. An equivalent relative fitness component can be computed for males in a similar way. In the baseline model, we assume that both species experience intraspecific competition. We later relax this assumption.

Mutualisms

Individuals of species *B* (or of the species derived from *B*) evaluate and select mutualistic partners of species *A* (or of the species derived from *A*), simulating common interactions between organisms that actively choose mutualistic partners (e.g., animals) and organisms being chosen (e.g., plants; Bronstein et al. 2006). Interactions are based on trait complementarity. For simplicity, we assume that higher complementarity occurs when $z_{A_i} = z_{B_j}$. Every individual *i* of species *B* interacts with a fixed number ω_{B_i} of individuals from species *A* bearing the most complementary traits. Therefore, the number ω_{A_i} of different partners with which each individual *i* of species *A* interacts is variable and defined by the attractiveness of its phenotype (z_{A_i}) to individuals of species *B* (Gómez and Perfectti 2012). The fitness component arising from the benefits gained from the mutualistic interactions for a female *i* of species *A* with phenotype z_{A_i} , $P_{\text{mut}}(z_{A_i})$, depends on the degree of trait complementarity between that female and the number ω_{A_i} of interacting interspecific individuals it encounters during its life span, as defined by the following equation:

$$P_{\text{mut}}(z_{A_i}) = \left(\frac{1 + \sum_{j=1}^{N_B} \rho_{ij} \exp[-(z_{A_i} - z_{B_j})^2]}{\max_p \left\{ 1 + \sum_{q=1}^{N_B} \rho_{pq} \exp[-(z_{A_p} - z_{B_q})^2] \right\}} \right)^\lambda, \quad (4)$$

with $p = 1, 2, \dots, N_{A_i}$ and in which $\rho_{ij} = 1$ if individual *i* interacts with individual *j* or 0 otherwise. The number of interspecific individuals interacting with the female *i* of the species *A* is thus $\omega_{A_i} = \sum_{j=1}^{N_B} \rho_{ij}$. Term N_{A_i} is the number of females within the population of the species *A*. Here the denominator rescales the values of P_{mut} , hence providing a proxy for the relative female fitness component arising from mutualistic interactions. The parameter λ measures the effect of the degree of phenotype matching on fitness. The negative effect of increased trait mismatching on fitness thus increases as λ increases. We assumed that λ varies between 0 and 1. We used $\lambda = 1$ as the maximal effect of phenotypic matching on fitness. In this case, equation (4) is similar to the equation describing the fitness consequences of phenotypic matching used in previous works (e.g., Yoder and Nuismer 2010). When $0 < \lambda < 1$, mismatched interactions are progressively less penalized under decreasing values of λ (appendix, fig. A1; appendix and figs. A1–A13 available online). If $\lambda = 0$, mutualism has no impact on the mating probability of individuals. The reproductive outcome of mutualistic interactions for a female *i* of species *B* is computed according to the same scheme.

Mate Choice, Reproduction, and Death

Each female of species *K* (with *K* being species *A* or *B* or the species derived from them) with phenotype z_{K_i} has a mating probability $P_{\text{mat}}(z_{K_i})$, determined by the reproductive penalty imposed by intraspecific competition $P_{\text{comp}}(z_{K_i})$ and the reproductive outcome of the mutualistic interaction, $P_{\text{mut}}(z_{K_i})$, as defined by

$$P_{\text{mat}}(z_{K_i}) = \frac{P_{\text{comp}}(z_{K_i}) \times P_{\text{mut}}(z_{K_i})}{\sum_{j=1}^{N_{K_i}} P_{\text{comp}}(z_{K_j}) \times P_{\text{mut}}(z_{K_j})}. \quad (5)$$

For each offspring, a parental female is sampled with replacement with a probability given by $P_{\text{mat}}(z_{K_i})$. That female mates with the male bearing the most similar trait value. The mating pair generates a single offspring individual with a trait value defined by the mean of the parental trait values plus or minus segregation variance, modeled as a random number sampled from a Gaussian distribution with mean $\bar{V}_A = 0$ and standard deviation $\sigma_{V_A} = 0.05$. All individuals die after reproducing, and their offspring become the next generation.

Number of Different Mutualistic Partners and Impact of Trait Matching on Fitness

Models of mutualisms often assume that only a single pairwise interaction between individuals occurs. Nevertheless, a variable number of individual partners may have important effects on the ecological and evolutionary dynamics of mutualisms (Guimarães et al. 2007; Gokhale and Traulsen 2012). We thus investigated the effect of partner number on adaptive diversification by varying the number of different individual mutualistic partners (ω_B) for each individual *i* of species *B*. Intimate mutualisms, such as those between ants and myrmecophytes, are cases in which individuals (a plant or ant colony) have low ω_B . In contrast, low-intimacy mutualists, such as nectarivorous insect pollinators, have large ω_B . One could expect individuals to interact with the same optimal partner multiple times because this partner provides the highest fitness benefit. However, in mutualisms among free-living species, individuals interact with multiple partners due to interspecific competition (Palmer et al. 2003), high temporal variation in partner availability (Tarayre 2007), increased predation risk when visiting the most rewarding partners (Jones 2010), and reward variability among partners, such as interindividual variability in amino acid composition of nectar within plant populations (Lanza et al. 1995).

In nature, the number of partners with which an individual interacts is variable. However, to test the effects of the number of interacting partners in a controlled way, we assumed that ω_B is fixed, meaning that all individuals of species *B* interact with the same number of different

mutualistic partners. On the other hand, individuals of species *A* have no constraints on the number of different partners with which they can interact; therefore, ω_A depends on the choice patterns of the individuals of species *B*. This difference implies an asymmetry between species regarding the number of individual mutualistic partners per individual. Asymmetry in the number of interspecific partners occurs, for example, when plants produce abundant resources that can be used by many individual animals, but each animal interacts with only a few individual plants (Bentley 1977; Weiblen 2002). Complementarily, we examined the case in which individuals of both species have constraints on the total number of partners during their lifetimes (appendix).

We also investigated the consequences for adaptive diversification of having variable impacts of the mutualism trait matching on fitness. Varying λ (eq. [4]) changes the effect of the degree of trait matching on the fitness component arising from the mutualistic interaction, thus affecting individuals' mating probabilities (fig. A1). High λ values simulate scenarios in which the degree of trait matching strongly affects the reproductive output of an individual, with mismatched individuals being highly penalized, as in the case of self-incompatible plants and specialized pollinators (Anderson and Johnson 2008). At the other extreme, minimal λ values simulate mutualisms in which the degree of trait matching has weak reproductive effects, as is likely the case for interspecific cooperative hunting, such as that between the badger *Taxidea taxus* and the coyote *Canis latrans* (Minta et al. 1992).

Simulation Experiments

We performed a sensitivity analysis (appendix) to identify the parameter combination resulting in greater species diversification. This parameter combination ($\sigma_A = \sigma_B = 0.58$, $\gamma = 10^{-3}$, $c = 0.74$) defined the baseline scenario for two simulation experiments designed to explore the hypothesis that mutualism attributes constrain adaptive diversification. In our simulations, a species was heuristically defined as any phenotypic cluster including reproductively isolated individuals that is differentiated from other phenotypic clusters by a distance of at least 0.2 units of z_k . Comparisons of species richnesses among simulations were possible because the number of emerging species reached asymptotic levels before 1,000 time steps. See the appendix for further details on species delimitation.

Experiment 1: Intimate Mutualisms, Mating Pool Composition, and Diversification

In the first simulation experiment, we modeled an intimate specialized mutualism to investigate how alternative re-

productive outcomes for individuals that fail to perform mutualistic interactions affect diversification. The first simulation group (group 1: control) modeled evolution in the absence of mutualism ($\omega_B = \lambda = 0$), with individual mating probabilities depending exclusively on P_{comp} . In groups 2 and 3, species coevolve through mutualism, defined by $\omega_B = \lambda = 1$. Therefore, in groups 2 and 3, each individual of species *B* interacts with only one mutualistic partner, and the degree of trait matching has a strong impact on its reproductive output. Individuals of species *A* may interact with an unrestricted number of interspecific individuals (ω_A). However, for low ω_B , some individuals of species *A* will not have any mutualistic interactions (appendix). Groups 2 and 3 exhibit contrasting potential reproductive consequences for individuals of species *A* that do not have any mutualistic interactions. In group 2, individuals without mutualistic partners are able to reproduce (i.e., the mutualism is not obligate). For individuals without mutualistic partners, the numerator of equation (4) is equal to 1, since in this case the summation of mutualistic trait matching effects is equal to 0. In group 3, individuals without mutualistic interactions do not survive to mate (i.e., the mutualism is obligate). We ran 50 simulation replicates in each group with $\sigma_A = \sigma_B = 0.58$, $\gamma = 10^{-3}$, $\theta_A = 0$, $\theta_B = 1$, $c = 0.74$, and $\lambda = 1$. Pairwise differences in the mean asymptotic richness between these groups were tested using Tukey's HSD test.

The asymptotic species richnesses of control simulations (group 1: $\omega_B = 0$, $\bar{S}_A = 7.5 \pm 1.1$ species; $\bar{S}_B = 7.3 \pm 0.94$ species) are not significantly different from the richnesses observed in simulations of nonobligate mutualisms (group 2), in which individuals that fail to engage in interspecific interactions remain in the mating pool ($\omega_B = 1$, $\bar{S}_A = 7.2 \pm 0.92$ species; $\bar{S}_B = 7.05 \pm 1.05$ species; Tukey's HSD test, $Q = 2.36$, $P > .050$ for S_A and S_B , $n = 150$ simulations). However, when individuals of species *A* that fail to engage in mutualistic interactions are not permitted to mate (obligate mutualisms, group 3), the mean asymptotic species richnesses are significantly lower than those of control simulations ($\omega_B = 1$, $\bar{S}_A = 6.75 \pm 0.91$ species; $\bar{S}_B = 6.60 \pm 0.83$ species; Tukey's HSD test, $Q = 2.36$, $P < .001$, $n = 150$ simulations).

Experiment 2: The Effect of Different Types of Mutualism on Diversification

To explore the effects of different types of mutualism on diversification, we simulated 30 scenarios (with 20 replicates for each) defined by the number of different individual partners, ω_B (1, 2, 4, 8, 16, 32, 64, 128, 256, and 512) and by the magnitude of the impact of trait matching on fitness, λ (0.01, 0.1, and 1). Since the maximum value of ω_B is relatively low, we assumed that, for the range of

ω_B values considered here, the net benefits of mutualism do not saturate under increased number of partners. Preliminary analyses showed that for $\omega_B > 4$ all individuals of species *A* interact (appendix, fig. A7). We investigated the scenario in which individuals of species *A* without mutualistic partners are able to mate (as in group 2 in experiment 1), controlling the potential confounding effect of removing individuals from mating pool in simulations in which $\omega_B < 4$ (experiment 1). To control for the effects of mutualisms on diversification, we ran 20 additional simulations without mutualistic interactions ($\omega_B = \lambda = 0$). In each replicate, we counted the asymptotic richness of species derived from *A* (S_A) and *B* (S_B) after 1,000 time steps. We tested the effects of ω_B and λ on diversification using general linear models (GLMs) in which the values of ω_B and λ were log transformed to improve normality and homoscedasticity.

Both the number of individual mutualistic partners (ω_B) and the effect of the degree of trait matching on fitness (λ) affect species richness emerging from adaptive diversification (figs. 1, 2). Richness is inversely correlated with the number of different individual partners, ω_B . Indeed, S_A (GLM, $F_{2, 617} = 322.4$, $P < .001$, $n = 620$) and S_B (GLM, $F_{2, 617} = 263.4$, $P < .001$, $n = 620$) decrease as individuals of species *B* interact with a greater number of mutualistic partners (i.e., with increasing ω_B values). An increased impact of the degree of trait matching on fitness (increasing λ) also constrains species diversification (GLM, $F_{2, 617} = 185.7$ and $F_{2, 617} = 309.9$, for S_A and S_B , respec-

tively; $P < .001$, $n = 620$; fig. 2). When trait matching has a strong impact on the mating probabilities of individuals ($\lambda = 1$), a higher number of different individual mutualistic partners (ω_B) leads to decreased phenotypic variance (fig. 1) and also progressively constrains the emerging species richness (fig. 2A). A decrease in diversification with the increase in the number of individual mutualistic partners (ω_B) is also observed when the impact of trait matching on mating probabilities (λ) is decreased by an order of magnitude (fig. 2B). Although species richness is lower when $\omega_B \geq 64$, extreme ω_B values do not impose additional constraints on species diversification at lower λ values (fig. 2B). The effect of ω_B on richness disappears when λ is very small (0.01) because the effect of the mutualism is not sufficient to impose the necessary stabilizing selection (fig. 2C).

Relaxation of Assumptions

We explored the dynamics of the model under the relaxation of different assumptions about mutualistic interactions, selection regimes, and population densities. Relaxing these assumptions allowed us to explore the dynamics of the IBM under alternative biological scenarios.

Phenotype Matching

In experiments 1 and 2, individuals of species *B* always choose a number ω_B of mutualistic partners that represent

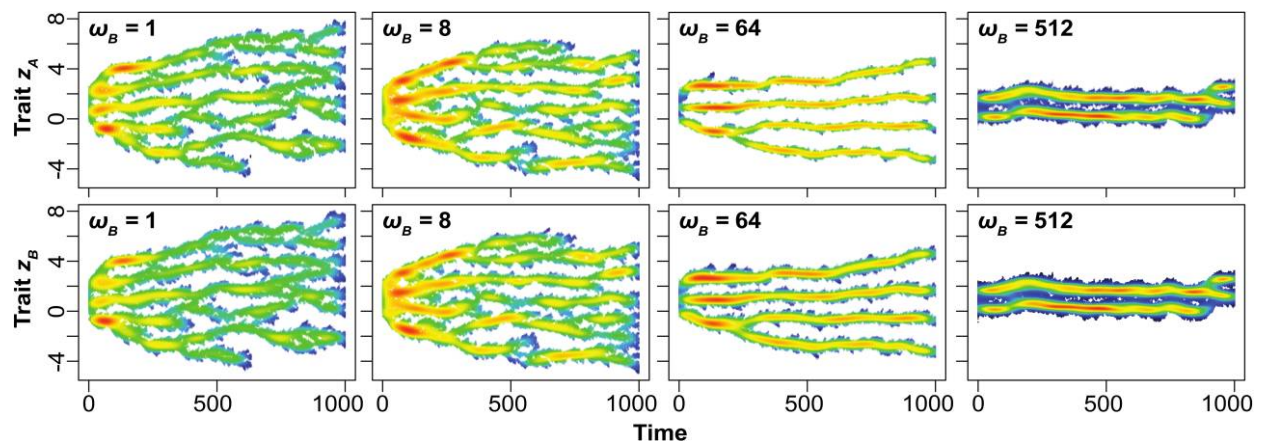


Figure 1: Mutualism attributes affect adaptive diversification. We consider sympatric populations of two mutualistic species, *A* and *B*, both experiencing intraspecific, frequency-dependent competition for resources. Mutualistic interactions are based on phenotypic matching, and the same trait mediates intraspecific competition and female mate choice. Individuals of species *B* choose a limited number (ω_B) of mutualistic partners, whereas individuals of species *A* have no constraints on the number of different interspecific individuals with which they interact. Here, the impact of mutualism trait matching on fitness is high because $\lambda = 1$ (see eq. [4]). Females mate assortatively, and the product of the penalty imposed by intraspecific competition and the profit gained from mutualism defines individual mating probabilities. The color temperature indicates the density of individuals, ranging from high (hot colors) to low (cool colors). $N_A = N_B = 600$, $\sigma_A = \sigma_B = 0.58$, $\gamma = 10^{-3}$, $\theta_A = 0$, $\theta_B = 1$, $c = 0.74$.

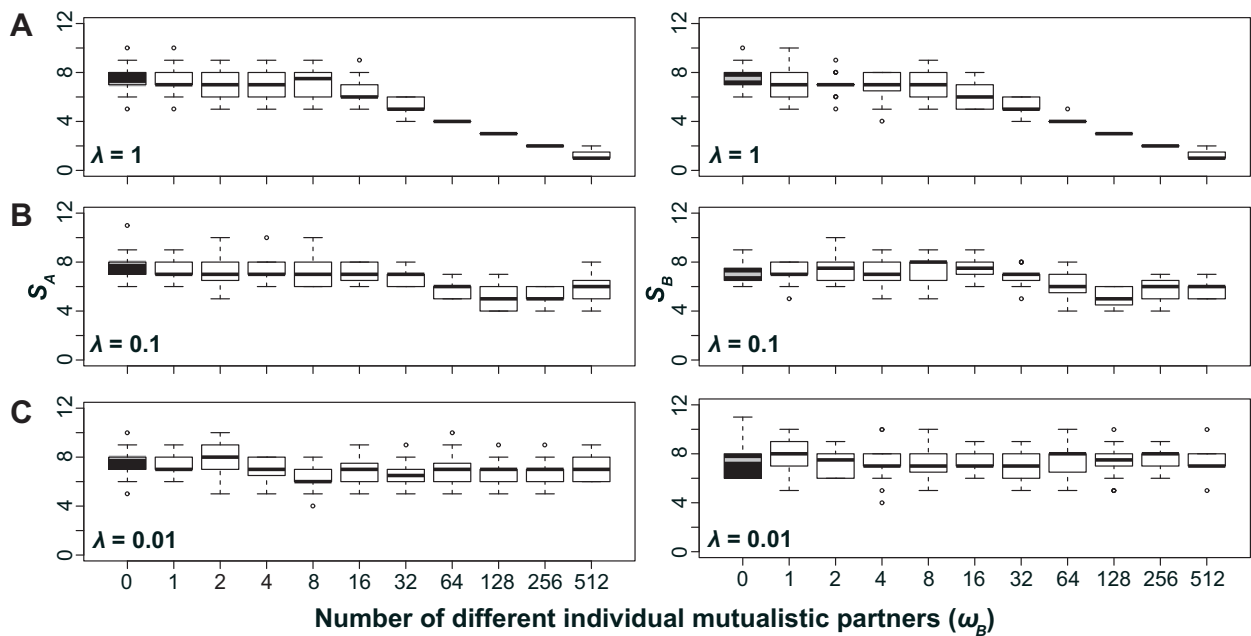


Figure 2: Species richnesses achieved in the simulation experiment under variable mutualisms. Asymptotic species richnesses obtained in simulations with different mutualism attributes, namely, the number of different interspecific partners of individuals of species B (ω_B) and the impact of mutualistic trait matching on the individual mating probabilities (λ). Each panel shows species richnesses under variable ω_B values for mutualisms in which the degree of trait matching has a high impact on fitness (A), has an intermediate impact on fitness (B), or has a low impact on fitness (C). Twenty replicate simulations were performed for each scenario. The horizontal lines inside the boxes indicate the medians. The boxes encompass the interquartile range, and error bars indicate the smallest (lower) and largest (upper) nonoutliers. Outliers are plotted separately as points.

the best trait matches in the entire population of species A . Therefore, individuals are assumed to be able to evaluate all existing interspecific individuals. We relaxed this unrealistic assumption by performing a simulation in which each individual i of species B randomly chooses its mutualistic partner(s) from a subset of the population of A formed by individuals within a certain phenotype range. This range is defined for each individual i of species B as a percentage ψ of individuals of species A bearing the traits most similar to its trait Z_{B_i} . We ran 20 replicates for each combination of four ψ values (15%, 30%, 45%, 60%) with four ω_B values (1, 8, 32, 64) and $\lambda = 1$. We then used a GLM to estimate the effects of ψ and ω_B in this set of simulations. This alternative phenotype-matching scheme leads to a more intense constraint on diversification due to mutualism than is observed in experiments 1 and 2. The lower the subset of potential partners ψ , the lower the final species richness (GLM, $F_{2, 317} = 135.2$ and $F_{2, 317} = 176.6$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 320$). Nevertheless, the constraints imposed by the number of partners (GLM, $F_{2, 317} = 87$ and $F_{2, 317} = 80.4$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 320$) still hold after relaxing the assumption of best-fit phenotype matching in our baseline model.

P_{mut} Computation

Similar constraining effects of increasing the number of mutualistic partners on diversification arise if the impact of mutualism on reproduction does not depend on the quantity of individual mutualistic partners but rather on how beneficial the interactions are on average, that is, if P_{mut} is computed using the mean instead of the sum to aggregate the effect of interaction events in equation (4) (appendix).

Males under Selective Pressures Arising from Ecological Interactions

In our baseline model, only females have mating probabilities defined by two fitness components arising from ecological interactions, P_{comp} and P_{mut} (eqq. [3]–[5]). Therefore, for males, mating probabilities are determined exclusively by females' choice, since each breeding female chooses a male with the most similar trait value as its sexual partner. In order to investigate if our model results hold if males are also affected by the selective pressures generated by ecological interactions, we explored the effects of the number of individual mutualistic partners, ω_B ,

and of the impact of the degree of trait matching on fitness, λ , when the male mating pool is formed by a percentage (50% or 25%) of the original male subpopulation. The probability that a male will remain in the population to form the mating pool is computed following equations (3)–(5), but with N_{A_m} and N_{K_m} , the number of males within the population of the species A and K , replacing N_{A_f} and N_{K_f} respectively. We found that the effects of ω_B and λ in these simulations in which ecological interactions also affect males' survival and in our baseline model are qualitatively the same (appendix).

*Both Species with Limited Numbers of
Individual Mutualistic Partners*

We relaxed the assumption that only species B has constraints on the number of mutualistic partners with which individuals interact. Increasing the number of interacting partners also reduces diversification if both species are constrained in the number interacting individuals ($\omega_A = \omega_B$; appendix).

Only One Species under Disruptive Selection

When we relaxed the assumption that both species are experiencing disruptive selection, similar effects of ω_B and λ on diversification emerge when only species B faces disruptive selection caused by intraspecific competition (appendix). However, diversification is even more constrained when species A , which is the one being chosen within the mutualistic interaction, experiences disruptive selection due to intraspecific competition (appendix).

Asymmetric Population Sizes

We explored the diversification dynamics when the population sizes of species A and B are asymmetric. We used values of $N_B < N_A$, leading to increased competition among individuals of species A for mutualistic partners. We ran 20 replicates for three values of N_B (75, 150, 300) and four ω_B values (1, 8, 32, 64) under $\lambda = 1$ and $N_A = 600$. The population size of species B (N_B) affects the diversification of both species. Lower N_B is associated with a lower final richness of species derived from species B (GLM, $F_{2,237} = 168.3$ and $F_{2,237} = 327.7$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 240$). This result is a consequence of stronger stabilizing selection imposed by the competition among individuals of A for the fewer individuals of B . After controlling for the effect of N_B , the number of partners, ω_B , still imposes constraints on diversification similar to those detected in experiment 2 (GLM, $F_{2,237} = 187.1$ and $F_{2,237} = 97.6$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 240$).

Stochastic Variation of Population Sizes

To relax the assumption of constant population sizes, we modeled two different scenarios for population variation across time. In the first model, the overall numbers of individuals N_B and N_A varied independently and randomly around a mean. At each generation, the number of individuals is the initial population size ($N_A = N_B = 600$) summed to a parameter e with a value sampled from a Gaussian distribution with a mean of 0 and a standard deviation of $\sigma_{P(K)}$. This stochastic variation in population size had a small but significant effect, constraining diversification (GLM, $F_{2,237} = 5.7$ and $F_{2,237} = 0.6$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 240$). After controlling for the effect of population fluctuations, the number of mutualistic partners, ω_B , still had an important effect of constraining diversification ($F_{2,237} = 467.2$ and $F_{2,237} = 297.7$ for \bar{S}_A and \bar{S}_B , respectively; $P < .001$, $n = 240$). In a second scenario, we modeled more drastic variations in the overall number of individuals. From initial population sizes $N_{0(A)} = N_{0(B)} = 600$, the number of individuals $N_{t(K)}$ of a species at generation t is $N_{t-1(K)} + V$, where V is a percentage of $N_{t-1(K)}$. At any given generation, V is randomly assigned to be positive or negative. We contrasted the diversification dynamics under two values of ω_B (8, 32) and V (1%, 5%). In the resulting population dynamics, population sizes are uncorrelated, independently assuming values much lower or much higher than the original sizes. Despite such severe variation in population sizes, the general trend of decreased species diversification following increasing ω_B persisted (appendix).

Discussion

The interplay between disruptive and stabilizing selection shapes the phenotypic variability of natural populations (Bürger 2002). These selective forces are thought to be equally common in nature (Kingsolver et al. 2001) and are likely to act together within populations (Felsenstein 1979). They thus have the potential to jointly affect the selective regimes underpinning the adaptive origin of new species. Indeed, conflicting selection pressures can affect the microevolutionary processes involved in phenotypic divergence and speciation (Lankinen and Larsson 2009). Our simulations indicate that, even under strong disruptive selection and assortative mating, mutualisms based on phenotype matching can constrain diversification in different ways.

First, mutualisms in which individuals have few partners can constrain diversification if the interaction determines which individuals are able to mate. Extreme phenotypes thus become less frequent in the mating pool even if they benefit from low intraspecific competition. Direct depen-

dence on mutualism for reproduction occurs when species rely on interspecific interactions for mating, as in the case of self-incompatible plants in relation to pollinators (Bond 1994). Additionally, in obligate mutualisms, individuals that fail to interact with partners suffer severe reproductive consequences. For example, ant queens that are excluded in the competition for a limited number of myrmecophyte plants are unable to survive and reproduce (Fonseca 1999). In other cases, plant individuals with maladapted myrmecophilic traits are attacked by herbivores and fail to reach reproductive size due to a lack of protection by ants (Léotard et al. 2008). Our analyses show that the emerging species richness depends on the population sizes of interacting species. Indeed, larger population sizes increase rates of adaptive diversification (Stevens et al. 2007). We thus expect that the magnitude of the constraints imposed on diversification by the exclusion of individuals without mutualistic interactions from the mating pool would be lower for species with larger population sizes.

Second, increasing the number of different mutualistic partners constrained species-level diversification even when we relaxed our biological assumptions regarding how phenotype matching occurs, population densities, and the number of species under disruptive selection. The generality of these results suggests that stabilizing selection may often inhibit the diversification caused by disruptive selection in mutualisms involving many individual partners. Here, the sources of stabilizing selection are increased suboptimal matches arising from an increased number of different individual mutualistic partners. As the number of different interacting individuals increases, the stabilizing selection imposed by the escalating effects of trait mismatch on extreme phenotypes progressively counterbalances the disruptive selection caused by intraspecific competition. If rare extreme phenotypes need many different mutualistic partners, they face a higher degree of interaction mismatches than do common intermediate phenotypes. Furthermore, the stabilizing effect is amplified as more players become involved in mutualistic interactions and a larger proportion of the extreme phenotypes of the population are affected by suboptimal choices; the magnitude of such mismatches also increases (fig. 3).

The effects of intraspecific competition favoring extreme phenotypes may thus be reduced or even suppressed when mutualistic interactions involving multiple players are an important factor affecting fitness. Our simulations also show that increasing values of ω_B , the number of different mutualistic partners with which the individuals of species *B* interact, constrain the overall phenotypic variance within a clade, leading to progressively lower phenotypic distances among the emerging species. Decreased phenotypic distances between similar, related species may lead to strong interspecific competition, constraining intrapopulation

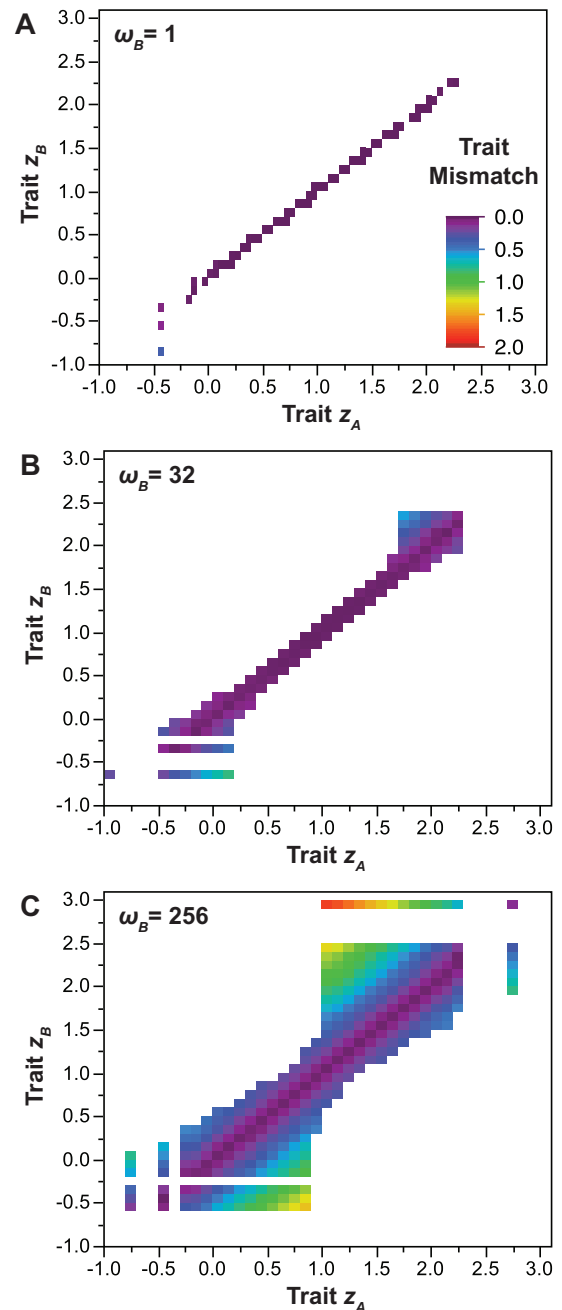


Figure 3: Phenotype mismatches in mutualistic interactions in which individuals of species *B* have different numbers of mutualistic partners (ω_B). Terms z_A and z_B are the values for the traits mediating the mutualism in species *A* and *B*, respectively. Panels show the distribution of trait mismatches for all interaction events within a time step t , when individuals of species *B* have a low number of different mutualistic partners (*A*), intermediate number of different mutualistic partners (*B*), or a high number of different mutualistic partners (*C*). The color gradient from purple (0) to red (2.00) represents increasing trait mismatch in interaction events. In all panels, $t = 1$, $\lambda = 1$, and $N_A = N_B = 600$.

variation. Thus, we hypothesize that selective pressures imposed by low-intimacy mutualisms add strength to the constraints imposed by interspecific competition to intrapopulation variation (Bolnick et al. 2003), potentially affecting ecological and evolutionary dynamics. For example, decreased phenotypic distances among the emerging species would impose sufficient interspecific competition to constrain species' niche width and avoid the continuous formation of extreme phenotypic clusters.

Our second simulation experiment suggests that adaptive diversification would emerge in mutualisms in which the degree of trait matching strongly affect fitness (high λ) and each individual interacts with few partners (low ω_B)—even if only one species experiences the disruptive selection regime. Conversely, the simulations predict that adaptive diversification in low-intimacy mutualisms (large ω_B) will often be constrained by strong stabilizing selection generated by phenotype mismatch in extreme phenotypes, counteracting the effect of disruptive selection. However, low-intimacy mutualistic assemblages hold up to 1 order of magnitude more species than high-intimacy assemblages in nature (fig. 4 and appendix). The departure between the patterns observed in nature and the predictions derived from our model provide insights on the role of different evolutionary processes in shaping the diversity of mutualistic assemblages.

Our model predicts that the species-rich assemblages formed by low-intimacy mutualisms are not likely to be a result of adaptive diversification promoted by intraspecific competition. As a consequence, other evolutionary processes are needed to explain the observed patterns of species richness in these systems. One possibility is that in low-intimacy mutualisms, which often form species-rich networks, a highly interactive set of generalist species drives the evolution of the whole assemblages (Bascompte et al. 2003; Guimarães et al. 2011) and favor, through convergence and complementarity of traits, the incorporation of new nonrelated species into the assemblages (Thompson 2009). Therefore, low-intimacy mutualistic systems can become species-rich by aggregating nonrelated species over time (Ramírez et al. 2011). Another nonexclusive hypothesis is that some low-intimacy mutualisms, such as seed dispersal by vertebrates, may indirectly promote diversification by providing predictable resources and broadening geographic ranges. For example, species of mutualistic primates have large geographic ranges, which favor high geographic speciation rates and low extinction rates (Gómez and Verdú 2012).

On the other hand, our first simulation experiment does predict constraints to diversification in high-intimacy, obligate mutualisms (when individuals that fail to interact with mutualistic partners are excluded from the mating pool), such as pollination by flower parasites. Comple-

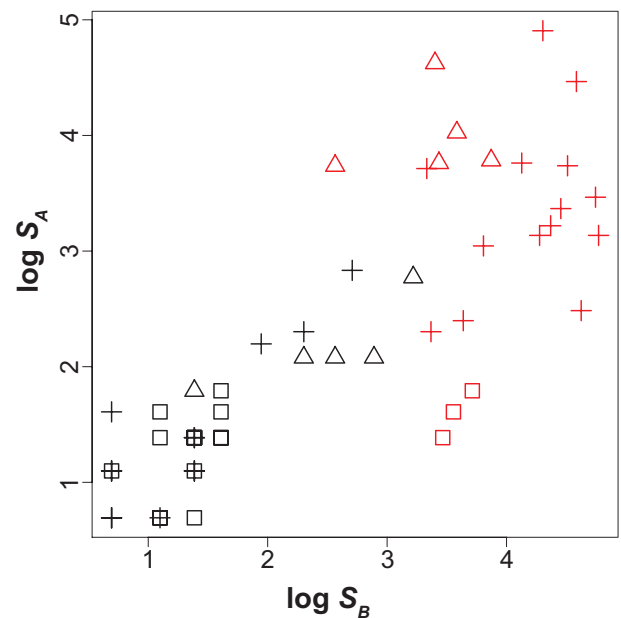


Figure 4: Species richness in natural mutualistic assemblages. Terms S_A and S_B indicate species richness for each group of mutualistic species (e.g., plants/pollinators). Black and red symbols indicate high- and low-intimacy mutualisms, respectively. Symbols represent different types of mutualism. Squares depict marine mutualisms (black = obligate interactions between anemonefish and their host species of sea anemones; red = cleaning mutualisms between cleaner species of shrimps and fishes and their fish clients). Triangles indicate ant-plant mutualisms (black = specialized protection mutualisms between ants and myrmecophyte plants; red = generalized ant-plant mutualisms, including protection mutualisms and ant-mediated seed dispersal). Crosses show pollination mutualisms (black = highly specialized, obligate interactions between plants and pollinating seed parasites; red = interactions between animal pollinators and flowering plants).

mentarily, other processes can also constrain species diversification in these high-intimacy mutualisms, leading to relatively species-poor systems. First, high-intimacy mutualisms can be more prone to species extinctions and coextinctions (Dáttilo 2012), which can contribute to lower local species richnesses despite a higher diversification potential. Additionally, high-intimacy mutualisms are embedded in tight coevolutionary processes involving complex sets of integrated traits (Thompson et al. 2013). As a consequence, high-intimacy systems are taxonomically constrained and have a very low potential to pull in nonrelated species into the interaction network. Indeed, events of addition of outside taxa to high-intimacy assemblages are few, even over tens of millions of years (Pellmyr 2003; Kawakita and Kato 2009).

The generality of our predictions rely on the major assumption that magic traits are involved in mutualistic interactions. An in-depth examination of this assumption

requires more data on phenotypic selection and mating preferences in mutualisms. However, there is empirical evidence suggesting that magic traits can be found in intimate interactions, such as size-based assortative mating in anemonefish subjected to intense intraspecific competition (Hattori 2012). Moreover, the costs of assortative mating often constrain sympatric speciation (Bolnick and Fitzpatrick 2007). These costs may be reduced in highly intimate mutualisms as female choosiness becomes more viable due to a reduction of risks (e.g., predation) and search time. Moreover, the greater morphological, physiological, and behavioral integration between mutualistic partners found under intimate specialized mutualisms may favor the occurrence of automatic magic traits—the case in which prezygotic reproductive isolation by assortative mating is a by-product of trait evolution under disruptive selection (Servedio et al. 2011). Indeed, assortative mating is likely to occur when individuals mate in time- or space-defined groups. For example, divergence in the timing of oviposition in relation to host phenology may initiate speciation in pollinating seed-parasitic globeflower flies (Ferdy et al. 2002) and the cospeciation of fig wasps and their hosts (Kiestler et al. 1984). Conversely, the strength of assortative mating may be constrained in low-intimacy mutualisms due to viability costs (Rymer et al. 2010). Weak assortative mating may thus be an additional limiting factor constraining adaptive diversification in low-intimacy systems.

In conclusion, we argue here that conflicting selection pressures generated by intra- and interspecific ecological interactions have important consequences for our understanding of adaptive diversification. We have shown a general effect in which stabilizing selection generated by mutualistic trait complementarity constrains the adaptive diversification caused by intraspecific competition. These results hold under various biological assumptions and represent a first step in the study of conflicting selection during diversification in mutualistic assemblages. However, although trait complementarity is common (Dalsgaard et al. 2008), other interaction mechanisms, such as trait differences (Yoder and Nuismer 2010) or the interaction mechanisms assumed in game theoretical models of mutualisms (e.g., Gokhale and Traulsen 2012) are also recurrent in mutualisms and may impose alternative selection regimes that will interact with the disruptive selection caused by intraspecific competition to produce distinct outcomes in terms of species diversity. Investigating the effects of such alternative interaction mechanisms on adaptive diversification is a promising line of research addressing the broader challenge of describing the fundamental role of competition in the evolution of mutualisms (Jones et al. 2012).

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A creamy-bellied thrush (*Turdus amaurochalinus*) feeding on fruits of the bangalow palm (*Archontophoenix cunninghamiana*) in the Atlantic Forest of Brazil. Photo credit: Pedro Jordano.