

Reconciling Santa Rosalia: Both Reproductive Isolation and Coexistence Constrain Diversification

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ABSTRACT: Understanding patterns of diversification necessarily requires accounting for both the generation and the persistence of species. Formal models of speciation genetics, however, focus on the generation of new species without explicitly considering the maintenance of biodiversity (e.g., coexistence, the focus of ecological studies of diversity). Consequently, it remains unclear whether and how new species will coexist following a speciation event, a gap limiting our ability to understand the rate-limiting controls of diversification over macroevolutionary timescales. To connect coexistence and speciation theory and assess the relative importance of ecological versus genetic constraints in diversification events, we develop a deterministic, three-locus, population-genetic model that includes a skewed distribution of available resources (to generate variation in fitness differences), frequency-dependent competition, and assortative mating. Both ecology and genetics play vital and interacting roles in shaping initial speciation events and long-term eco-evolutionary outcomes. Ecological constraints are especially important when fitness differences are large and competition remains strong among dissimilar phenotypes. Ephemeral species can occur in our model and are typically lost because of competitive exclusion, a result demonstrating that species persistence may serve as the rate-limiting control of long-term diversification rates. More broadly, our model adds evidence that the unification of ecological and evolutionary (including genetic) perspectives on biodiversity is needed to predict large-scale patterns.

Keywords: asymmetric selection, competitive exclusion, ephemeral speciation model, MacArthur resource competition model, sympatric speciation.

Introduction

Both ecologists and evolutionary biologists seek to understand patterns of biodiversity. Despite this shared goal,

many researchers in these fields take dramatically different perspectives on the topic. Ecologists have long focused on understanding how niche availability and overlap facilitate coexistence between competing species. Nearly 70 years ago, G. Evelyn Hutchinson asked, “why are there so many species?” He proposed that niche availability allows speciation, and limited niche availability ultimately constrains species richness (Hutchinson 1959). In the past decades, modern coexistence theory has formalized how coexistence is the outcome of two competing forces: niche differences (i.e., differential resource usage) facilitate coexistence, whereas fitness differences (i.e., competitive dominance) prevent coexistence (Chesson 2000).

Speciation geneticists, however, have taken a different perspective. Twenty years after Hutchinson’s “homage to Santa Rosalia” (Hutchinson 1959), Joseph Felsenstein provided a seminal contribution to our understanding of diversification, which he set up in direct contrast to the ecological perspective. Felsenstein (1981) argued that coexistence only sets an upper bound on species richness and showed how recombination provides a powerful homogenizing force to prevent speciation. This work steered the next 40 years of microevolutionary speciation research to focus heavily on genetic constraints on the evolution of reproductive isolation (Butlin et al. 2021).

Speciation genetics has thus developed largely in isolation from ecological perspectives on diversity. Macroevolutionary studies, however, have a long history of seeking to incorporate ecological perspectives into the study of diversification. Numerous authors have discussed the role of ecological competition as a driver of extinction, which potentially causes diversification rates to decline with species richness (Mayr 1965; MacArthur and Wilson 1967; MacArthur 1969; Rosenzweig 1975; Sepkoski 1978). More recent work has focused on understanding the role of

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ecological processes in shaping phylogenetic patterns (Weir and Schluter 2007; Cavender-Bares et al. 2009; Maruvka et al. 2013; Pennell and Harmon 2013; Nuismer and Harmon 2015; Cutter and Gray 2016; Drury et al. 2016; Li et al. 2018; Aristide and Morlon 2019). For example, patterns of persistence resulting from the degree of ecological differentiation of new species are sufficient to generate a wide range of phylogenetic patterns, such as either increasing or decreasing lineage accumulation rates (McPeck 2008).

The importance of ecological persistence has largely failed to gain traction within speciation genetics, however, leaving much work to be done to synthesize our understanding of the processes that generate biodiversity (speciation) with the processes that maintain biodiversity (coexistence). In particular, the mechanism by which species form or become extinct is often the provenance of speciation genetics or community ecology, respectively, and is rarely made explicit in macroevolutionary models (Sepkoski 1978; Harvey et al. 2019; Louca and Pennell 2020). The failure of speciation genetics to incorporate ecological perspectives on biodiversity may thus drive a disconnect between the microevolutionary study of speciation and macroevolutionary patterns. Evidence of this disconnect comes from macroevolutionary net diversification rates in *Drosophila* and birds being independent of the rate at which clades evolve reproductive isolation (Rabosky and Matute 2013). Furthermore, despite sexual selection's potential role in reproductive isolation, evidence regarding whether it facilitates speciation in macroevolutionary studies is equivocal and depends on methodological and taxonomic choices (Kraaijeveld et al. 2011).

These disconnects may follow from microevolutionary studies focusing heavily on the build-up of reproductive isolation, even though this need not be the rate-limiting control of the speciation process (Dynesius and Jansson 2014; Harvey et al. 2019). To contribute to long-term diversification, population splitting and the build-up of reproductive isolation must be followed by the persistence of reproductively isolated lineages (Dynesius and Jansson 2014; Rabosky 2016). Matching evidence that neither initial splitting (Singhal et al. 2022) nor the build-up of reproductive isolation (Rabosky and Matute 2013) predicts macroevolutionary diversification rates, the ephemeral speciation model hypothesizes that species persistence is the rate-limiting control of diversification (Rosenblum et al. 2012). This would follow from populations often splitting and becoming isolated but rarely persisting, either for ecological (e.g., competitive exclusion or stochastic extinction) or genetic (e.g., hybrid collapse) reasons.

Both theory (e.g., Liou and Price 1994; Kirkpatrick 2000; Servedio and Bürger 2014; Irwin 2020; Irwin and Schluter 2022) and studies of natural populations (Seehausen et al. 1997; Taylor et al. 2005; Walters et al. 2008; Frei et al. 2022)

have shown that hybrid collapse is one possible outcome of secondary contact of sister species. However, these results are typically not discussed in connection with the ephemeral speciation model, and it remains unclear whether and under what conditions species fail to persist for ecological reasons. Filling these gaps and formalizing the conceptual ephemeral speciation model would help to unify ecological and evolutionary perspectives on biodiversity and, because persistence has been largely neglected in microevolutionary studies of speciation (Dynesius and Jansson 2014; Harvey et al. 2019), also help to integrate micro- and macroevolutionary studies of speciation.

A better understanding of the interactions between coexistence and speciation could also lead to advances in community ecology. In his influential synthesis, Vellend (2016) considers speciation to be one of four fundamental processes of community ecology, but our understanding of speciation's role in shaping ecological communities remains limited. Understanding whether speciation can produce two species not capable of coexisting could shed light on the origin of nonequilibrium ecological communities, an important step given that naturally co-occurring species pairs often appear unable to stably coexist in reciprocal invasion tests (see supplement 2 in Simha et al. 2022). Existing ecological models that consider speciation sometimes make unrealistic assumptions about the speciation process that can alter conclusions (Kopp 2010; Rosindell et al. 2010). Thus, assessing coexistence in a robust genetic model of speciation that explicitly includes the build-up of reproductive isolation is an important frontier for community ecology.

The importance of integrating community ecology with speciation genetics for advancing our understanding of biodiversity has been recognized (Gavrilets 2014; Hubert et al. 2015; Germain et al. 2021; Porretta and Canestrelli 2023), and some microevolutionary studies have begun this integration. Irwin and Schluter (2022) demonstrated an important role of genetics for species persistence in a model of secondary contact by showing that insufficient assortative mating is more frequently the cause of failure to coexist than is insufficient niche differences. Their model, however, does not consider the build-up of reproductive isolation but rather assesses the mechanism behind reproductively isolated populations failing to persist. Work that does explicitly model the build-up of reproductive isolation with the potential for competitive exclusion has demonstrated that species persistence is a crucial component to understanding diversification (Aguilée et al. 2013). These models often simulate adaptive radiation, where dramatic changes in niche availability over the course of the simulation lead to a sharp separation between a phase of rapid growth in species richness and a phase dominated by extinction (Gavrilets and Vose 2005; Aguilée

et al. 2018). The focus on adaptive radiation and species-rich communities in these studies makes it hard to understand the mechanism driving persistence or extinction in specific speciation events and for single species pairs.

Here, we assess how diversification dynamics play out in a minimal model that allows for both the initial evolution of reproductive isolation and the possibility of competitive exclusion and hybrid collapse. Specifically, we develop and analyze a deterministic genetic model that includes dynamic population density and a skewed resource distribution to vary fitness differences. We focus on a simple proof-of-concept model to serve as a foundation on which to build intuition (Gavrilets 2003; Servedio et al. 2014) on the interplay of speciation and coexistence as well as the relative importance of ecological versus genetic constraints on diversification.

Overall, outcomes of the model are often idiosyncratic, with both ecology (e.g., the distribution of resources and the strength of resource competition) and genetics (e.g., the genetic architecture and potential to hybridize) playing vital roles in shaping eco-evolutionary outcomes—both during initial speciation events and in whether species will persist. As one example, we find that competitive exclusion can follow a speciation event, suggesting that speciation can give rise to nonequilibrium ecological communities and providing proof of concept that persistence may serve as a rate-limiting control of macroevolutionary net diversification rates. We also demonstrate that genetic constraints are the primary drivers of eco-evolutionary outcomes when assortative mating is weak and competition kernels are narrow, whereas ecological constraints dominate when the resource distribution is broad or highly skewed (leading to large possible fitness differences) and competition kernels are broad. Our results make clear that a fuller view of the speciation process requires integrating ecological perspectives on niche availability and coexistence with microevolutionary perspectives on genetics and reproductive isolation.

Model

Model Overview

We begin by providing a nontechnical overview of the model and its assumptions before formally developing the equations in the next section. We broadly follow Bürger et al. (2006) in developing a three-locus, diallelic, diploid, discrete-time model. To serve as a bridge between models on the genetics of speciation and models on ecological coexistence, we include both explicit genetics with recombination as well as density-dependent ecological competition with dynamic population density.

Our model includes 27 possible genotypes, each of which can have a unique phenotype. Initially, the system

undergoes frequency-independent stabilizing selection. Loosely, the function controlling stabilizing selection can be thought of as setting the carrying capacity or distribution of available resources for any possible phenotype. In contrast with past approaches, we include the possibility that this distribution is asymmetric (skewed), which alters the possible fitness differences between the phenotypes. Selection also includes a density-dependent component. We assume that more similar phenotypes compete more strongly with a maximum competition coefficient of 1 for identical phenotypes. Sexual reproduction occurs through phenotype matching based on a “magic trait” (Gavrilets 2004; Servedio et al. 2011); females prefer to mate with males that have a phenotype most similar to their own and use the trait involved in ecological competition to choose their mate. We assume strict polygyny with no costs to choice, meaning that all females have equal reproductive success. Offspring are produced using the standard assumptions of Mendelian inheritance.

Model Description

Genetics. Each individual has a single (one-dimensional) phenotype that controls its ecology and mating prospects. We assume an individual’s phenotype is controlled by three diallelic loci L_1 , L_2 , and L_3 . Locus L_i confers a phenotypic effect of ℓ_i , such that individuals with the first allele have their phenotype decreased by $-\ell_i$ and individuals with the second allele have their phenotype increased by $+\ell_i$. We assume absence of dominance, such that a heterozygote with one copy of each allele at a given locus is exactly intermediate to the homozygotes. Loci are additive, such that one must simply sum the phenotypes conferred by each locus in order to calculate an individual’s phenotype. Based on these assumptions, we can, without loss of generality (Bürger et al. 2006), scale the overall range of phenotypes to be bounded in absolute value by 0.5. Thus, individuals that are homozygous for the first allele at each locus have phenotype -0.5 , individuals that are homozygous for the second allele at each locus have phenotype 0.5 , and the phenotypic effects ℓ_i simply set the relative contribution of each locus to an individual’s phenotype. We explain our choices of the ℓ_i in the “Analysis” section below.

Competition. Ecological dynamics and competition are based on a MacArthur-style consumer-resource model (MacArthur and Levins 1967). Resources are treated implicitly, and an individual’s phenotype is assumed to control its access to and ability to exploit resources (Ranjan and Klausmeier 2022). This results in frequency-independent stabilizing selection that we assume is controlled by the fitness function

$$\mathcal{S}(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{1}{2\sigma^2}\left(x + \frac{k\sigma\sqrt{2/\pi}}{\sqrt{1+k^2}}\right)^2\right] \times \text{Erfc}\left[-\frac{k}{\sigma\sqrt{2}}\left(x + \frac{k\sigma\sqrt{2/\pi}}{\sqrt{1+k^2}}\right)\right]. \quad (1)$$

The term $\mathcal{S}(x)$ is the probability density function of the skew normal distribution (a skewed unimodal distribution; fig. 1*a*) with mean 0, shape parameter k , and scale parameter σ . Setting the shape and scale parameters directly does not permit clear interpretation, so we parameterize stabilizing selection by setting the variance V and skewness K of \mathcal{S} and calculating k and σ using

$$V = \left(1 - \frac{2k^2}{\pi(1+k^2)}\right)\sigma^2, \quad (2)$$

$$K = \frac{k^3(4-\pi)\sqrt{2}}{(k^2(\pi-2) + \pi)^{3/2}}. \quad (3)$$

In calculating the fitness of a genotype, we scale \mathcal{S} to have a maximum of 1 (which must be done numerically). We refer to this scaled distribution as S and show how S changes with variance and skewness in figure 1*a*: as skewness increases, negative phenotypes begin to have an advantage over positive phenotypes until, in extreme cases, selection becomes directional.

Past approaches typically assume that S is normal (has zero skewness; i.e., $k = K = 0$; Dieckmann and Doebeli 1999; Bürger et al. 2006), although skewness emerges naturally from mechanistic consumer-resource models (Abrams et al. 2008) and has been observed in both phylogenetically and functionally diverse examples (Mountford 1968; Boag and Grant 1984; Weis and Abrahamson 1986; Yoshimura and Shields 1995). Importantly, as seen in figure 1*a*, skewness alters fitness differences between phenotypes and thus may have important implications for coexistence and evolutionary ecology (Abrams et al. 2008; Urban et al. 2013). In particular, with a symmetric fitness function and competition kernel with maximum of 1 (the case considered previously; Dieckmann and Doebeli 1999; Bürger et al. 2006), evolutionary branching (where a single population evolves to a fitness peak, at which point frequency-dependent disruptive selection splits the population in two) cannot deterministically result in fitness differences and the newly formed species are thus guaranteed to ecologically coexist.

Although frequency-independent stabilizing selection limits the competitive ability of each genotype, frequency-dependent competition can also alter competitive hierarchies. Consistent with past approaches, we assume that more similar phenotypes compete more strongly, with

$$\alpha(x, y) = \exp[-c(x - y)^2] \quad (4)$$

controlling the strength of competition between individuals having phenotype x and phenotype y (fig. 1*b*). Note that the maximum strength of competition of 1 is achieved when a phenotype competes with itself ($\alpha(x, x) = 1$) and that competition affects both phenotypes equally ($\alpha(x, y) = \alpha(y, x)$). The parameter c controls the width of the competition kernel. When c is small, competition is strong even between dissimilar phenotypes (the competition kernel is broad), but when c is large, competition is strong only for similar phenotypes and dissimilar phenotypes compete only weakly (the competition kernel is narrow; fig. 1*b*). The frequency-dependent nature of competition becomes clear by computing the average strength of competition experienced by a given phenotype x ,

$$\bar{\alpha}(x) = \sum_{y \in P} \alpha(x, y)f(y), \quad (5)$$

where $f(y)$ is the frequency of phenotype y in the system and the sum is taken over the set of all possible phenotypes P .

Mating. Females mate assortatively, preferring males that have the same phenotype as their own. The probability that a female with phenotype x accepts a male with phenotype y as her mate upon encounter is

$$\Pi(x, y) = \exp[-a(x - y)^2]. \quad (6)$$

The parameter a controls a female's preference strength. With high a females strongly prefer to mate with matching males, whereas with low a females are more accepting of males with different phenotypes (fig. 1*c*).

We assume that females choose their mates through a series of random male encounters, which results in mating also being frequency dependent. We also assume that all females will eventually obtain one mate (there is no cost to choice) and have equal mating success. Let genotype g have frequency $p(g)$ and phenotype x_g . Then the probability that a given female with genotype g ultimately mates with a male with genotype h is

$$Q(g, h) = \frac{\Pi(x_g, x_h)p(h)}{\sum_{z \in G} \Pi(x_g, x_z)p(z)}, \quad (7)$$

where G is the set of all genotypes. These mating assumptions generate sexual selection in males but not in females (Bürger and Schneider 2006).

Dynamics. Finally, we explain how the above assumptions lead to ecological and evolutionary dynamics. We assume that the population has an intrinsic growth rate of ρ and that κ is inversely related to the strength of density-dependent

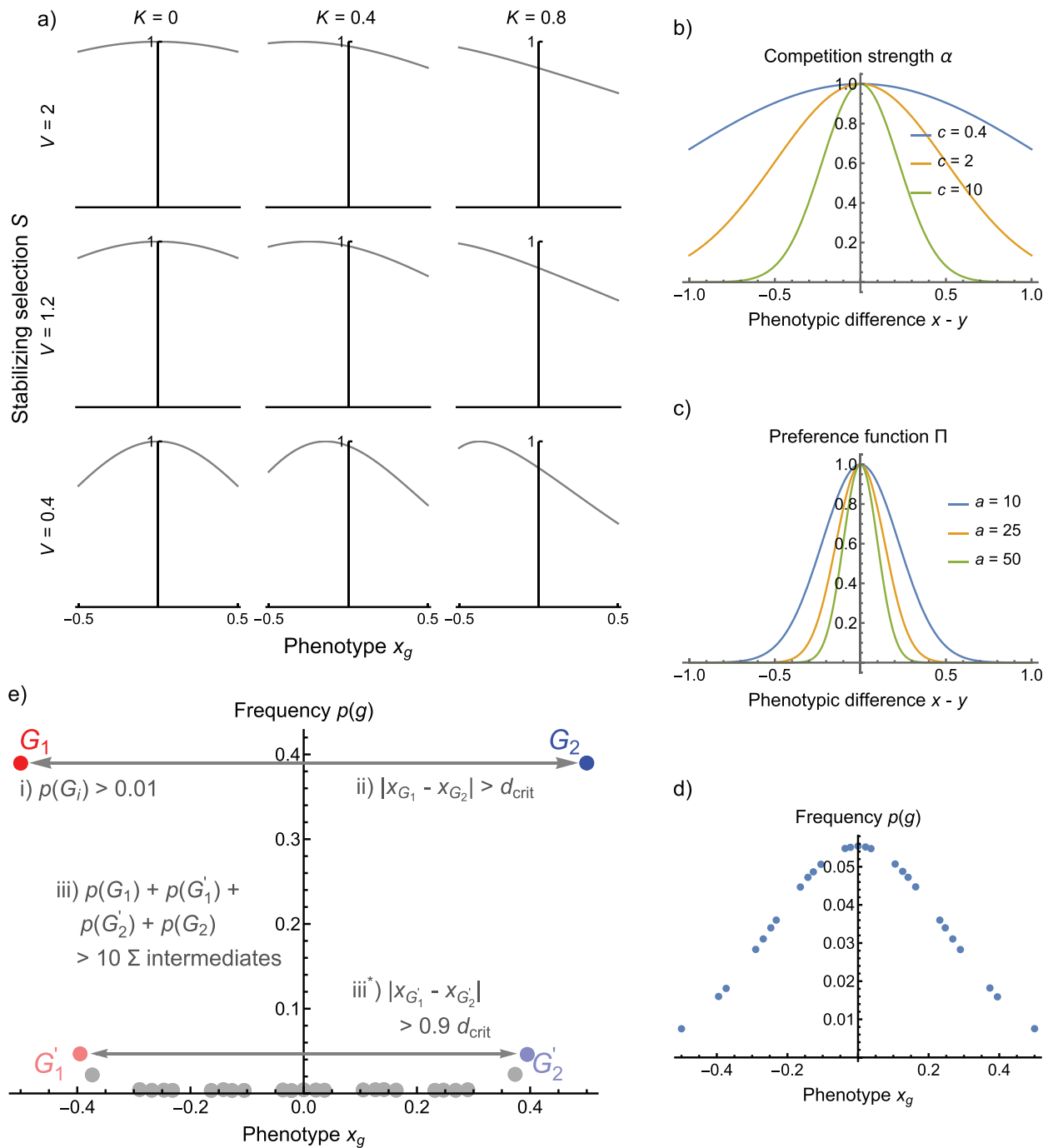


Figure 1: Overview of the model. *a*, Stabilizing selection function S plotted over a sample of possible parameters. Rows indicate different variances V , and columns indicate different skewness K . *b*, Strength of competition α for a range of competition kernel widths (see key). *c*, Preference function Π for a range of preference strengths (see key). *d*, Initial conditions (frequency $p(g)$ vs. phenotype x_i) used for the numerical iteration of the recursion equations. *e*, Quantitative criteria for speciation, with red and blue points denoting different species. Criteria i–iii are labeled on the panel; “intermediates” in iii refers to all gray circles, and iii* is given an asterisk because it is applied only when $p(G_1), p(G_2) > 0.001$.

population regulation. Let N_t be the overall density of the population at time t , such that $N_t f(x)$ is the density of individuals with phenotype x at time t . Using the model for logistic growth from Bürger et al. (2006), this results in individuals with phenotype x having absolute fitness of

$$W(x) = \left(\rho - \frac{\bar{\alpha}(x)N}{\kappa} \right) S(x). \quad (8)$$

The mean population fitness can then be calculated as $\bar{W} = \sum_{x \in G} W(x)f(x)$. We plot this realized fitness function in figures S1–S3 (figs. S1–S4, S1.1–S1.4, S3.1–S3.3, S4.1–S4.8, S5.1–S5.3, S6.1–S6.3 are available online) to demonstrate the role of both access to resources and competition. Disruptive selection is more likely with a broad resource distribution S and a narrow competition kernel α ; high skewness often results in directional selection.

Let $p_t(g)$ be the frequency of genotype g at time t . Then the genetic dynamics follow

$$p_{t+1}(g) = \frac{1}{\sum_{u,v,w \in G} p'_t(u)Q'(u,v)R(uv \rightarrow w)} \times \sum_{u,v \in G} p'_t(u)Q'(u,v)R(uv \rightarrow g). \quad (9)$$

Here, $p'_t(g) = p_t(g)W(x_g)/\bar{W}$ denotes genotype frequencies after selection, and Q' indicates that equation (7) is computed using frequencies after selection. The term $R(uv \rightarrow g)$ is the proportion of matings between parental genotypes u and v that produce an offspring with genotype g under Mendelian inheritance with diploid genetics. The initial term is simply a normalization to ensure $\sum_g p_{t+1}(g) = 1$. Finally, the population density is updated with

$$N_{t+1} = \bar{w}N_t \sum_{u,v,w \in G} p'_t(u)Q'(u,v)R(uv \rightarrow w). \quad (10)$$

Equations (9) and (10) provide a complete description of model dynamics.

Analysis

Numerical Procedure. Because of its complexity, the model is analytically intractable except for special cases, even in the absence of skew (Bürger et al. 2006). As such, we primarily rely on the numerical iteration of recursion equations. Unless otherwise specified, we iterate the model until none of the genotype frequencies change by more than 10^{-8} in one time step, at which point we treat the final genotype frequencies as the equilibrium. For most analyses, we consider initial conditions of a single broad species with a large degree of intraspecific variation (fig. 1*d*). Namely, we assume that $p_0(g) \propto \exp[-8x_g^2]$. To avoid having perfect symmetry in initial conditions, we add a small random number drawn from a normal distribution with mean 0

and standard deviation 0.001 to each frequency, which must be scaled so that $\sum_{g \in G} p_0(g) = 1$. We use a fixed random seed to ensure that initial conditions are identical for every run.

Parameters. Similar to the procedure above, we use a fixed seeded random set of phenotypic effects. Initially, we assume that $\ell_1 \approx 0.21$, $\ell_2 \approx 0.25$, and $\ell_3 \approx 0.54$, although we explore the effect of genetic architecture below. These numbers can be interpreted as the proportions of the phenotype controlled by loci 1–3, respectively (see fig. 1*d* for possible phenotypes).

We focus our analysis on the shape of the stabilizing selection function, which largely controls external ecological conditions (e.g., distribution of resources) in our model, using a wide range of $0.2 \leq V \leq 2$ and $0 \leq K \leq 0.9$ (fig. 1*a*) in steps of 0.2 and 0.1, respectively. We consider a broad range of competition kernel widths ($c = 0.4, 2, 10$; fig. 1*b*). Our widest competition kernel results in all attainable phenotypes competing strongly, whereas our narrowest competition kernel results in only very similar phenotypes competing appreciably. Finally, we consider preference strengths of $a = 10, 25$, and 50 (fig. 1*c*). Note that even $a = 10$ corresponds to strong preferences (fig. 1*c*), as is necessary for sympatric speciation in the model (Bürger et al. 2006). Throughout, we assume $\rho = 2$ and $\kappa = 10,000$.

Definition of Speciation. Finally, we must develop a quantitative measure of speciation. We primarily use a definition of speciation developed by Bürger et al. (2006), which they found largely agreed with the “manual” assignment of speciation from inspecting the final genotype distribution as well as with an unrelated linkage disequilibrium–based measure of speciation. Broadly, our definition of speciation requires that (i) species are sufficiently common, (ii) species have sufficiently different phenotypes such that hybridization occurs rarely, and (iii) intermediate phenotypes are sufficiently uncommon such that the species exchange genes through hybrids only infrequently (fig. 1*e*).

First, we identify potential species by finding peaks in the genotype distribution whose frequency is at least 0.01 (fig. 1*e*, blue and red). This satisfies condition i and makes it likely that any species is sufficiently common to be detected and influence the evolutionary ecology of the system.

Let G_1 and G_2 be the genotypes of two adjacent peaks with frequency >0.01 (i.e., there is no genotype conferring a phenotype intermediate to x_{G_1} and x_{G_2} whose frequency is also >0.01). To satisfy condition ii above, we further require that $|x_{G_1} - x_{G_2}| < d_{\text{crit}} = (-\ln(0.01)/a)^{1/2}$ (fig. 1*e*, top gray line). It can be shown from equation (6) that the preceding inequality is exactly the condition for which a G_1 female accepts a G_2 male as her mate with probability

<0.01 upon encounter (i.e., hybridization is rare). Note that d_{crit} is a decreasing function of a , such that stronger preferences allow for “good species” to be closer together in phenotype space.

The final set of conditions ensure that genes also cannot be exchanged between G_1 and G_2 through intermediaries (condition iii). Assume without loss of generality that $x_{G_1} < x_{G_2}$. Define G'_1 to be the genotype whose phenotype is directly adjacent to G_1 in the direction of G_2 (i.e., $x_{G_1} < x_{G'_1}$; fig. 1e, pink). Analogously, define G'_2 to be the genotype whose phenotype is directly adjacent to G_2 in the direction of G_1 (i.e., $x_{G_2} > x_{G'_2}$; fig. 1e, light blue). The terms G'_1 and G'_2 are of interest in the case that the species containing G_1 and G_2 includes intraspecific variation, so that for G_1 and G_2 to be in separate species, G'_1 and G'_2 must also be reproductively isolated. Furthermore, let I be the set of all genotypes i such that $x_{G_1} < x_i < x_{G_2}$. Then for G_1 and G_2 to be considered separate species, we require that $p(G_1) + p(G_2) + p(G'_1) + p(G'_2) > 10 \sum_{i \in I} p(i)$; that is, intermediaries are in sufficiently low frequency that genes are rarely exchanged between G_1 and G_2 through them (iii in fig. 1e). As an additional constraint (iii*), in cases where $p(G'_1), p(G'_2) > 0.001$ (i.e., there is some degree of intraspecific variation), we require that $|x_{G'_1} - x_{G'_2}| < 0.9d_{\text{crit}}$ (fig. 1e, bottom gray line), which helps to ensure that more similar morphs of the two species (when they exist) rarely hybridize. Only when all of the quantitative criteria described above are met do we consider G_1 and G_2 to be members of different species. The criteria can be applied successively to adjacent peaks to allow for the possibility of more than two species in the model.

As with any quantitative definition of speciation, there is, of course, some degree of arbitrariness to our choices. However, we confirmed that qualitative conclusions drawn throughout are not highly sensitive to small changes in the speciation criterion (app. S1; apps. S1–S6 are available online).

Asexual Model

To help disentangle the relative importance of ecology and genetics in the speciation process, we develop an analogous model, identical in every way except that reproduction is clonal (the “asexual model”). The asexual model only includes viability selection from the full model considered above (henceforth, the “sexual model”); thus, it removes any influence of sexual reproduction, hybridization, and recombination. The nature of reproduction in the asexual model means that each genotype can be considered a unique species. The asexual model is explained in detail in appendix S2.

We use the asexual model to uncover the dynamics predicted when only ecological forces are acting. In par-

ticular, we can use the asexual model to analytically determine whether ecological coexistence is possible between a pair of genotypes assuming that they reproduce clonally and hence cannot hybridize (app. S2). As we show below, these “asexual coexistence” and “asexual exclusion” outcomes will be key to understanding mechanisms driving dynamics with sexual reproduction.

Results

Conditions Favoring Speciation

We begin by considering only the sexual model. Figure 2 provides an overview of the model’s results. Two conclusions that have been drawn previously are apparent. First, strong assortative mating (high a) facilitates speciation (fig. 2). Assortative mating is required to prevent frequent hybridization leading to homogenization (Felsenstein 1981; Bürger et al. 2006). Second, a narrow stabilizing selection function (i.e., narrow resource supply distribution, low V) prevents speciation (fig. 2). A sufficiently broad distribution of resources ensures that species are capable of persisting in a wide range of phenotype space (MacArthur and Levins 1967; Meszén et al. 2006). In other words, this leads to more usable niche space.

Speciation Does Not Guarantee Coexistence. Darker blue squares in figure 2 are of special interest because they correspond to cases where speciation occurs but only a single species persists at equilibrium. In appendix S3, we assess why one of the species fails to persist by determining whether coexistence occurs in the asexual model. If coexistence is possible, then we conclude that hybridization is necessary for the failure to persist; otherwise, we conclude that competitive exclusion is sufficient for the failure to persist.

In most (47 of 54) cases, we find that competitive exclusion is the reason that all but one species fail to persist (app. S3). This provides an explicit demonstration that speciation (even sympatric) does not imply stable ecological coexistence. We refer to cases of speciation occurring only to have a single species at equilibrium as “ephemeral speciation.” Importantly, ephemeral speciation is not a case of partial divergence failing to complete: it corresponds to a speciation event initiating and completing (i.e., two “good species” form) only to have a failure of persistence follow (most often because of competitive exclusion). Thus, from the perspective of modern coexistence theory, sympatric speciation events may produce species pairs that have insufficient niche differences to make up for the degree of fitness differences.

Figure 3a–3d (first row) shows example dynamics from a case of ephemeral speciation (video S1; videos S1–S9 are

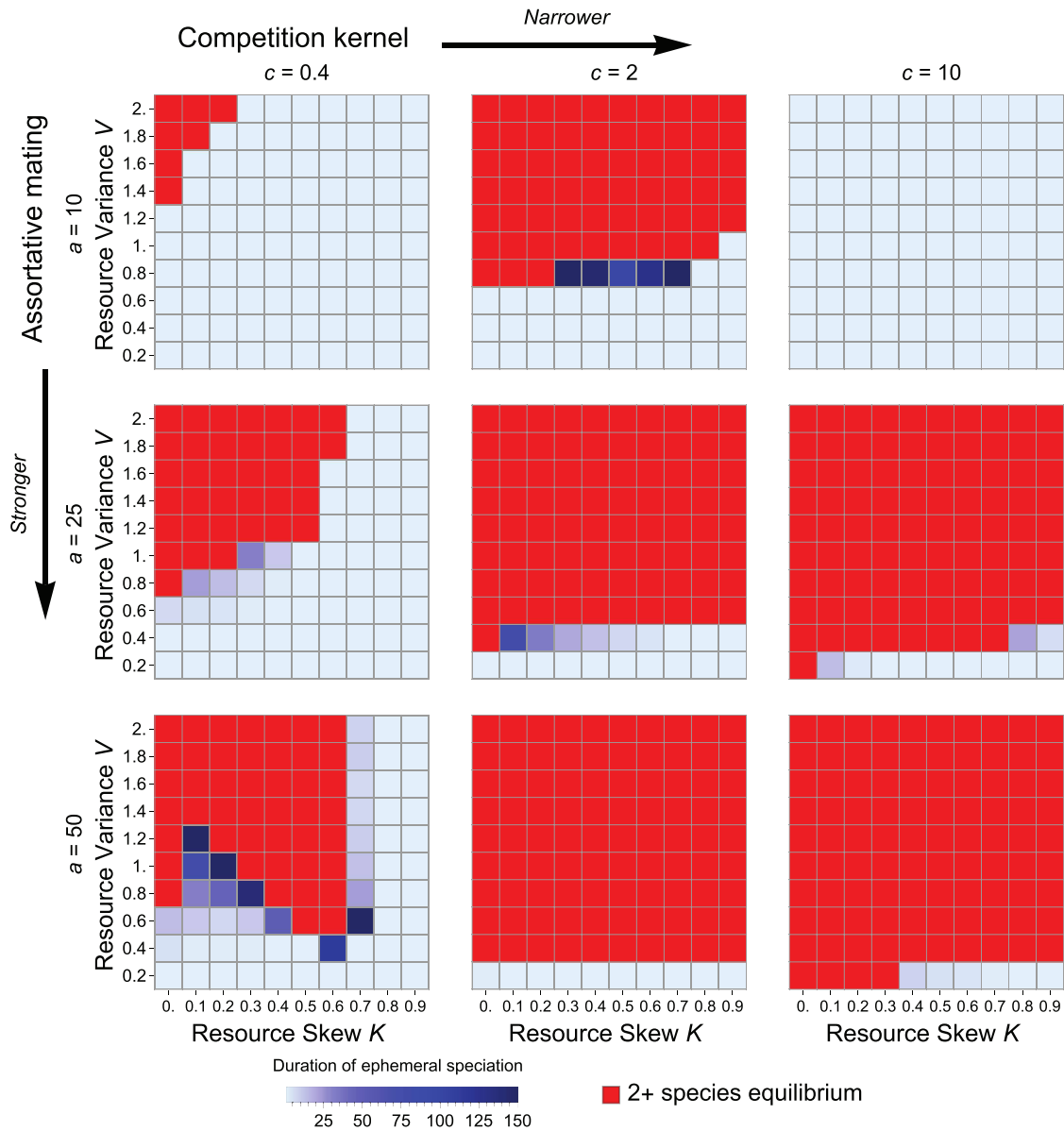


Figure 2: Equilibrium outcomes from the model. Rows correspond to different levels of preference strength a (strongest preference on bottom), and columns correspond to different competition kernel widths c (narrowest competition kernels on right). Each panel is a 10×10 grid of variance in S , V (y -axis) and skewness in S , K (x -axis). Red indicates at least two species at equilibrium (and thus speciation), and blue indicates only one species at equilibrium. The shading of blue represents how many time steps for which there were separate species before only one species persisted (see key). Darker colors correspond to a longer duration of ephemeral speciation; the lightest shade of blue indicates that speciation never occurred.

available online). Initially, two species form that are far apart in phenotype space and capable of ecological coexistence (i.e., coexistence is stable between the most common two phenotypes in the asexual model; fig. 3*b*, red and black). However, in the middle of phenotype space, competition becomes quite weak because of nearby phenotypes reaching a very low frequency, allowing for a third species to rise in frequency (fig. 3*c*, blue). This third species increases in fre-

quency not because of hybridization (the probability that the extreme species mate with one another upon encounter is $<10^{-20}$); rather, it increases in frequency because of favorable ecological conditions (weak competition and near-peak frequency-independent fitness). However, the intermediate species is able to competitively exclude the others (fig. 3*c*, 3*d*) and thus is the only species present at equilibrium (fig. 3*d*).

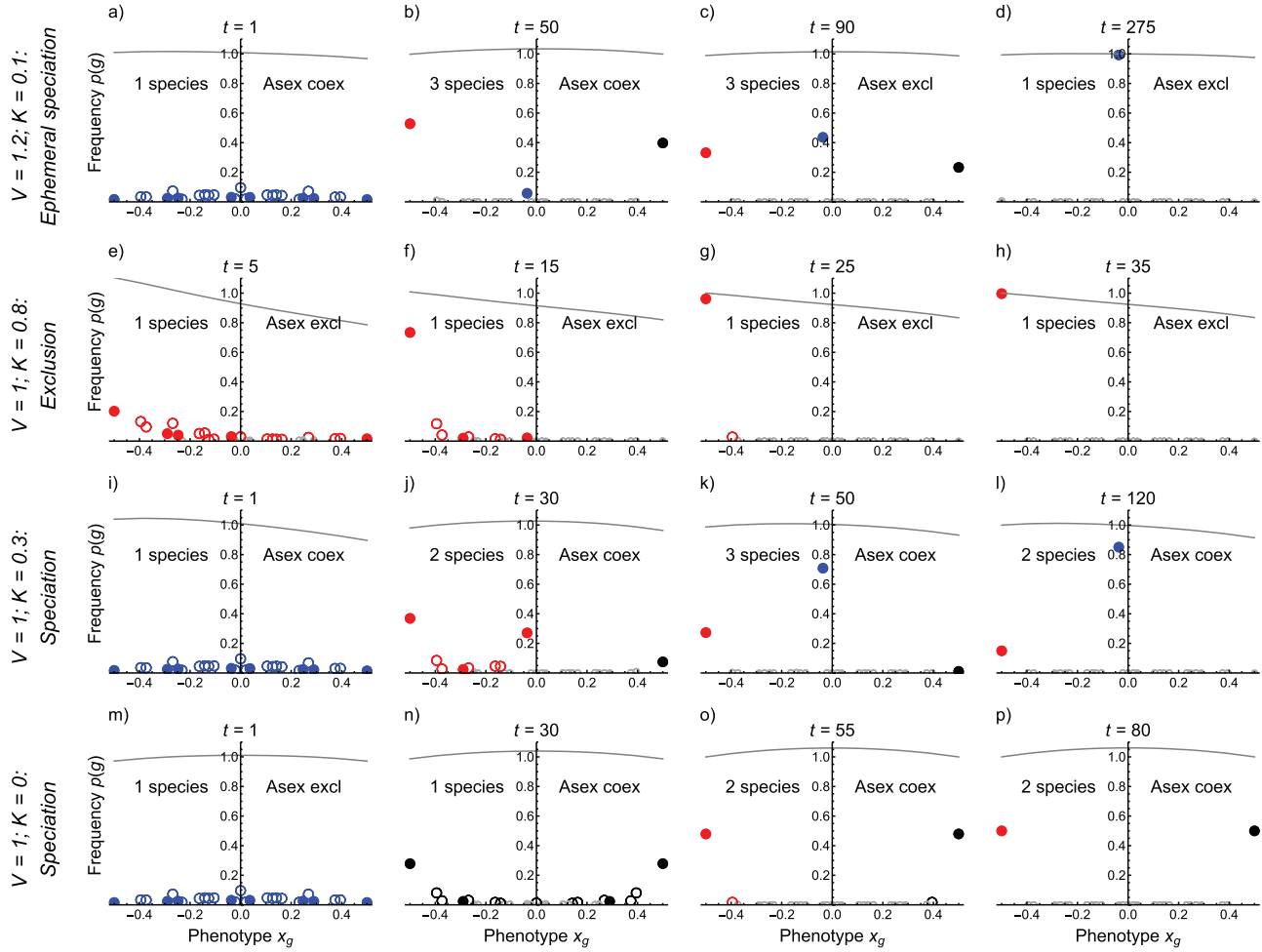


Figure 3: Snapshots of the genotype distribution, exploring the causes of speciation and/or exclusion. Each row corresponds to one set of parameters shown through time (parameters listed to left of row; time step shown above each panel; $a = 50$, $c = 0.4$). The gray line corresponds to the realized fitness of each phenotype $W(x_g)$ (eq. [8]). The number of species at the given time step is listed to the left of the y-axis, with phenotypes having frequency greater than 0.01 color coded on the basis of the most common phenotype of the species that they belong to (red = extreme negative; blue = intermediate; black = extreme positive). Phenotypes that are rare (frequency less than 0.01) are always colored gray for convenience, although in reality these might be best characterized as belonging to one of the species. Heterozygous genotypes are shown as open circles, and homozygous genotypes are shown as closed circles. If the two most common phenotypes are capable of coexisting in the asexual model, then “Asex coex” is labeled to the right of the y-axis; otherwise, “Asex excl” is labeled when one of the two most common phenotypes excludes the other in the asexual model (see app. S2 for more details). Animations of these time series are shown in videos S1–S4. We show these results not because they are generalizable/insensitive to parameters but rather because they provide clear examples of the eco-evolutionary drivers in various situations: *a–d*, ephemeral speciation with loss driven by competitive exclusion; *e–h*, strong skew in the resource distribution preventing speciation; *i–l*, stable coexistence with low skew between relatively similar species; *m–p*, stable coexistence with no skew between highly divergent species.

Skewed Resource Distributions Disfavor Speciation. A novel result from our model is that skewed selection tends to disfavor sympatric speciation (fig. 2). Especially with a broad competition kernel ($c = 0.4$; first column), speciation is rarely initiated once skew in stabilizing selection (the distribution of resources) becomes too great. Because skew results in larger maximum fitness differences in the model, this hints at the fact that the factors promoting coexistence may be similar to the factors promoting evolutionary di-

vergence. Figure 3*e–3h* (second row) shows why speciation does not occur with too high of skew (video S2). In our model, skew creates fitness differences that favor negative phenotypes (figs. S1–S3). Thus, positive phenotypes are never able to increase in frequency, despite their release from competition (fig. 3*e–3h*).

There are, however, a number of nuances regarding the role of skew in shaping equilibrium outcomes. Although we see below that these results are largely idiosyncratic

and sensitive to small parameter changes, they are still valuable to explore as case studies of interactions between ecological and genetic features of the population during the process of speciation.

Genetics plays a role in skew not universally disfavoring speciation. In the bottom left panel of figure 2 ($a = 50$, $c = 0.4$), with variances in S from 0.8 to 1.2, skew has a nonmonotonic influence on equilibrium outcomes. As explained above, with very high skew speciation is not initiated. As skew is decreased (but still high), two species form and persist at equilibrium. One example of this is seen in figure 3*i–3l* (video S3). Similar to the case of ephemeral speciation above (fig. 3*a–3d*), two species initially form followed by an intermediate third species increasing in frequency (fig. 3*j*, 3*k*). The intermediate species has a relatively large fitness advantage over the positive species, which it drives to extinction (fig. 3*k*, 3*l*). However, skew means that the fitness difference between it and the negative species is small enough that they are capable of ecological coexistence (albeit with the negative species at lower frequency; fig. 3*l*). As we saw above, with less skew the fitness difference becomes large enough that competitive exclusion results (fig. 3*a–3d*). This explains why less skew leads to fewer species at equilibrium in this case.

But why does no skew result again in two species at equilibrium in the bottom left of figure 2? Figure 3*m–3p* demonstrates that in this case an intermediate species never increases in frequency, with the two extreme phenotypes coexisting ecologically (video S4). Now, the genotypes with the highest fitnesses according to the stabilizing selection function (the distribution of resources) are in the middle of phenotype space because there is no skew to provide an advantage to individuals with negative phenotypes. However, the most intermediate phenotypes correspond to heterozygous genotypes. With strong assortative mating, individuals with this phenotype most often mate with one another. However, heterozygotes do not breed true, and only half of offspring in these matings generate individuals with the same genotype. Since homozygotes breed true, this results in an asymmetry that makes it harder for heterozygotes to increase in frequency in the sexual model. Thus, there are two extreme homozygous species present at equilibrium.

To summarize, a general trend exists with greater skew in resource distributions being less favorable for speciation, although this is not universally true (fig. 2), in part because of genetic constraints.

Competition Kernel Width Interacts with Preference Strength. This interplay between ecological and genetic constraints becomes especially clear in the final result that we highlight from figure 2: narrow competition kernels

(high c) facilitate speciation with strong assortative mating (second and third rows; $a = 25$, 50) but prevent speciation with weaker assortative mating (first row; $a = 10$). In general, narrow competition kernels are expected to lead to more disruptive selection (figs. S1–S3; Bürger 2005), which, in turn, should facilitate divergence. Why then do narrow competition kernels result in no speciation with preference strength $a = 10$ despite the fact that most ecological parameters result in speciation for a broader competition kernel ($c = 2$)? Narrow competition kernels mean that genotypes can pack more tightly into phenotype space and still coexist (Meszéna et al. 2006; Szabó and Meszéna 2006; Barabás and D’Andrea 2016). In other words, they allow for more phenotypic variation to be maintained. However, if assortative mating is too weak, then the presence of tightly packed phenotypes will result in matings between different genotypes. The result is a single species with a high degree of intraspecific variation (video S5). Thus, the interaction between preference strength a and the width of the competition kernel c demonstrates that specific ecological conditions (here, narrow competition kernels) lead to increased importance of genetic constraints on speciation (here, frequent hybridization).

Disentangling the Effect of Genetics and Ecology

A common theme above is that the origin and persistence of species is an interplay between ecological and genetic constraints, and a mechanistic understanding of outcomes requires both ecological and evolutionary perspectives. This conclusion, however, does not mean that both ecological and genetic drivers (or preventers) of speciation are always equally important. We compare the sexual and asexual models to tease apart when ecological versus genetic factors dominate.

The first comparison that we draw between the sexual and asexual models is the number of species at equilibrium. Whether the two models predict equal species richness depends on the width of the competition kernel. With broad competition kernels ($c = 0.4$), the two models typically predict the same number of species at equilibrium (fig. 4*a*). As the competition kernel narrows (larger c), the asexual model permits more and more species at equilibrium (fig. 4*a–4c*). Thus, with broad competition kernels, ecological constraints primarily drive species richness (i.e., sexual reproduction plays little role in altering the number of species in the system). However, with narrow competition kernels, genetic constraints begin to play an important role in limiting species richness (i.e., if not for sexual reproduction, many more species would persist in the system).

As we saw above, narrow competition kernels mean that phenotype space can be tightly packed with coexisting genotypes. Under asexual reproduction, this tight packing

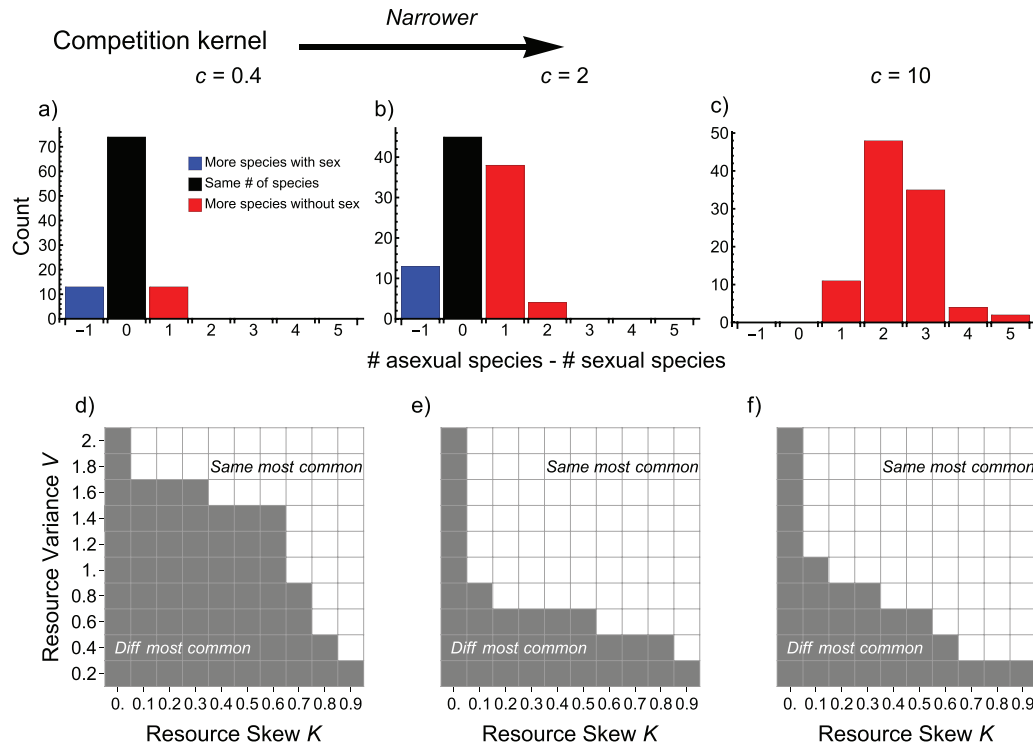


Figure 4: Comparing model outcomes with and without sexual reproduction. The first row ($a-c$) represents the difference between the number of species at equilibrium with asexual reproduction and the number of species at equilibrium with sexual reproduction ($a = 50$) for three different competition kernel widths (larger c corresponds to narrower competition kernels). Red indicates more species with asexual reproduction, black indicates the same number of species with both forms of reproduction, and blue indicates more species with sexual reproduction. The second row ($d-f$) shows whether the two models predict that the same (white) or different (gray) phenotype will be the most common at equilibrium for different variances of S , V (y -axis), skewness of S , K (x -axis), and different competition kernel widths (as shown across the top).

corresponds to high species richness. However, under sexual reproduction, tight packing results in frequent mating between different genotypes, which has a homogenizing effect that limits species richness (video S5). With broad competition kernels, genotypes can coexist only if they are far apart in phenotype space, in which case hybridization is quite rare and thus relatively inconsequential.

One potentially surprising result from figure 4a and 4b is that sexual reproduction can occasionally lead to more species than asexual reproduction (blue bar), running counter to the view that sex homogenizes the population. This counterintuitive result can be understood by a genetic constraint encountered previously: heterozygotes do not breed true. In these cases, the equilibrium reached in the asexual model would be equivalent to a heterozygote being fixed in the sexual model (fig. S4). Of course, a monomorphic population for a heterozygote is not a stable equilibrium with sexual reproduction, and thus the model with sexual reproduction can result in two species for the same parameters (fig. S4).

The second comparison that we draw between the sexual and asexual models is the identity of the most common phenotype. We use the most common phenotype as a coarse measurement of the state of the system, corresponding to the “dominant” species/genotype. The two models predict the same most common phenotype with broad and highly skewed stabilizing selection functions (i.e., broad and skewed resource distributions). In contrast, the two models predict a different most common phenotype with narrow and relatively symmetric stabilizing selection functions (i.e., narrow and symmetric resource distributions; fig. 4d–4f).

Highly skewed resource distributions correspond to the strongest ecological constraints in our model, resulting from larger possible fitness differences (figs. S1–S3). Thus, it is no surprise that sexual reproduction does not alter the most common phenotype in the face of these strong ecological constraints. In contrast, narrow resource distributions mean that there is little available niche space (MacArthur and Levins 1967; Meszéna et al. 2006), and thus species

must pack fairly tightly in phenotype space to coexist. As we have seen above, it is under such conditions with tight packing that genetic constraints become especially important because genotypes interbreed more frequently, leading to more recombination.

As another comparison to demonstrate the importance of both ecology and genetics in shaping model outcomes, we explore different genetic architectures in appendix S4. The relative frequency of various outcomes is largely consistent across genetic architectures (fig. S4.1), as are the conditions shaping the relative importance of genetic versus ecological constraints (figs. S4.6–S4.8; cf. fig. 4). Nevertheless, changes to phenotypic effects leads to notable changes in how the resource distribution influences equilibrium outcomes (figs. S4.2–S4.4; cf. fig. 2), underscoring an important role of genetics and providing another demonstration that mechanistic insights into speciation requires knowledge of both ecology and genetics.

Discussion

We develop and analyze a model aimed to bridge the gap between ecological and microevolutionary perspectives on biodiversity. Indeed, we find that both the initiation of speciation events and the long-term outcome of species persistence can be understood only as a complex interplay between both ecological and genetic constraints. Highly skewed resource distributions, which lead to larger fitness differences, typically act to prevent the initiation of speciation, suggesting that in some cases ecological and evolutionary limits on biodiversity act synergistically. This is not universal, however, as we show that speciation can occur only to have competitive exclusion remove diversity from the system. This latter point has important implications for understanding the connection between micro- and macroevolution, demonstrating that both speciation and coexistence can serve as separate controls on species richness.

Our model provides insights into the mechanisms and stages in which ecology and genetics can influence the speciation process and resulting ecological communities. Overall, we find that when the resource distribution is highly skewed or broad and competition is strong even between dissimilar phenotypes, model outcomes are dominated by ecological constraints rather than genetic constraints. In such cases, fitness differences generated by the resource distribution prevents the initiation of speciation events. Genetic constraints become most important when competition is strong only between similar phenotypes and assortative mating is weaker. Here, although intraspecific variation can be maintained, tight phenotype packing prevents speciation, resulting in fewer species at equilibrium with sexual reproduction compared to asexual reproduction.

Even after speciation events occur, however, species are not guaranteed to persist. We demonstrate both ecological (competitive exclusion) and genetic (hybrid collapse) cases of persistence failing, although competitive exclusion is more common. We caution that this last conclusion may not generalize to more quantitative phenotypes or weaker preferences. Importantly, the failure to persist occurs with no change to external environmental conditions (unlike, e.g., Aguilée et al. 2011) and is solely due to dynamics intrinsic to the system. Although there is considerable empirical evidence of species persistence failing because of hybrid collapse, such examples typically follow environmental change (Seehausen et al. 1997; Taylor et al. 2005; Seehausen 2006; Walters et al. 2008; Frei et al. 2022); here, we demonstrate that this need not be the case.

To deconstruct the mechanisms shaping model outcomes, we focused on developing a simple model. Simplicity, of course, comes with a trade-off of realism. As one example, we have focused exclusively on magic traits, which facilitate divergence in some (Gavrilets 2004), but not all (Servedio and Bürger 2020; Aubier et al. 2023), scenarios. Although many examples of magic traits exist in nature (Servedio et al. 2011) and theory suggests that they may be selected (Thibert-Plante and Gavrilets 2013), they are, of course, not ubiquitous. Nevertheless, simulations from a related model produce very similar results with or without magic traits (Dieckmann and Doebeli 1999). Thus, our focus on magic traits is unlikely to bias conclusions. Second, we assume that only three loci control the evolving trait. The differences that we observe when we change the genetic architecture (app. S4) are likely sensitive to the low number of possible genotypes (and thus phenotypes). With more continuous variation and fewer constraints on accessible phenotypes, we predict that these changes (figs. S4.2–S4.4) may not occur. Third, we have ignored any influence of demographic stochasticity, which may drive rare species extinct either by preventing their initial invasion or by precluding their stable persistence (Mayr 1963; Ito and Dieckmann 2007; Germain et al. 2021). Fourth, by focusing our model on sympatric speciation, assortative mating had to be quite strong, which is a limitation of the analysis (Bürger and Schneider 2006; Bürger et al. 2006).

This focus on sympatric speciation runs counter to empirical evidence that some degree of spatial structure is common in the majority of speciation events (Barraclough and Vogler 2000; Bolnick and Fitzpatrick 2007; Phillimore et al. 2008; Cardillo et al. 2016; Vargas et al. 2023). However, in principle sympatric speciation seems the most likely to produce two species capable of persisting, since it requires that competitive exclusion not occur before the speciation process is complete. In this sense, providing proof of concept that competitive exclusion may follow

speciation is perhaps strengthened by the focus on sympatric speciation. Similarly, studies of hybrid collapse typically focus on secondary contact scenarios (Abbott et al. 2013; Irwin 2020; Irwin and Schluter 2022); here, we show that these genetic failures to persist can even occur after sympatric speciation. Nevertheless, persistence (including coexistence; Germain et al. 2021) is still important following allopatric speciation (Aguilée et al. 2011) because the ability to expand ranges in secondary contact provides an important limit on diversification rates (Weir and Price 2011). Thus, our study has implications for speciation with geographic barriers. We show that our general conclusions hold in a secondary contact scenario in appendix S5. Relatedly, many models of speciation suggest diversification in divergent ecological conditions (Felsenstein 1981; Schluter 2009; Nosil 2012). In our model, this could best be approximated by a bimodal distribution of resources. Again, we find that our general conclusions hold if resources are bimodally distributed, although ephemeral speciation is less common (app. S6).

Despite calls for integrating community ecology with speciation research (Gavrilets 2014; Germain et al. 2021), much work remains to unify these related fields. One goal of our study was to demonstrate how to consider community dynamics simultaneous with and immediately following a speciation event in a formal model. Indeed, we show that various factors shaping ecological coexistence interact with and control the speciation process. This focus led us to consider the evolution of extrinsic reproductive isolation; however, intrinsic reproductive isolation may be particularly important for the persistence of species over macroevolutionary timescales. Thus, understanding interactions between ecology and the evolution of intrinsic reproductive isolation is an important avenue for future research (Anderson et al. 2023). We admit that our perspective has been that of evolutionary biologists, and more integration and connection to the ecological literature is needed. Recent studies have provided a framework for understanding the importance of evolution to modern coexistence theory (Hart et al. 2019; Pastore et al. 2021; Yamamichi et al. 2022, 2023); similar studies in the context of speciation would be valuable contributions. Still, some implications for community ecology are already apparent. Many cases of co-occurring species may not represent stable coexistence but rather be the result of transient dynamics (Hubbell 2001; Leibold and McPeck 2006; Simha et al. 2022). Our finding that speciation can produce two species incapable of coexistence provides one potential explanation for the origin of these nonequilibrium ecological communities.

In our case, we mainly incorporated ecological features relevant to modern coexistence theory through the variance and skewness of the resource distribution (and also through a bimodal resource distribution; app. S6). As is

clear from figure 1a, the maximum possible fitness difference over the range of possible phenotypes increases with skew. It is worth noting, however, that skew is not necessary to lead to fitness differences after a speciation event. Only when a population splits into two similar phenotypes that evolve away from one another (e.g., evolutionary branching in adaptive dynamics models) would skew be necessary to generate fitness differences due to the asymmetry that it introduces (coexistence is guaranteed in past models with branching because there is no skew in the carrying capacity and competition coefficients are less than 1; e.g., Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000). In our model, such a split occurs only under a very restricted and extreme set of conditions (Bürger and Schneider 2006). As a result, asymmetries—and thus fitness differences—can develop even without skew. Incorporating skew into models of adaptive speciation and evolutionary branching would be a valuable future step.

Recent evidence suggests a disconnect between micro- and macroevolutionary studies—microevolutionary processes that contribute to diversification do not predict macroevolutionary patterns (Rabosky and Matute 2013; Rabosky 2016). The ephemeral speciation model provides a potential solution to this disconnect by positing that population persistence (e.g., competitive exclusion or hybrid collapse) limits macroevolutionary measures of diversification (Rosenblum et al. 2012). Our study provides a formal demonstration in a simple model that either ecological or genetic failure of population persistence can, in principle, control macroevolutionary diversification rates. This provides an important proof of concept of the theoretical validity of the ephemeral speciation model, which we show can occur not only in the secondary contact scenarios (app. S5) often associated with ephemeral speciation but also in sympatric speciation events. Of course, an abstract model of a single-phenotype axis that rarely predicts more than three species does not provide an answer to the question of what limits macroevolutionary diversification. However, it provides a necessary foundation on which to build and a complement to past work demonstrating that nonequilibrium eco-evolutionary diversification dynamics can result from scenarios with more species and higher dimensional phenotypes (Doebeli and Ispolatov 2017). Under what conditions ecological or genetic factors provide the ultimate control on macroevolutionary diversification rates in nature remains an important outstanding question that requires bringing empirical data to bear.

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Statement of Authorship

B.A.L. conceived of the project. All authors provided conceptualization and modified the model that had been developed previously by R.B. B.A.L. led the analysis and wrote the first draft of the manuscript, which was edited by all authors.

Data and Code Availability

Data and code for replication have been deposited in Zenodo (<https://doi.org/10.5281/zenodo.10040665>; Lerch et al 2024).

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