

# Coevolution-induced selection for and against phenotypic novelty shapes species richness in clade co-diversification

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## Abstract

Coevolution can occur because of species interactions. However, it remains unclear how coevolutionary processes translate into the accumulation of species richness over macroevolutionary timescales. Assuming speciation occurs as a result of genetic differentiation across space due to dispersal limitation, we examine the effects of coevolution-induced phenotypic selection on species diversification. Based on the idea that dispersers often carry novel phenotypes, we propose and test two hypotheses. (1) *Stability hypothesis*: selection against phenotypic novelty enhances species diversification by strengthening dispersal limitation. (2) *Novelty hypothesis*: selection for phenotypic novelty impedes species diversification by weakening dispersal limitation. We simulate clade co-diversification using an individual-based model, considering scenarios where phenotypic selection is shaped by neutral dynamics, mutualistic coevolution, or antagonistic coevolution, where coevolution operates through trait matching or trait difference, and where the strength of coevolutionary selection is symmetrical or asymmetrical. Our key assumption that interactions occur between an independent party (whose individuals can establish or persist independently, e.g., hosts) and a dependent party (whose individuals cannot establish or persist independently, for example, parasites or obligate mutualists) yields two contrasting results. The stability hypothesis is supported in the dependent clade but not in the independent clade. Conversely, the novelty hypothesis is supported in the independent clade but not in the dependent clade. These results are partially corroborated by empirical dispersal data, suggesting that these mechanisms might potentially explain the diversification of some of the most species-rich clades in the Tree of Life.

**Keywords:** coevolution, dispersal limitation, macroevolution, metacommunity, natural selection, phenotypic novelty, species interaction, symbiosis

## Introduction

The natural world is filled with interactions between different species. Many such interactions are bipartite, where two interaction parties play two distinct roles, for example, the interactions between herbivores and plants, parasites and hosts, pollinators and angiosperms, and predators and prey. Bipartite interactions can potentially result in coevolution, that is, reciprocal evolutionary change in two or more interacting species driven by natural selection (Thompson, 2005). Coevolution is a multi-faceted process that can be characterized from many perspectives, including phenotypic evolution (Parchman & Benkman, 2002), partnership specificity (Cook & Rasplus, 2003), and community assembly (Endara et al., 2017). Another such perspective is diversification, that is, two coevolving lineages can codiversify when they are allowed enough time. This has been an active area of research since the seminal “escape-and-radiate” hypothesis, which states that rapid diversification of phytophagous insects or their host plants often follows a significant shift in interaction partners as a result of the new ecological opportunity that the new partner opens up (Cogni et al., 2022; Ehrlich & Raven, 1964). Later theories have suggested ways by which macroevolutionary dynamics may be generated by processes at the local scale. One such theory is the geographic mosaic theory of coevolution, which emphasizes that coevolutionary dynamics can

occur not only between interacting populations (e.g., plants and pollinators) but also between geographically connected populations (Thompson, 2005). It is therefore plausible that speciation could arise out of coevolutionary mosaics (Hembry et al., 2014; Thompson et al., 2017). Specifically, local coadaptation could potentially decrease the chance of mating between populations, paving the way for reproductive isolation and consequently speciation (Thompson et al., 2017). However, whether speciation is more likely to be enhanced or impeded by coevolution remains unclear (Harmon et al., 2019; Hembry & Weber, 2020; Janz, 2011).

Coevolution can be shaped by the direct fitness outcomes of species interactions, which can vary in at least three ways. First, species interactions may benefit both parties (mutualism) or benefit one party at the cost of the other (antagonism). Second, coevolution can be characterized by whether they are mediated by trait difference or trait matching (Yoder & Nuismer, 2010). Under the trait-difference scenario (in the strict sense of the term following Yoder & Nuismer, 2010), a species’ fitness is maximized when its trait value is very different from that of its interaction partner. Examples of the trait-difference scenario include antagonistic interactions in which predators and prey evolve increasingly strong weaponry and defense against each other (Vermeij, 1994) as well as mutualistic arms races in which both partners gain

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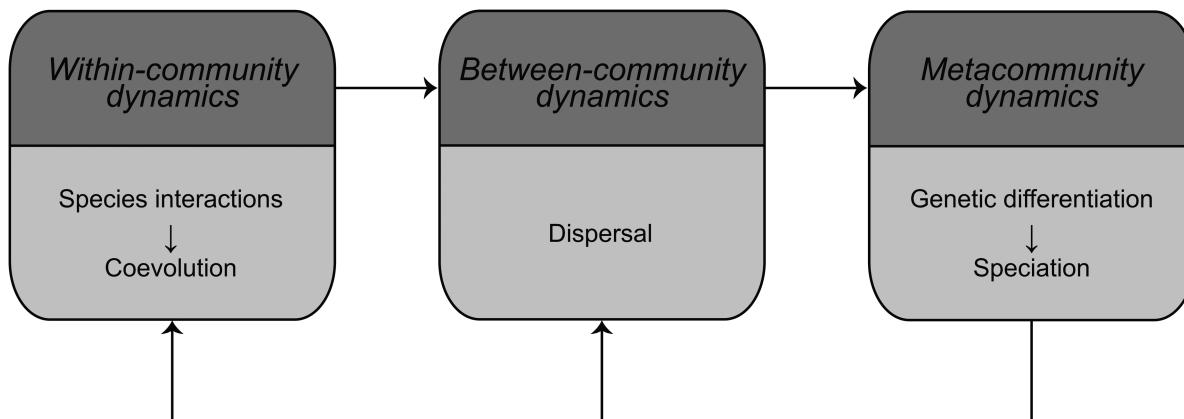
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more benefits from their partner when they have a greater trait value than that of their interaction partner, for example, a longer tongue in moth pollinators and a longer nectary spur in flowers (Whittall & Hedges, 2007). Under the trait-matching scenario (again, in the strict sense of the term following Yoder & Nuismer, 2010), on the other hand, a species' fitness is maximized when interacting species' traits closely match each other. Antagonistic examples of this scenario include brood parasitism where parasitic birds, such as cuckoos, lay similar-looking eggs in the nests of birds of other species and rely on them for the raising of their young (Langmore et al., 2003), whereas mutualistic examples include obligate pollination mutualisms where pollinating insects' ovipositor length tends to match their host plants' ovary wall thickness (Althoff & Segraves, 2022). Third, the strength of natural selection imposed by a species interaction can be symmetrical or asymmetrical for the interacting parties, with the selection sometimes being much stronger on one party than on the other (Andreazza et al., 2017; Brodie & Brodie, 1999; Endara et al., 2017).

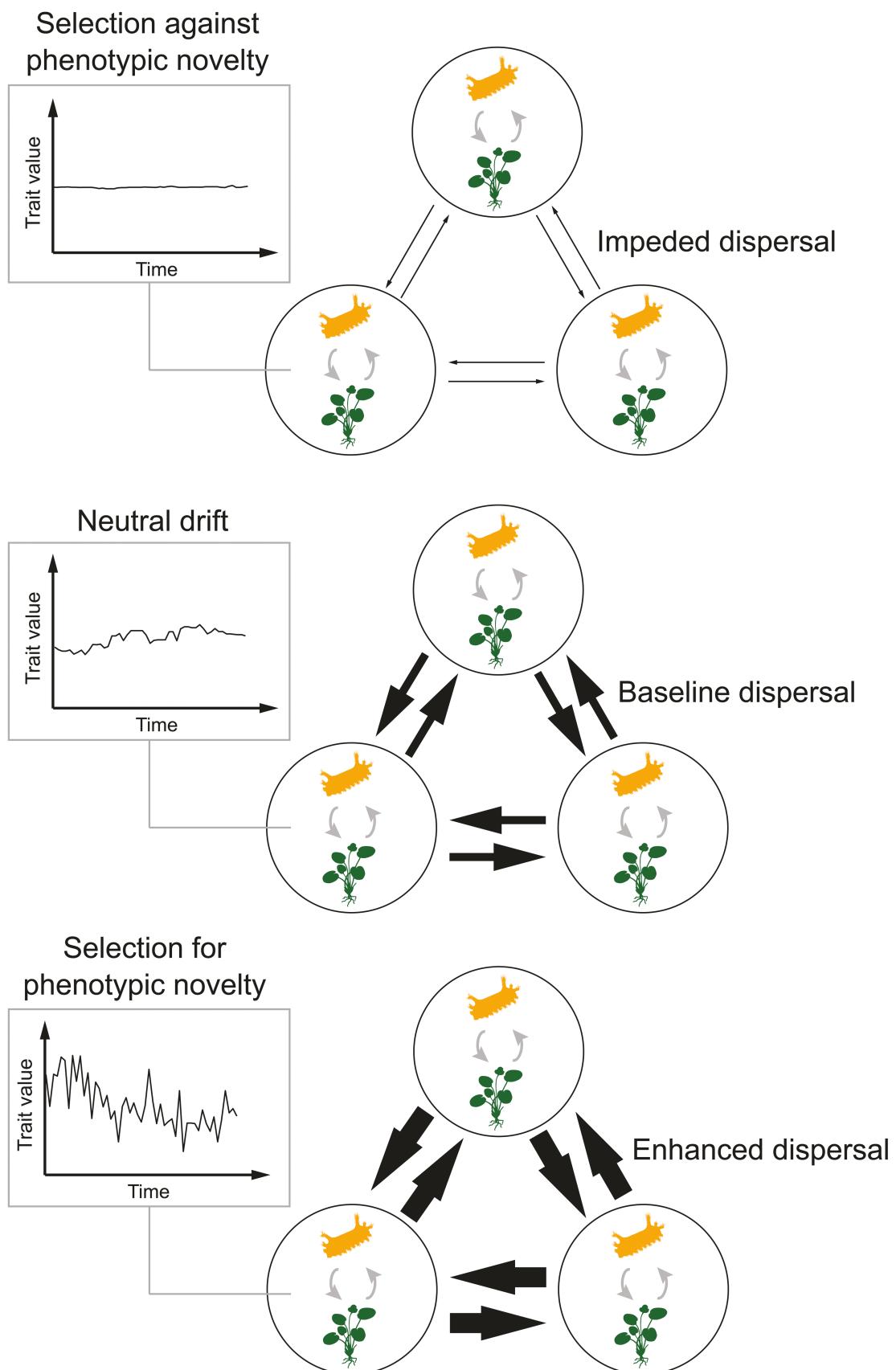
Coevolution, by definition, entails natural selection, and natural selection can occur at the phenotypic level (i.e., phenotypic selection). Phenotypic selection can occur when different phenotypes differ in fitness. These fitness differences can manifest as differential reproduction or survival. For example, plants with traits matching those of their pollinators tend to have higher reproductive success than those with nonmatching traits (Althoff & Segraves, 2022; Garibaldi et al., 2015; Peralta et al., 2020). Trait variation has also been linked to parasitism-induced host death in some cases, with large-bodied hosts having higher parasite loads and thus higher mortality rates (Cable et al., 2007). Thus, different regimes of phenotypic selection can potentially arise from different fitness outcomes of species interactions as a result of trait variation. Prior literature has looked at the microevolutionary effects of different selective regimes on coevolution (Hembry et al., 2014), for example, by focusing on phenotypic diversification (Yoder & Nuismer, 2010). However, although persistent phenotypic selection has the potential to shape species richness through macroevolution (Kingsolver & Pfennig, 2007), a theory is lacking on whether and how

different schemes of phenotypic selection induced by coevolution drive or impede the macroevolutionary accumulation of species richness (i.e., species diversification). The geographic mosaic theory of coevolution points to the possibility of coevolutionary diversification of clades while leaving the exact mechanisms largely unexplored (Thompson, 2005). Given that certain types of species interactions are essential to the biology of many organisms (e.g., herbivory to the biology of phytophagous insects), a better understanding of how coevolution shapes diversification through phenotypic selection could potentially explain the diversification of many clades. Here, we consider a general mode of speciation where dispersal limitation causes genetic differentiation across space, eventually leading to speciation (Etienne & Alonso, 2005; Hubert et al., 2015; Maliet et al., 2020; Manceau et al., 2015; Moran, 1962; Rosindell et al., 2015). Based on this mode of speciation, our model considers how within-community coevolutionary dynamics shape between-community dispersal dynamics and eventually shape speciation dynamics across an entire metacommunity (Figure 1).

We propose two novel hypotheses regarding how phenotypic selection shapes dispersal and consequently shapes species accumulation through speciation (Figure 2). The idea that selection against phenotypic novelty, for example, stabilizing selection, limits dispersal has been supported both empirically and theoretically (Huisman & Tufto, 2012; Lopez et al., 2008; Scheepens et al., 2010; Tufto, 2000, 2001; Yeaman & Whitlock, 2011; Zaccarello et al., 2020). This makes intuitive sense, as dispersers often carry novel phenotypes and thus should be expected to be selected against when selection disfavours phenotypic novelty (and selected for when selection favours phenotypic novelty). This leads to the hypothesis that selection against phenotypic novelty limits dispersal and causes stronger genetic differentiation across space and eventually a higher species richness accumulation through speciation (i.e., *stability hypothesis*). The same intuition can lead to a contrary hypothesis that selection for phenotypic novelty enhances dispersal and causes weaker genetic differentiation across space and eventually a lower species richness accumulation through speciation (i.e., *novelty hypothesis*).



**Figure 1.** Our model describes the interplay (shown as arrows) between processes at three scales: within-community, between-community, and across a metacommunity. Within a community, species interactions can result in coevolution and thus generate selective pressure for individuals belonging to both interacting parties. Between communities, individuals disperse and populations exchange genes. Across an entire metacommunity, genetic differentiation occurs between different communities and eventually results in speciation.



**Figure 2.** Hypothesized links between selective regime (within-community) and dispersal (between-community). A metacommunity is composed of multiple communities (circles) connected through dispersal (black straight arrows). Species interactions (grey curved arrows) occur within each community. The size of a straight arrow indicates the level of dispersal. Compared to neutral drift as the baseline, selection against novelty is hypothesized to impede dispersal (stability hypothesis) whereas selection for novelty is hypothesized to enhance dispersal (novelty hypothesis), as dispersers often carry novel phenotypes and thus should be expected to be selected against when selection disfavours phenotypic novelty (and selected for when selection favours phenotypic novelty). Note that these hypotheses themselves do not involve a coevolutionary context.

To test these hypotheses in the context of two coevolving clades, we built an individual-based model for the coevolutionary accumulation of species richness across two-dimensional space. We considered different coevolutionary scenarios, including those where the interaction is mutualistic versus antagonistic, where the interaction is mediated by trait difference versus trait matching, and where coevolutionary selection is symmetrically versus asymmetrically strong for the interacting parties. In bipartite interactions such as antagonisms and mutualisms, one partner is often more dependent on the other than the other way around. For example, many antagonistic interactions occur between antagonistic symbionts (e.g., parasites, pathogens) and their hosts without which they cannot survive (Schmid-Hempel, 2021). Even in mutualistic interactions, the mutual dependence of interaction partners can be highly asymmetrical (Bascompte et al., 2006; Bronstein, 2015). Given this, we built into our model the differences between independent and dependent interaction partners. We assumed that the independent party's individuals, for example, hosts, can establish or persist in a community independently, whereas a dependent party's individuals cannot establish or persist in a community without the independent party, for example, parasites or obligate mutualists. Our simulation results suggest potential mechanisms for the diversification of some of the most species-rich groups in the Tree of Life (Table 1).

## Materials and methods

### Model description

**Partnership between independent and dependent individuals**  
In the model, we consider the partnership between independent and dependent individuals. An independent individual can partner with multiple dependent individuals, but a dependent individual can only partner with one independent individual. An independent individual does not need to partner with any dependent individual for survival, but a dependent individual needs the one and only independent individual that it partners with for survival. This is modelled in two ways. First, during dispersal, an independent individual could survive where no dependent individuals are present; however, a dependent individual dies where no independent individuals are present. Second, during competition, when an independent individual dies, so do all of its dependent partners; however, when a dependent individual dies, its independent partner does not die. It is important to note that, in nature, the party that interacts with multiple individuals may not necessarily be the independent (less dependent) party.

**Table 1.** Examples of species interactions that may be described as independent–dependent partnerships and the species richness estimates for the independent and dependent parties.

Interaction	Independent party (species richness)	Dependent party (species richness)	Reference(s)
Host plants and herbivorous insects	Plants (ca. 374,000)	Herbivorous insects (over 500,000)	Bernays (2009); Christenhusz and Byng (2016)
Host and parasites	Hosts (NA)	Parasites (ca. 6,000,000)	Dobson et al. (2008)
Host plants and mutualistic mites	Some plants (NA)	Mutualistic mites (NA)	Romero and Benson (2005)
Corals and Symbiodinium	Corals (ca. 10,661 estimated for Anthozoa)	Symbiodinium (NA)	Bánki et al. (2023)
Insects and gut microbes	Insects (ca. 5,500,000)	Gut microbes (NA)	Stork (2018)

### Dispersal

The model starts with two populations each belonging to one of the interacting parties (the independent and dependent) placed at the central site of a  $n \times n$  grid, where each cell represents a geographic site. Each individual, independent or dependent, has the opportunity to disperse only at birth and moves to one of the four neighbouring sites or else remain at the same site (with the probabilities of upward, downward, leftward, rightward, and no movement all being equal). As previously mentioned, if a dependent individual moves to a site where no independent individuals are present, it dies; however, if it moves to a site where at least one independent individual is present, the dependent individual randomly chooses an independent individual to partner with among the independent individuals available at that site. The entire grid forms a metacommunity composed of  $n \times n$  communities (sites) connected through dispersal.

### Sexual reproduction and speciation

The genetic model follows a previous model built for the diversification of a single clade (Aguilée et al., 2018), but with simplifications. Each independent or dependent individual is diploid and has a given number of  $L_{dist}$  loci determining its genetic distance from another individual, with genetic distance defined as the number of loci at which two individuals carry completely different alleles. A new mutation can arise at any of these loci at a fixed probability  $\mu_{dist}$ . To determine whether two individuals are genetically incompatible enough to be considered reproductively isolated, we calculated the genetic distance between two individuals. The genetic distance is considered sufficient for reproductive isolation if greater than a fixed genetic distance threshold  $T_{dist}$ . These features allowed speciation through genetic differentiation across the grid.

Both independent and dependent individuals are hermaphrodites and reproduce sexually. For independent individuals or dependent individuals, each mating attempt occurs within each site following these steps: (a) two individuals with the highest fitness are chosen regardless of whether they have reproduced before (see “Fitness outcomes of species interactions” for how fitness is decided; for simplicity, we did not choose a more complicated reproduction model); (b) the two parents successfully reproduce  $n_{offsp}$  offspring if they are not reproductively isolated. These steps are repeated until  $n_{mat}$  mating attempts are made, regardless of whether mating attempts result in successful reproduction. For each offspring, the genotypes of the genetic distance loci are determined by Mendelian independent assortment of parental alleles. Given that dependent individuals die along with their independent

partner but not vice versa, it is necessary for  $n_{offspr}$  and  $n_{mat}$  to be greater for the dependent individuals than for the independent individuals so that the dependent individuals do not die out.

### Genetics of phenotype

Each independent or dependent individual has one locus determining its ecological phenotype which consists of a single quantitative trait. Mutation occurs at each of these loci, with the mutated allele value drawn from a normal distribution with a mean equal to the parent allele value and a standard deviation equal to  $\sigma_{eco}$ . For each offspring, the genotype of the ecological phenotype locus is determined by Mendelian random segregation of parental alleles.

### Competitive death

Many types of antagonisms and mutualisms occur between a consumer and a resource, such as herbivory, parasitism, or pollination (Bronstein, 2015). Given that populations cannot grow infinitely in consumer-resource systems due to resource competition (Abrams, 2009), we consider there to be a growth rate of zero when population size reaches carrying capacity. In the model, resource competition occurs among dependent individuals partnering with the same independent individual (e.g., parasites on the same host) and among independent individuals within the same site. The number of mutually competing individuals  $n$  cannot grow above carrying capacities  $K_{independent}$  or  $K_{dependent}$ . We ensured this by assigning  $n_{independent} - K_{independent}$  or  $n_{dependent} - K_{dependent}$  individuals to death (where  $n_{independent}$  and  $n_{dependent}$  are the numbers of mutually competing individuals, for independents and dependents, respectively), on a lowest-fitness-first basis (see “Fitness outcomes of species interactions” for how fitness is decided). Again, when an independent individual dies, so do all of the dependent individuals that partner with it; however, when a dependent individual dies, its one and only independent partner does not die.

### Fitness outcomes of species interactions

We allowed different modes of phenotypic selection to arise from species interactions with different fitness outcomes (Figure 3). For either antagonisms or mutualisms, the fitness of phenotypes was modelled as the result of either (a) trait difference: how different the two interacting phenotypes were (the direction of phenotypic difference between interacting parties matters), or (b) trait matching: how closely two interacting trait values matched each other (the direction of phenotypic difference between interacting parties does not matter). Following Yoder and Nuismer (2010), the fitness of a focal individual  $i$  interacting with  $n$  antagonist or mutualist individuals  $j_1, j_2, \dots, j_n$  can be expressed as

$$w_i(z_i, z_{j1}, z_{j2}, \dots, z_{jn}) = w_0 + \sum_{k=1}^n \frac{\xi}{1+e^{-\alpha(z_i-z_{jk})}} \quad (1)$$

under trait difference, or

$$w_i(z_i, z_{j1}, z_{j2}, \dots, z_{jn}) = w_0 + \sum_{k=1}^n \xi e^{-\alpha(z_i-z_{jk})^2} \quad (2)$$

under trait matching, where  $z_i$  and  $z_{j1}, z_{j2}, \dots, z_{jn}$  are phenotypic trait values of interacting individuals,  $w_0$  is the focal individual  $i$ 's fitness in the absence of the interaction,  $\xi$  is the cost or benefit to the focal individual (positive if beneficial, negative if costly), and  $\alpha$  determines the sensitivity of the

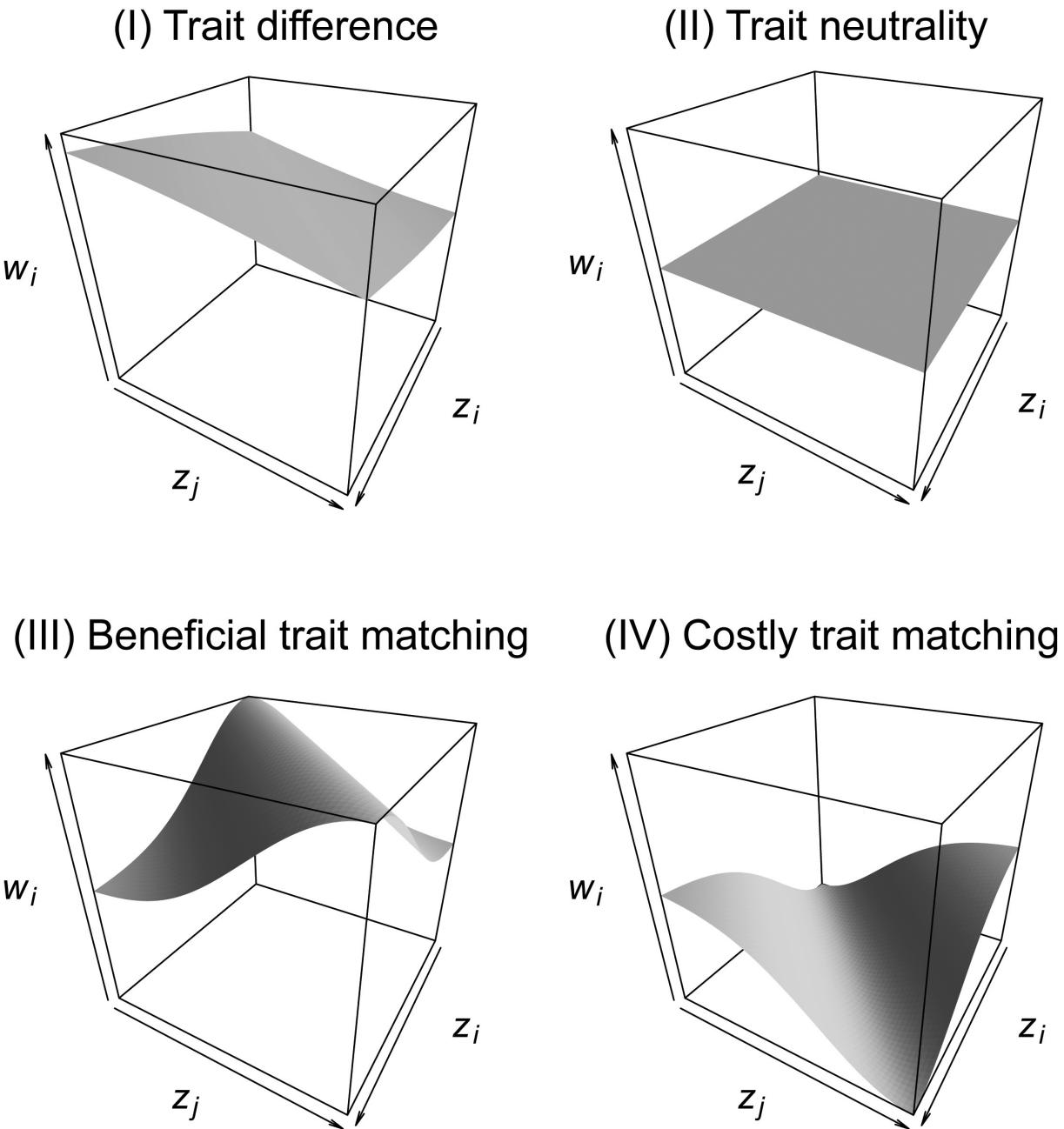
fitness outcome to the difference between interacting trait values (i.e., deviation from fitness neutrality). The strength of coevolutionary selection can sometimes be highly asymmetrical, that is, much weaker on one interacting party than on the other (Andreazzi et al., 2017; Brodie & Brodie, 1999; Endara et al., 2017). Here, we considered the extreme case of asymmetrical coevolutionary selection by allowing either the independents' or dependents' individual fitness to be unaffected by trait values, that is, trait neutrality (Function II in Figure 3). A fully factorial design would need  $4^*4 = 16$  scenarios to include all the combinations of the 4 fitness functions. We simulated a total of 9 possible scenarios (Table 2) to include all possible combinations except 7 combinations of which no or few empirical cases are known, that is, those where one clade's fitness follows trait difference while the other's follows trait matching (again, in the strict sense of these terms following Yoder & Nuismer, 2010) or where the interaction is costly for the dependent clade.

### Simulations

The model was implemented and the simulation results were analyzed in the R language (v4.0.0; R Core Team, 2020). All simulations were run on the University of Arizona High-Performance Computing clusters. We ran 96 replicates for each of the 9 scenarios, totalling 864 simulations. Each simulation was run for 1,500 generations. For each of the 9 simulated scenarios, t-tests comparing the distributions of mean species richness during the 1,401th–1,450th generations versus the 1,451th–1,500th generations found no statistically significant difference ( $P > 0.05$ ,  $n = 96$  replicates for each of the two distributions being compared). This confirmed that the duration of simulation (1,500 generations) was enough for simulations to reach a stationary state in terms of species richness, despite the ongoing fluctuations in species richness near the end of simulation (see Supplementary Figs. S1–S8 for fluctuations in species richness over time). For these simulations, we employed parallel computation using the R package doParallel (v1.0.17; Microsoft Corporation and Weston, 2022). All custom code used in this work is available as a Supplementary File (File S1) and on GitHub ([https://github.com/yichaozeng/Macro\\_Coevolution](https://github.com/yichaozeng/Macro_Coevolution)). All the constants used in the simulations are provided in Supplementary Table S1.

### Identifying selective regimes based on rates of phenotypic evolution

To identify the schemes of phenotypic selection for each scenario, we recorded the phenotypic values of all independent and dependent individuals at the central site of the  $n \times n$  grid during the entire duration of each simulation (1,500 generations). We then quantified the change in mean trait value during each generation,  $\Delta z$ , as a measure of the rate of phenotypic evolution.  $\Delta z$  is conventionally referred to as step difference and is measured in haldanes, that is, standard deviations per generation on a timescale of one generation (Gingerich, 2019a, 2019b). For example, a  $\Delta z$  value of 2 haldanes means that the change in mean trait value from Generation 1 to Generation 2 is two times the standard deviation of the trait distribution at Generation 1. We further took the absolute value of  $\Delta z$  to get  $|\Delta z|$ . We then averaged  $|\Delta z|$  across the entire duration of simulation to get the mean step difference  $|\Delta z|$  as a measure of rate of phenotypic evolution. We determined the minimum and maximum for the  $|\Delta z|$  of the entirely neutral scenario (Scenario



**Figure 3.** Fitness as a function of interacting trait values. Using four fitness functions, we simulate scenarios of trait difference (I), trait neutrality (II), and trait matching (III & IV).  $w_i$ , the fitness of the focal individual  $i$ , is treated as a function of  $z_i$ , which denotes the trait value of the focal individual  $i$  itself, and  $z_j$ , which denotes the trait value of individual  $j$  (individual  $i$ 's interaction partner). Function I: Equation 1,  $\xi = 0.1$ ,  $\alpha = 1$ ,  $n = 1$ . Function II:  $w_i = 0$ . Function III: Equation 2,  $\xi = 0.1$ ,  $\alpha = 1$ ,  $n = 1$ . Function IV: Equation 2,  $\xi = -0.1$ ,  $\alpha = 1$ ,  $n = 1$ . For this model, Function II, where individual fitness is constant and independent from trait values, is equivalent to Equation 1 or 2 when  $\alpha = 0$  regardless of the value of  $\xi$ . Following Yoder & Nuismer (2010), the fitness function is not dependent on whether the interaction is beneficial or costly when coevolution operates through trait difference (Function I). In all panels, the ranges of the  $z_i$  and  $z_j$  axes are between 0 and 2 and the range of the  $w_i$  axis is between -0.1 and 0.1.

$i$ , where both the independents' and dependents' fitness are held constant and do not depend on trait values). We treated simulations in which  $|\Delta z|$  is greater than the neutral maximum as experiencing selection for novelty and those in which  $|\Delta z|$  is less than the neutral minimum as experiencing selection against novelty. It is noteworthy that selection against phenotypic novelty, by our definition, does not entail that all populations converge on the same trait optimum. Instead, it simply entails slower rates of evolution within populations. Under this selective regime, two populations can both have

extremely low rates of evolution while having extremely different optimum trait values around which trait values fluctuate. It is also noteworthy that here we did not observe selective regimes per se but instead focused on measuring rates of evolution. This is justified by the fact that our model was set up in a way such that different rates of evolution are necessarily results of different selective regimes. Specifically, the only difference across scenarios is the fitness function dictating selective regimes while the strength of all other factors potentially affecting rates of evolution (e.g., population size,

**Table 2.** Nine scenarios are simulated to encompass the trait difference and trait matching mechanisms and symmetrical and asymmetrical selective strengths, with real-world biological examples explained in the second paragraph of the Introduction section.

Scenario	Trait difference, trait neutrality, or trait matching	Symmetry of selective pressure	Outcome of interaction	Fitness function for the independent (see Figure 3)	Fitness function for the dependent (see Figure 3)
a	Difference	Symmetrical	Mutualism or antagonism	I	I
b	Difference	Asymmetrical	Mutualism or antagonism	I	II
c	Difference	Asymmetrical	Mutualism or antagonism	II	I
d	Matching	Symmetrical	Mutualism	III	III
e	Matching	Asymmetrical	Mutualism	III	II
f	Matching	Asymmetrical	Mutualism or antagonism	II	III
g	Matching	Symmetrical	Antagonism	IV	III
h	Matching	Asymmetrical	Antagonism	IV	II
i	Neutrality	Symmetrical	Mutualism or antagonism	II	II

genetic architecture, generation time, and mutation rate) are the same across scenarios.

#### Degree of dispersal limitation, genetic distance between sites, and species richness

We quantified the degree of dispersal limitation as the proportion of native individuals among all individuals, with higher proportions of native individuals indicating stronger degrees of dispersal limitation. We define a native individual as an individual that inhabits the same site at which it was born. Specifically, what we measured was realized dispersal rather than dispersal per se, because we are interested in the contribution of dispersal to local gene pools, which is contingent on successful establishment of the dispersers following dispersal. The degree of dispersal limitation we refer to is the degree to which dispersal success is limited. Then, we computed genetic distance between any two sites (i.e., between the two populations inhabiting the two sites) by taking the mean genetic distance between any two individuals from the two sites (i.e., the two populations). We then computed the genetic distance between all sites by taking the mean genetic distance between any two sites. To quantify the species richness that each clade had accumulated at the end of the simulation, we considered populations to belong to a single species if their genetic distance did not exceed the genetic distance threshold for speciation  $T_{dist}$  (for details, see “Sexual reproduction and speciation”).

For the degree of dispersal limitation (the proportion of native individuals), we took the mean over the entire 1,500 generations of simulation because it is the cumulative effect of dispersal that is of interest. For genetic distance between sites and species richness accumulation, we took the mean over the last 10 generations of simulation because we are interested in them as the eventual results of multiple generations of dispersal and speciation.

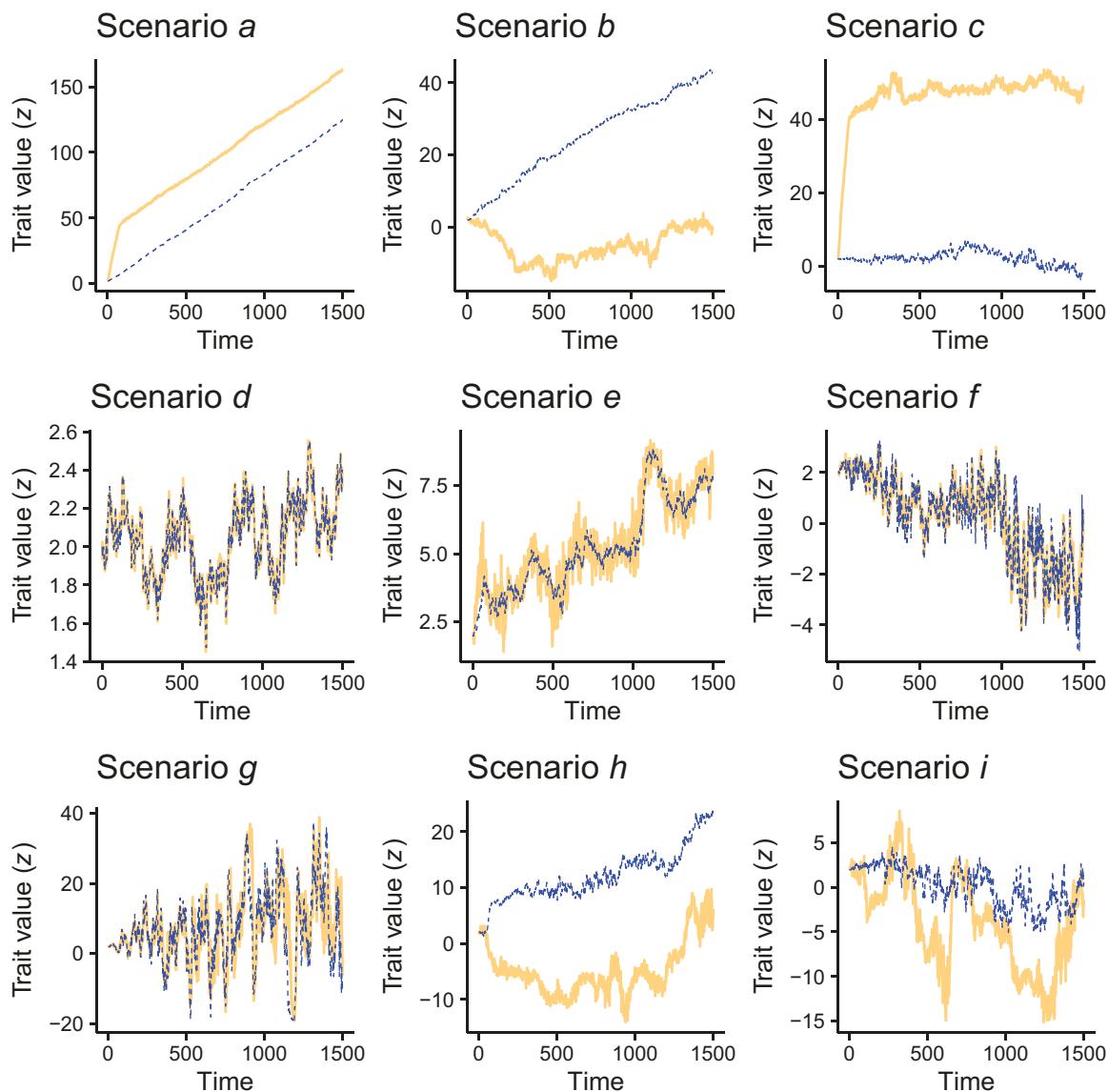
## Results

Each of the nine simulated scenarios generated a unique coevolutionary trajectory within communities (Figure 4). Scenario *a* was characterized by rapid and continuous reciprocal escalation of trait values in the two clades characteristic of an arms race. Scenario *b* was characterized by trait escalation in the independent clade and an initial decrease in trait value followed by a random walk (in the sense that it is not

seemingly different from a trajectory typical of the neutral scenario, same wherever else a random walk is mentioned) in the dependent clade. Scenario *c* was characterized by trait escalation followed by a random walk in the dependent clade and a random walk in the independent clade. Scenarios *d–f* were characterized by varying degrees of temporal trait stationarity in the two clades. Scenario *g* was characterized by a dramatic fluctuation in trait value in both clades characteristic of coevolutionary cycling. Scenario *h* was characterized by a tendency for the host trait value to not overlap with that of the dependent. Scenario *i* was characterized by a random walk underlain by neutral dynamics in both clades. By using a neutral fitness function (Function II in Figure 3), we also included scenarios where the trait value of at least one interacting partner does not closely follow that of the other interacting partner (Scenarios *b, c, e, f, h, i*).

We analyzed the effects of selective regime on the degree of dispersal limitation, genetic distance between sites, and species richness accumulation. These analyses revealed the mechanisms by which coevolution shaped species richness (Figure 5). Quantification of the mean step difference  $|\Delta z|$  as a measure of rate of phenotypic evolution showed that the 9 scenarios generated all three schemes of phenotypic selection in the two clades, that is, neutral drift, selection against novelty, and selection for novelty. For each of the relationships of interest (Figure 5A–C), we performed a loess regression to visualize nonlinearities, but also two localized simple linear regressions to quantify the average effects of selection against novelty and selection for novelty (Supplementary Fig. S19).

In the independent clade (Figure 5D–F; Supplementary Fig. S19D–F), compared to neutral drift, selection against novelty resulted in relatively weak increases in the degree of dispersal limitation (slope = -1.47 percentage/haldane,  $P = 0.0013$ , left line in Supplementary Fig. S19D), genetic distance between sites (slope = -0.1664 loci/haldane,  $P = 0.208$ , left line in Supplementary Fig. S19E), and species richness accumulation (slope = -16.4918 species/haldane,  $P = 0.00117$ , left line in Supplementary Fig. S19F). However, compared to neutral drift, selection for novelty resulted in relatively strong reductions in the degree of dispersal limitation (slope = -12.11 percentage/haldane,  $P < 2e-16$ , right line in Supplementary Fig. S19D), genetic distance between sites (slope = -7.60415 loci/haldane,  $P < 2e-16$ , right line in Supplementary Fig. S19E), and species richness accumulation (slope = -181.4629 species/haldane,  $P < 2e-16$ , right line in Supplementary Fig.



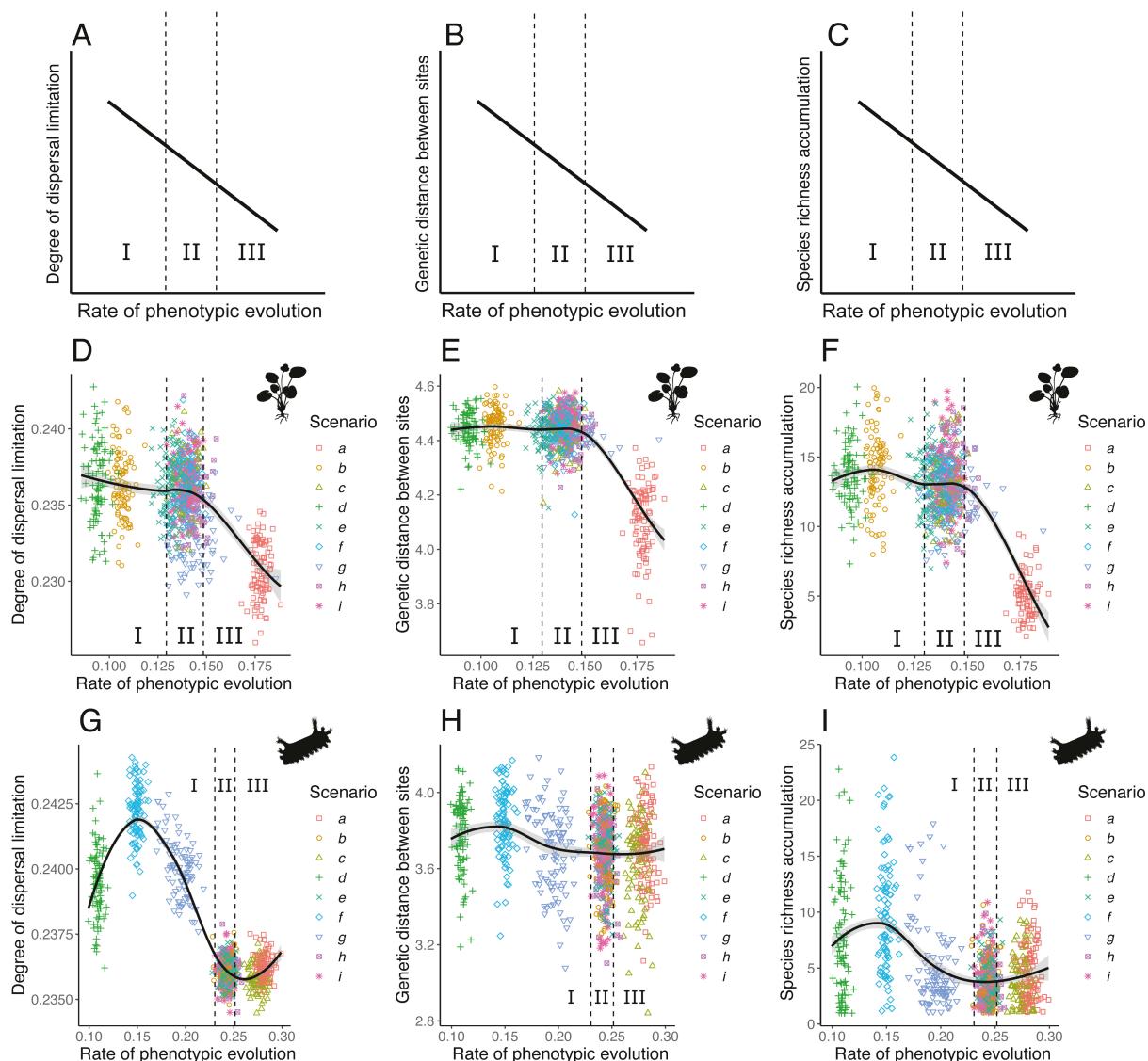
**Figure 4.** Coevolutionary trajectories within communities in each of the nine simulated scenarios (*a–i*). Solid lines indicate the mean trait value calculated for individuals at the central community (site) of the  $n \times n$  grid in one of the 96 replicates for each scenario. Dashed and solid lines are used to indicate the independent and dependent trait values, respectively.

**S19F**). These results suggest that the predominant mechanism shaping species richness in the independent clade is one where selection for novelty reduces the degree of dispersal limitation, which reduces the genetic distance between sites, eventually resulting in reduced species richness accumulation (i.e., the *novelty hypothesis*).

In the dependent clade (Figure 5G–I; Supplementary Fig. S19G–I), compared to neutral drift, selection against novelty resulted in relatively strong increases in the degree of dispersal limitation (slope =  $-3.755$  percentage/haldane,  $P < 2e-16$ , left line in Supplementary Fig. S19G), genetic distance between sites (slope =  $-1.0355$  loci/haldane,  $P = 2.87e-12$ , left line in Supplementary Fig. S19H), and species richness accumulation (slope =  $-35.7923$  species/haldane,  $P < 2e-16$ , left line in Supplementary Fig. S19I). The effect of selection against novelty showed strong nonlinearity, with the highest degree of dispersal limitation, genetic distance between sites, and species richness accumulation being achieved by intermediately rather than extremely strong selection against novelty (Fig. 5G–I). However,

compared to neutral drift, selection for novelty resulted in relatively weak reductions or even a slight increase in the degree of dispersal limitation (slope =  $-0.00114$  percentage/haldane,  $P = 0.993$ , right line in Supplementary Fig. S19G), genetic distance between sites (slope =  $-0.08698$  loci/haldane,  $P = 0.853$ , right line in Supplementary Fig. S19H), and species richness accumulation (slope =  $6.4800$  species/haldane,  $P = 0.375$ , right line in Supplementary Fig. S19I). These results suggest that the predominant mechanism shaping species richness in the dependent clade is one where selection against novelty increases the degree of dispersal limitation, which increases the genetic distance between sites, eventually resulting in increased species richness accumulation (i.e., the *stability hypothesis*).

Specifically, the *novelty hypothesis* explained how species richness accumulation was reduced for the independent clade in the coevolutionary scenarios of mutualistic or antagonistic arms races where selective pressure is comparable between the independent and dependent individuals, that is, a classical arms race, and in the scenario of antagonistic trait matching where selective



**Figure 5.** Expected and observed relationships between selective regime, degree of dispersal limitation, genetic distance between sites, and species richness accumulation. Selective regimes (neutral drift, selection against novelty, or selection for novelty) are determined by rate of phenotypic evolution. To visualize how selective regimes are determined based on rates of phenotypic evolution, each panel is divided into three areas I, II, and III, each corresponding to selection against novelty (low rates of evolution), neutral drift (intermediate rates of evolution), and selection for novelty (high rates of evolution). (A)–(C): Expected relationships—a significantly negative slope is predicted based on the stability and novelty hypotheses. (D)–(F): Observed differences between selection regimes in the independent clade. (G)–(I): Observed differences between selection regimes in the dependent clade. In (D)–(I), black lines with grey ribbons show loess regressions with 95% confidence intervals (with 96 replicates per scenario/colour).

pressure is comparable between the independent and dependent individuals (Fig. 5D–F; Supplementary Fig. S19D–F; Scenarios *a* & *g* in Table 2). The *stability hypothesis* explained how species richness was increased for the dependent clade in the coevolutionary scenario of mutualistic trait matching where selective pressure is comparable between the independent and dependent individuals, the scenario of mutualistic or antagonistic trait matching where selective pressure is weak for independent individuals, and the scenario of antagonistic trait matching where selective pressure is comparable between the independent and dependent individuals (Fig. 5G–I; Supplementary Fig. S19G–I; Scenarios *d*, *f* & *g* in Table 2).

## Discussion

Here we have shown that coevolution shapes species richness through two different mechanisms depending on whether the

clade of interest is independent or dependent. In the independent clade, selection for novelty enhances dispersal, which impedes genetic differentiation across space, eventually impeding species richness accumulation through speciation (i.e., the *novelty hypothesis*). In the dependent clade, selection against novelty impedes dispersal, which enhances genetic differentiation across space, eventually enhancing species richness accumulation through speciation (i.e., *stability hypothesis*). These results arose through two simple rules governing the dynamics of independent-dependent interactions: (1) one independent individual can pair with multiple dependent individuals but not vice versa; (2) a dependent individual dies in the absence of an independent partner but not vice versa. These rules should be applicable to a wide variety of systems including intimate host-phytophagous-insect interactions, most host-parasite interactions, most host-pathogen interactions, and some obligate interactions between mutualists and

their hosts, although they do not apply to more generalized interactions such as the dispersal of seeds by frugivores or the interactions between plants and generalist pollinators.

The concept of selection for and against phenotypic novelty, to the best of our knowledge at least, has not been directly touched on in the coevolutionary literature. However, these two selective regimes are related to several existing concepts in the literature. For example, previous models have explored the conditions for coevolutionary stable states (which also entail slow rates of evolution) to be achieved, although these models did not consider dispersal or speciation across space as we did (Day & Burns, 2003; Gilchrist & Sasaki, 2002; Vasco et al., 1987). The concept of selection for phenotypic novelty is also related to cases of trait lability in coevolution. One such case is classical arms race where there is reciprocal escalation of trait values in brood parasites and hosts, predators and prey, and pollinators and plants (e.g., Dawkins & Krebs, 1979; Vermeij, 1994; Whittall & Hedges, 2007). Another such case is coevolutionary cycling where there is persistent alternation between different trait states, for example, between high and low trait values in hosts and parasites (Ashby & Boots, 2015; Ashby & Gupta, 2014; Prado et al., 2009). Thus, this work can be seen as a new step along these lines of thinking.

Empirical data partly corroborate our results that coevolution-induced selection for and against phenotypic novelty differentially affects the dispersal of independent and dependent individuals, suggesting that our model provides a potential mechanistic explanation for these patterns of dispersal. The results of our model tend to match several empirical observations about ant–plant, ant–bacterium, and plant–fungus mutualisms. First, our model shows that coevolution-induced selection against novelty impedes the dispersal of dependent individuals only. This matches large-scale observations that only specialized mutualism (high dependence on mutualistic partners) is associated with a reduced likelihood of successful establishment beyond native ranges (Nathan et al., 2023). Second, our model shows that coevolution-induced selection for novelty enhances the dispersal of independent individuals only. This matches large-scale observations that only generalized mutualism (low dependence on mutualistic partners) is associated with an increased likelihood of successful establishment beyond native ranges (Nathan et al., 2023). We show that coevolution-induced selection for and against novelty can generate these widely observable patterns. This suggests that coevolution-induced selection for and against novelty, as well as their macroevolutionary consequences as shown in our model, may be prevalent in nature.

It is useful to understand these results in light of environmental selection and trait multidimensionality. Some traits under coevolutionary selection may be simultaneously under selection from other factors in the environment. Selection imposed by the environment can either favour or disfavour phenotypic novelty—a stable environment can select against phenotypes deviating from a fixed environmental optimum and thus disfavour phenotypic novelty (Kopp & Matuszewski, 2014), whereas a fluctuating environment can potentially select for phenotypic novelty (De Villemereuil, 2020). Disruptive selection along an environmental gradient has itself been shown as a mechanism driving speciation (Doebeli & Dieckmann, 2003). It would be interesting for future research to explore the interactive effects of coevolutionary selection and environmental selection on co-diversification, as has been pointed

out in cases where biotic interactions drive speciation in tandem with spatial isolation (Hembry et al., 2014; Kay and Sargent, 2009). In addition, species interactions are sometimes better modelled using multi-dimensional traits (Eklöf et al., 2013). The trait difference mechanism can have similar effects on phenotypic evolution to those of the trait matching mechanism when the trait of interest is multidimensional (Yamamichi et al., 2019). Therefore, selection for novelty underlain by the trait difference mechanism might be less common in systems with higher trait dimensionalities.

These results may provide mechanistic insights into the diversification of some extremely diverse clades that fit the description of a dependent clade. Specifically, explaining the origins of the diversity of phytophagous insects and parasites has long been an active area of research (Ehrlich & Raven, 1964; Hardy & Otto, 2014; Kawahara et al., 2023; Poulin & Morand, 2000; Weinstein & Kuris, 2016), and our model provided a novel, alternative explanation for their staggering diversity: selection against novelty induced by coevolution selects against dispersers, reducing dispersal success and consequently enhancing genetic differentiation across space that is necessary for speciation. This is conceptually similar to the notion that local coadaptation can reduce the chance of mating between populations and this reduction in gene flow can promote reproductive isolation and consequently speciation (Thompson et al., 2017). However, we furthered this notion by showing that this is likely to be the case only for clades that fit our assumption about dependence such as phytophagous insects, parasites, pathogens, or obligate mutualists that depend on their hosts, but is unlikely to be the case for clades that fit our assumption about independence such as some hosts of mutualists or victims of phytophagous insects, parasites, and pathogens. Overall, the mechanisms from this model provide potential mechanisms by which coevolution may have had a profound impact on the diversification of phytophagous insects and parasites, although the prevalence of coevolution in insect herbivory and parasitism has yet to be confirmed by empirical evidence.

Our results suggest that the diversity of clades that fit our description of an independent clade (e.g., plants, hosts of parasites and pathogens, or the facultative hosts of obligate mutualists) could also be explained in the light of coevolution. The effect of coevolution on an independent clade's diversity, under our model assumptions, is likely negative as shown in the *novelty hypothesis*. It is interesting in this light that independent clades, for example, clades of angiosperms, are often more species-poor than their dependent clades, e.g., clades of phytophagous insects (Bernays, 2009; Christenhusz and Byng, 2016), although many other mechanisms likely contribute to this asymmetry in richness. This decelerating effect of coevolution on diversification that we show here has not been explored before, as classic coevolutionary hypotheses such as the escape-and-radiate hypothesis tended to focus on the accelerating effects of coevolution on diversification (Ehrlich & Raven, 1964).

Comparing our model to previous models provides some additional implications. We show that a classical arms race impedes the accumulation of species richness in the independent clade but has no effect in the dependent clade. Our results focusing on species richness are seemingly in contrast with the results of a previous study showing that the classical arms race neither promotes nor inhibits phenotypic diversification (Yoder & Nuismer, 2010). We also show that selection

for novelty also predicts a decrease in species richness in the independent clade in the scenario of antagonistic trait matching where selective pressure is comparable between the independent and dependent individuals. This also seems to contrast with the previous model which showed that coevolution promotes phenotypic diversification when trait matching is costly, for example, as in competition or antagonisms (Yoder & Nuismer, 2010). In short, we want to point out that we looked at species diversification while Yoder & Nuismer (2010) looked at phenotypic diversification. Since the two papers examined two different aspects of diversification, their results are not directly comparable because the two processes can be decoupled from each other over macroevolutionary time. On a different note, the idea that having multiple partners imposes a constraint on diversification when the interaction is governed by mutualistic trait matching has been shown in a nonspatially explicit model previously (Raimundo et al., 2014). This agrees with the results of our spatially explicit model and suggests that the lack of support for the *stability hypothesis* in the independent clade could potentially arise through similar mechanisms. Overall, the new model contributes to an ongoing effort to integrate metacommunity ecology with macroevolution in general (McPeek, 2008; Reijenga et al., 2021) and for independent-dependent systems in particular (Forister & Jenkins, 2017).

Our model provides an alternative or supportive explanation for some long-standing hypotheses. In the seminal escape-and-radiate hypothesis (Ehrlich & Raven, 1964), a lineage, independent or dependent, that acquires a new defense or counter-defense (i.e., key innovations) may then rapidly radiate into a new adaptive zone. We show a different picture here—coevolutionary spatial dynamics can continuously enhance or impede speciation without involving sporadic key innovations. Whether coevolutionary diversification occurs in a punctuated fashion (as described by the escape-and-radiate hypothesis) or a steady fashion (as shown in our model) remains open to debate. Future empirical research would be needed to gauge the generality of each mode of coevolutionary diversification. There are also long-standing hypotheses that dependents should be more specialized the more intimate their interactions with their independents are (Ollerton, 2006; Thompson, 1994). These hypotheses generally predict that dependents should be more species-rich than independents, which is consistent with our results suggesting that coevolution generally impedes diversification for an independent clade and enhances diversification for a dependent clade. However, these hypotheses related to interaction intimacy are agnostic to the geography of speciation. It is also clear that a single independent can contain a multitude of niches for different dependents (Farrell & Sequeira, 2004), so the asymmetry in richness is less surprising regardless of the specific mechanisms of diversification.

Changing some of the assumptions of key parameters will likely generate results that are different than ours. We acknowledge that the model assumes independence-dependence as the only difference between the interacting parties. However, interacting parties likely differ in other factors such as speciation threshold, dispersal ability, mutation rate, and maximum population size (carrying capacity) in reality. Any extreme disparities in these factors between the two interacting parties, or the evolvability of these factors, could potentially give rise to conclusions that are different than ours. While lab or field experiments will likely prove

unsuitable for exploring these possibilities given the timescale of species diversification (usually over several million years), computer experiments under biologically realistic assumptions could generate new insights in these directions. One of the interesting hypotheses to be tested computationally may be whether this study's different conclusions for independents and dependents under the assumption of dispersal limitation apply to extremely well-dispersed groups such as plankton in the world's oceans (Saulsbury et al., 2024).

In conclusion, here we show that there are two general mechanisms of coevolutionary diversification: coevolution-induced selection against novelty enhances the accumulation of species richness in dependent clades, whereas coevolution-induced selection for novelty impedes the accumulation of species richness in independent clades. The model provides a new line of thinking in bridging symbiotic biology, coevolution, metacommunity ecology, and macroevolution. Given that symbiotic relationships between a more dependent party and a less dependent party permeate the natural world (Margulis, 1998), these general mechanisms of coevolutionary diversification could potentially explain the diversification of many clades in the Tree of Life.

## Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

## Data availability

No real data were used for this study.

## Author contributions

Yichao Zeng (Conceptualization [Lead], Data curation [Lead], Formal analysis [Lead], Investigation [Lead], Methodology [Lead], Software [Lead], Validation [Lead], Writing—original draft [Lead], Writing—review & editing [Lead]), and David Hembry (Writing—original draft [Supporting], Writing—review & editing [Supporting])

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## Conflicts of interest

None declared.

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