Evolutionary diversification of ecological specialists under informed resource choice

Raphaël Scherrer[1,*], Joris Damhuis[1], G. Sander van Doorn[1], and Rampal S. Etienne[1]

[1]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, the Netherlands

[*]Corresponding author: raphael.scherrer@evobio.eu

Abstract

Behavior can be an important modulator of eco-evolutionary dynamics and genetic evolution that is not always taken into account in models of evolutionary diversification. On the one hand, classical models for the evolution of ecological specialization have been extended to account for flexible behavioral aspects such as diet choice or matching habitat choice, but only in a subset of all spatial settings relevant for adaptive speciation. On the other hand, models of adaptive speciation have been synthesized to encompass different types of spatial settings — either promoting diversification through within-habitat frequency-dependent forces arising from competition, or between-habitat local adaptation independent of competition — albeit with non-flexible behavior. Here, we study individual-based simulations of the emergence of multiple resource specialist strategies, when individuals are allowed to choose their resource based on profitability in a two-resource, two-habitat environment, inspired from previous models of adaptive diversification. We join other authors in finding that active resource choice favors resource conservatism and the maintenance of a single specialist when individuals are already somewhat specialized on one resource. When individuals start off as generalists, however, active resource choice maintains the convergence stability of the generalist branching point — meaning that selection leads to the diversification of two specialists — in the face of strong ecological trade-offs, where evolution towards a single specialist would have otherwise been favored without resource choice. Active resource choice also turns frequency-independent processes of diversification (relying on local adaptation) into frequency-dependent ones (relying on competition) when resources are spatially restricted. Consequently, the chances of ecological divergence in spatially heterogeneous scenarios are maximized at intermediate levels of resource choice accuracy, where frequency-dependent selection balances out selection for resource conservatism. Finally, we find that active resource choice promotes divergence when resources are compartmentalized within microhabitats, by avoiding the waste of energy that foraging in poor microhabitats represents.

Keywords — ecological specialization, optimal foraging, frequency-dependent selection, speciation, resource compartmentalization, matching habitat choice

Introduction

The adaptive diversification of ecologically specialized species is critical for the emergence and maintenance of biodiversity on Earth (Hutchinson, 1959; Tilman, 1982; Schluter, 2000). Many of the species found in the world's most diverse ecosystems are ecological specialists, i.e., species having evolved adaptations to efficiently utilize specific ecological niches in their environment (as opposed to generalists, which can use a broader panel of niches but exploit any single one somewhat less efficiently, Rosenzweig, 1981). Examples of particularly specialized species include hummingbirds feeding on the nectar of flowers (Tinoco et al., 2017), phytophagous insects feeding on specific host plants (Del Campo et al., 2003; Lewinsohn & Roslin, 2008), or galling crabs living on particular species of corals in shallow reefs (Bravo et al., 2024). The prevalence of ecological specialization in nature makes unraveling the mechanisms underlying the diversification of species into ecological specialists a key step for a thorough understanding the origins of biodiversity (Schluter, 2000).

Under adaptive speciation theory, the divergence of species or morphs specializing on distinct ecological niches is predicted by factors such as habitat heterogeneity in the type of available resources (Nosil, 2012; Rettelbach et al., 2013), and/or frequency-dependent selection arising from interspecific competition for limited resources (Dieckmann & Doebeli, 1999; Dieckmann et al., 2004; Rueffler et al., 2006). In divergent selection, the diversification of specialist ecotypes is driven by distinct habitats having different resources present, thus favoring local adaptation to the most abundant resource in the environment (Nosil, 2012; Rettelbach et al., 2013). In frequency-dependent selection, intraspecific competition for resources creates an advantage to adapt towards under-utilized resources, which may result in a split of multiple specialized ecotypes within the population (Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999; Rueffler et al., 2006; Weissing et al., 2011). Key to these selective forces leading to the diversification of specialist ecotypes is the existence of physiological or utilization trade-offs among resources or niches, such that no biologically attainable combination of traits can fully adapt a species to all niches — adaptation to one niche must come at a cost in terms of adaptation to another niche (Levins, 1962; Egas et al., 2004; Rueffler et al., 2006).

As an evolved property of organisms, behavior can be instrumental in achieving a high fitness through the active choice of resources (Stephens & Krebs, 1986), whether those resources are food (Parent et al., 2014), habitats (Morris, 2003; Ronce, 2007; Edelaar et al., 2017), mates (Andersson, 1994; Reynolds & Fitzpatrick, 2007) or breeding sites (Turelli et al., 1984). The ability to modulate foraging efforts or habitat exploitation through behavior has been documented not just in animals, but also in bacteria (Moreno-Gámez, 2022), fungi (Fukasawa & Ishii, 2023) and even plants (Kelly, 1992), and has been recognized as an important factor affecting the dynamics of selection, possibly directing genetic evolution (Rueffler et al., 2007; Edelaar et al., 2008; Edelaar & Bolnick, 2012; Bolnick & Otto, 2013). For example, while ecological generalists are predicted to evolve under weak physiological trade-offs when behavior is random (i.e. organisms cannot modulate how they experience the environment, Levins, 1962; Rueffler et al., 2006), this is no longer true when optimal foraging or matching habitat choice is considered. Instead, adaptive choice behavior tends to favor ecological specialists and not generalists whenever individuals can direct their efforts towards the resource or niche they are good at exploiting, which in turn modifies the selection pressures to promote specialization even more (Rueffler et al., 2007; Ravigné et al., 2009).

Most of previous work on eco-evolutionary dynamics in the face of active choice behavior has focused on exploring rules for the coexistence of specialists and generalists in the context of multiple resources in a single habitat (building on optimal foraging theory, e.g. Stenseth, 1984; Matsuda and Namba, 1989; Abrams, 1999; Svanbäck and Bolnick, 2005; Rueffler et al., 2007), or in the context of multiple habitats containing one resource each (habitat selection models, e.g. Brown, 1990, 1996; Ravigné et al., 2004, 2009). The few models combining both contexts focus on establishing the conditions for the ecological coexistence of specialist species once they already exist as separate ecotypes, but do not focus on the mechanisms of adaptive diversification resulting in the emergence of such ecotypes (Vincent et al., 1996; Abrams, 2006). Some models of adaptive speciation do combine both within-habitat frequency-dependent selection and between-habitat divergent adaptation in driving the emergence of distinct ecotypes (e.g. Rettelbach et al., 2013), but they have not yet been extended to account for flexible behavior.

In this study, we use individual-based simulations to ask how the propensity of resource choice affects the likelihood of evolutionary divergence of ecological specialists. We developed a model with two resources and two habitats, allowing us to explore the continuum from within-habitat, competition-driven diversification to between-habitat diversification driven by adaptation to local resources (similar to Rettelbach et al., 2013). Our model imposes a certain level of adaptive decision making upon resource encounter, mediated by the accuracy with which the profitability of each resource is assessed by consumer organisms. In turn, the profitability of a resource depends on some underlying ecological trait of the individual, and is subject to a utilization trade-off between resources (similar to Rueffler et al., 2007). We investigate the interaction between modes of diversification and resource choice ability by varying choice accuracy and resource partitioning among habitats. We study the generality of our findings across strengths of the utilization trade-off between resources and rates of resource discoverability (which is akin to search time during foraging).

Methods

The model

We consider a population of individuals living across two separate habitat patches connected by dispersal (Fig. 1A). In each habitat, two resources are available for individuals to feed on. The concentration R_{ij} of resource i in habitat j is given by the matrix

$$\boldsymbol{R} = \{R_{ij}\} = \begin{pmatrix} 1 & h \\ h & 1 \end{pmatrix} \tag{1}$$

where h is the habitat symmetry parameter ($0 \leq h \leq 1$). When $h = 1$, both resources are equally distributed between habitats. As h decreases, resources become increasingly restricted to a single habitat, until, when $h = 0$, resource 1 is only found in habitat 1 and resource 2 in habitat 2 (Fig. 1A).

A population of consumers dwells in this landscape. Each individual has a certain quantitative trait x, which indirectly determines its affinity for each resource through a utilization trade-off, such that a value of x increasing the affinity for one resource reduces the affinity for the other, and vice versa. For any given resource i, this affinity, or consumption rate, is given by

$$C_i(x) = \exp\Big(-s\left(x - x_i^{\text{opt}}\right)^2\Big) \tag{2}$$

where x_i^{opt} is the trait value needed for maximum consumption of resource i ($x_i^{\text{opt}} = -1$ for resource 1 and $+1$ for resource 2), and s is the trade-off strength parameter ($s \geq 0$), controlling the widths of the two Gaussian curves (Fig. 1B). The higher the value of s, the narrower the curves and the stronger the trade-off. Because they promote ecological specialization, utilization trade-offs between resources or ecological niches are critical components of adaptive speciation models (Levins, 1962; Rueffler et al., 2006).

The population consists of N individuals. The size of the population is fixed, and generations are discrete and non-overlapping, meaning that at each generation, all adults die and are replaced by N newborns, which will be the adults of the next generation. Reproduction is asexual, and the parents of the newborns are sampled from a weighted lottery where, for each offspring, the probability of an individual to be sampled as the parent of that offspring is proportional to the amount of resource accumulated by that potential parent during its lifetime (which we thus assume to be a measure of its reproductive success).

Resource accumulation occurs during a feeding season, within which individuals must choose one resource to feed on, and can only utilize that resource. To make this choice, individuals evaluate their expected gains from choosing one resource over the other. They then choose the resource that is most profitable to them with a certain probability (see below). The perceived gains of an individual on a particular resource depend on the affinity of that individual for that resource (Eq. 2) and how much of that resource is available in the local habitat. This, in turn, depends on how many individuals have already chosen that same resource, and on the consumption rates of these individuals. The perceived profitability of a resource is the following share of the available resource, proportional to the focal individual's consumption rate relative to others,

$$C_i(x) \Big/ \sum_{k \in S_{ij}} C_i(x_k) \ , \tag{3}$$

where the sum is over all individuals k from the set S_{ij}, containing all individuals living in habitat j and having chosen resource i thus far.

The amount of resource shared among individuals is not necessarily all of the resource that is present in the habitat. If this were the case, it could result in cases where a few migrants arriving in a new, previously unoccupied habitat, would automatically enjoy a large fitness benefit from feeding on some locally abundant resource, simply because of a lack of local competition and despite possibly having low consumption rates for that resource. Such situations are reminiscent of models of *soft selection*, in which the spread of alleles depends more on local, relative fitness than on global, absolute fitness (Levene, 1953; Ravigné et al., 2004; Reznick, 2016). This may of course occur in nature, but in this study we wanted to be able to modulate the degree to which individuals are also impacted by their absolute fitness — a hallmark of *hard selection* (Dempster, 1955; Ravigné et al., 2004) — irrespective of any local relief from competition. Notably, models of hard selection are much less prone to the coexistence of multiple genotypes than models of soft selection, and this distinction was shown to be important for the evolution and coexistence of ecological specialists and generalists (Ravigné et al., 2004, 2009). To fine-tune the behavior of our model along this continuum, we introduce a new parameter, the resource discovery rate δ, which controls how much of the total resource in a habitat is available to the population of consumers. This amount of resource discovered is given, for resource i in habitat j, by

$$R_{ij}^{\mathrm{D}} = R_{ij} \left(1 - \exp\Big(- \delta \sum_{k \in S_{ij}} C(x_k) \Big) \right) \ , \tag{4}$$

which is a saturating function of the cumulative consumption rate $\sum_{k \in S_{ij}} C(x_k)$ of all consumers having chosen that resource, asymptotically reaching R_{ij} (Fig. 1C). The resource discovery rate δ is therefore the initial slope of this saturating curve ($\delta > 0$), and could be interpreted as the approximate amount of resource i that would be found by a single hypothetical individual, alone in the habitat and with consumption rate $C_i(x) = 1$ (the maximum achievable consumption rate).

During a feeding season, individuals are taken in random order, and make their decision based on their perceived share (Eq. 3) of the resources discovered so far (Eq. 4) by all individuals earlier in the queue. To limit the influence of the order in which individuals are choosing, each generation consists of n_{R} feeding rounds, or seasons, where a new random order is sampled every time.

Once the perceived profitability has been calculated for each resource for a given individual in the feeding queue, the individual chooses one of the two resources to exploit. At this point, the resource with the higher perceived profitability may be considered a better option for the individual (but see below). The individual then picks that better resource with probability

$$P_{\text{best}} = (1 - \beta)\, P_0^{\text{best}} + \beta \tag{5}$$

where β is the resource choice accuracy, determining the weight of the perceived profitability in the decision-making process of the individual ($0 \leq \beta \leq 1$). If $\beta = 1$, individuals always choose the most advantageous resource. If $\beta = 0$, profitability is irrelevant, and resource choice then depends on the probability of encountering the better resource, P_0^{best}. This probability is in turn given by

$$P_0^{\text{best}} = {}^{1}\!/_{2}\,(1 - \alpha) + \alpha\, R_{\text{best}} \big/ R_{\text{tot}} \tag{6}$$

where R_{best} is the total concentration of the better resource in the local habitat (R_{1j} or R_{2j}), R_{tot} is the sum of both total resource concentrations ($R_{1j} + R_{2j}$), and α is the resource abundance weight parameter, determining how much the probability of encounter of a resource is determined by its abundance ($0 \leq \alpha \leq 1$). When $\alpha = 1$, the probability of encounter of a resource is equal to its abundance relative to the other resource, $R_{\text{best}} \big/ R_{\text{tot}}$ (Fig. 1D). When $\alpha = 0$, this probability is ${}^{1}\!/_{2}$, irrespective of resource abundances. Note that the probability of encounter of the best resource is also ${}^{1}\!/_{2}$ whenever $h = 1$, regardless of α, because in that case the resource concentrations in each habitat are equal. Hence, parameter α really only makes a difference when $h < 1$ (i.e. $R_{1j} \neq R_{2j}$). Scenarios where $\alpha \neq 1$ and $R_{1j} \neq R_{2j}$ could correspond, for example, to situations where resources can be found in two particular species of trees, both occupying equal surfaces in the habitat, but with different yields of usable resource per unit area. Note that although parameter β controls the probability of accurately choosing the better of the two local resources given their known profitability, for all intents and purposes this is equivalent to the accuracy with which individuals perceive this profitability (i.e. in this study choice accuracy is indistinguishable from assessment accuracy).

Actual resource gains are not distributed until all individuals have chosen which resource to utilize. This means that the actual gains individuals receive may not be the same as the gains they expected upon choosing a resource based on perceived profitability. Once all individuals have chosen (i.e. at the end of a feeding season), the final amounts of resource discovered R_{ij}^{D} are computed (as per Eq. 4) and individuals receive their share, proportional to their consumption rate relative to others (as per Eq. 3). The next feeding season then starts, where individual choice occurs in a new random order. The gains from all the feeding seasons are accumulated to constitute a total amount of resource obtained across seasons. This amount of accumulated resources then serves as the weight in the weighted lottery of asexual reproduction.

During the reproduction step, each newborn individual is an almost identical clone of its parent, albeit with a potential mutation applied to it. Mutations occur at rate μ (the per capita mutation rate) and affect the value of trait x. When a mutation occurs, a deviation is sampled from a normal distribution with standard deviation σ_x (the mutational standard deviation) and applied to the trait value of the newborn. Newborns at first inherit their parent's habitat, but after mutation has occurred, can disperse to the alternative habitat with probability m (the per capita migration rate).

Analysis

We tracked the mean trait value in the population through time across simulations, as well as measures of ecological isolation and spatial isolation between nascent ecotypes (i.e. clusters of individuals above versus below the mean trait value of the whole population at a given time). We refer to the clear separation and divergence of both ecotypes along the ecological trait axis x as *evolutionary branching*, which is diagnosed based on the value of the ecological isolation statistic.

The degree of ecological isolation is measured by

$$\mathrm{EI}_0 = 1 - \frac{N_1\,V_1 + N_2\,V_2}{N\,V} \tag{7}$$

where N_i is the number of individuals in ecotype i, V_i is the variance in trait value x within ecotype i, N is the total population size and V is the total variance in x across the entire population. This statistic ranges between 0 (full overlap) and 1 (full clustering). However, due to the impossibility of both ecotypes to overlap in trait value (the mean trait value being a hard cut-off between the two), EI_0 rarely goes below $2/\pi \approx 0.64$ (which can be shown to be the value the statistic should take in a perfectly normally distributed population split in two halves), which renders interpretation difficult. To correct for that, we rescaled EI_0 into

$$\mathrm{EI} = \big(\mathrm{EI}_0 - 2/\pi\big)/\big(1 - 2/\pi\big)\ , \tag{8}$$

which technically ranges between $1/(1-\pi/2) \approx -1.75$ and 1, but will typically be around 0 for a unimodal, normally distributed sample of trait values.

The degree of spatial isolation between the two ecotypes is computed as

$$\mathrm{SI} = \left| \frac{n_{11}\,n_{22} - n_{12}\,n_{21}}{\sqrt{n_{1\cdot}\,n_{2\cdot}\,n_{\cdot 1}\,n_{\cdot 2}}} \right| \tag{9}$$

where n_{ij} is the number of individuals from ecotype i in habitat j, $n_{i\cdot}$ is the total number of individuals in ecotype i (across both habitats) and $n_{\cdot j}$ is the total number of individuals in habitat j (across both ecotypes). This statistic quantifies the restriction of each ecotype to one habitat, and ranges between 0 (for complete habitat overlap of the ecotypes) and 1 (for complete spatial separation).

Adaptive dynamics In parallel, interpretation of the simulations was aided with numerical analyses based on adaptive dynamics theory (Metz et al., 1992; Geritz et al., 1998), a body of mathematical tools used to predict the effect of selection on eco-evolutionary dynamics (see Appendix). We used these to verify our simulations when compared to dynamics derived independently from the simplest case of no resource choice ($\beta = 0$).

Simulations

Simulations were run across various combinations of parameters for a total of $T_{\max}$ generations, with each simulation starting with N identical individuals with initial trait value x_0. Unless specified otherwise in the figures, parameters and their values are as per Table 1.

Specifications

The simulation code in this study was written in the programming language C++20 using standard libraries. Analyses were performed both within the simulations as well as externally, in the R computing environment, version 4.3.3 (R Core Team, 2025). See accompanying code for details.

Results

Symmetric habitats under random choice

We first focus on the case of high habitat symmetry ($h = 1$) where both resources are in equal concentrations in each habitat. Until further notice, we also focus on $\alpha = 1$, in which resources are encountered proportionately to their local abundance (we relax this assumption at the end of this section). Figure 2 shows an example outcome of one simulation in such a case, with intermediate resource choice accuracy β. Analysis of the adaptive dynamics of a deterministic approximation of the model shows general agreement with our stochastic individual-based simulations in the simple case of absence of active resource choice ($\beta = 0$, Fig. S2).

When resource choice is fully random ($\beta = 0$), the strength s of the utilization trade-off between resources determines whether evolutionary branching takes place (Fig. 3, S3). If the trade-off is very weak, a population of generalists evolves, capable of utilizing both resources equally well (i.e. with trait values close to $x = 0$, Fig. 3, S3A). This happens when $s < 0.5$, as in that case the average consumption rate over both resources is maximized at a generalist strategy when each resource is encountered half of the time (Fig. S3C). If the trade-off is very strong (and how strong is too strong depends on the resource discovery rate δ, see Fig. 3), the penalty for deviating from the original phenotype is so high that the population remains specialized on the one resource it is already well adapted to (here, resource 1, when the population starts at $x_0 = -0.9$, Fig. 3, S3A). Branching occurs when the trade-off is strong enough that the total consumption of a specialist (e.g. $x \approx \pm 1$) exceeds that of a generalist ($s > 0.5$), but weak enough that generalists first enjoy a frequency-dependent advantage from utilizing the under-exploited alternative resource (e.g. resource 2), in a population mostly consisting of specialists of one resource (e.g. resource 1). A generalist phenotype then replaces the initial specialist, but loses its advantage once it becomes common, as specialists are now favored that could exploit each resource more fully. Since a specialist of a single resource would restore the asymmetric depletion of the resources that favored generalists in the first place, the only stable outcome is the emergence of two alternative specialists, each depleting its own respective resource — evolutionary branching has occurred ($s = 1$ in Fig. S3A). Because both resources are present in equal quantities in both habitats, the newly split divergent ecotypes diversify in sympatry and spatially overlap (Fig. 3C, S3B). These results are in agreement with the predicted adaptive dynamics of the model in the absence of active resource choice ($\beta = 0$, Fig. S2A).

Resource choice in symmetric habitats

The first notable effect of a nonzero resource choice accuracy β is to prevent the evolution of a generalist phenotype under weak trade-offs ($s < 0.5$), instead promoting branching into two specialists (Fig. 3, S4). As individuals become better at picking the most advantageous resource, the same frequency-dependent advantage as described previously pushes individuals slightly less well adapted to the initially preferred resource 1 to actively choose the alternative resource 2 once the former becomes depleted (Fig. S4). Because the trade-off is relatively weak, individuals choosing the alternative resource for which they are rather maladapted enjoy a similar fitness as those choosing the depleted resource (Fig. S4B). In turn, this splits the population into two groups, with individuals from one end of the phenotypic spectrum consistently exposed to their originally preferred resource, and individuals from the other end consistently driven to the alternative resource by competition. Biased exposure to different resources at both ends of the phenotypic spectrum leads to the adaptive divergence of two alternative specialist strategies, this time without a generalist phase (Fig. S4A); branching occurs.

The second clear effect of resource choice is a reduction in the maximum trade-off strength s still allowing branching (Fig. 3, S5). That is, under high trade-offs which would have normally favored frequency-dependent branching under random choice ($\beta = 0$), increasing choice accuracy β prevents branching, and increases the probability that the population will remain as a single resource specialist instead. When the trade-off is strong, the most advantageous resource will often be the resource the initial population of specialists is already adapted to (here, resource 1), because deviating from that specialized phenotype (and adapting to resource 2) comes at a heavy cost (Fig. S5). For branching to occur, this cost must be offset by the frequency-dependent advantage gained from avoiding competition for the depleted resource, and this advantage must be strong enough to compensate for the fact that higher choice accuracy β reduces exposure to the under-exploited resource (i.e. the trade-off must be weaker). The same mechanism of active, behavioral bias in exposure operates that favors two specialists over one generalist under weak trade-offs (as presented in the previous section), except that under strong trade-offs, the frequency-dependent advantage to utilize the under-exploited resource is no longer sufficient for adaptation to that resource to occur.

Asymmetric habitats under random choice

The maximum trade-off strength still allowing branching slightly goes down as habitat asymmetry increases ($h < 1$) when resource choice is random ($\beta = 0$, Fig. 3). In asymmetric habitats (low h), one resource is rare and the other is common in any given habitat (e.g. with $h = 0.1$ resource 1 is encountered $10/(10 + 100) \approx 9\%$ of the time in habitat 2 and the same is true for resource 2 in habitat 1). Therefore, specialist individuals migrating into a yet unoccupied habitat find themselves with their preferred resource (the one they are already well adapted to) being the rare one. If the preferred resource is encountered too rarely, and the alternative, maladaptive abundant resource is utilized most of the time, the fitness of foraging individuals is no longer sufficient to spread and establish a viable population in the new habitat (Fig. S6). Instead, the population remains mostly restricted to its ancestral habitat, with few migrants arriving at each generation in the alternative habitat (here at rate $m = 0.01$, see Methods and Table 1), but rarely leaving offspring for the next generation (owing to a low fitness after all feeding rounds, Fig. S6D). Branching no longer occurs where more symmetric habitats (higher h) would have promoted it, and the strength s of the trade-off must be lowered to increase the fitness of specialists of one resource utilizing the other resource, and allow branching again. Once the trade-off is appropriately reduced, branching can occur in asymmetric habitats, and involves both a high degree of spatial isolation between diverging ecotypes, as well as rapid ecological divergence, without an intermediate generalist phase (Fig. S7). Then, the rare encounter of one resource in each habitat selects against generalists and for specialists. We note that the frequency-dependent advantage of utilizing the under-exploited resource disappears in highly asymmetric habitats, as adaptation to a new resource occurs when its utilization becomes more advantageous than the alternative, much-too-rare ancestral resource, regardless of its state of depletion. In asymmetric habitats, branching is driven more by frequency-independent local adaptation than by frequency-dependent disruptive selection arising from competition.

Resource choice in moderately asymmetric habitats

In moderately asymmetric habitats where the rare resource is still discoverable by a non-negligible minority of individuals (i.e. here, when $h = 0.1$ and $\delta = 0.04$), increasing the resource choice accuracy β restores the frequency-dependent advantage of generalists, leading to branching under stronger trade-offs, but only up to a point ($\beta \approx 0.25$ in Fig. 3), beyond which the maximum trade-off allowing branching decreases again (Fig. 3, S8). This is because as β increases, individuals pick the preferred but rare resource more often after migrating to a new habitat (when the rare resource is rare but not too rare, picking that resource pays off, but non-choosy individuals, i.e. $\beta = 0$, would typically not encounter it). That rare resource, in turn, is sufficiently rare that a few accurate choosers are enough to deplete it, now giving a frequency-dependent fitness advantage to individuals choosing the alternative resource and favoring adaptation to it — branching occurs. When choice accuracy β becomes high (beyond the apparent threshold of $\beta \approx 0.25$), however, the same phenomenon happens as in symmetric habitats ($h = 1$), where individuals choose the preferred resource (the one they are already well adapted to) so often, and exposure to the alternative resource is so reduced, that a higher consumption efficiency on the latter is no longer beneficial (Fig. S8). As a result, the breadth of trade-off values allowing branching peaks at intermediate levels of resource choice accuracy β.

This effect of resource choice on frequency-dependent disruptive selection in asymmetric habitats is further exemplified when the migration rate m is reduced. As the rate of migration decreases, the pattern described above becomes more pronounced, and branching occurs under stronger trade-offs at intermediate choice accuracies β (except this time the peak is located at $\beta \approx 0.3$, Fig. S9, S10). Under reduced migration, two things happen (Fig. S10). First, competition intensifies in the ancestral, highly populated habitat, as fewer individuals leave every generation, thus generally reducing fitness and lowering the representation of this habitat in the reproductive pool compared to the new habitat (which experiences less competition), and therefore amplifying the frequency-dependent advantage of adaptation to the alternative resource in the new habitat. This intensification of competition due to less emigration is negligible in the new habitat, which is too poorly populated. In contrast, and second, reduced (im)migration decreases competition for the rare resource in the new habitat, thereby increasing the fitness of individuals utilizing it. With increased fitness from choosing the ancestral resource, the depletion of that resource triggers the frequency-dependent advantage of utilizing the alternative, more common resource. Through these two processes, reduced migration amplifies the strength of frequency-dependent selection driving branching, when selection takes place in asymmetric resource availability conditions (i.e. when habitat asymmetry is moderate and the rarity of the rare resource is not prohibitively high). Importantly, the migration rate does not affect other model outcomes across parameter space (Fig. S9), strengthening the idea that the observed effect of resource choice accuracy on branching in asymmetric habitats is indeed mediated through its role as modulator of frequency-dependent selection.

The phenomenon of branching being most favored at intermediate resource choice accuracy also relies on the rare resource not being completely unavailable. If that resource is rare, but can still be discovered a non-negligible proportion of the time (e.g. $h = 0.1$ and $\delta = 0.4$), then the preferred resource is depleted even at low choice accuracy, and branching occurs under a similar range of trade-offs as in symmetric habitats (Fig. 3). If the rare resource is too rare (e.g. $h = 0.01$), or moderately rare but too difficult to discover (e.g. $h = 0.1$ and $\delta = 0.004$), it is never advantageous enough to be depleted, in which case there is no rise in maximum trade-off allowing branching, because frequency-dependent selection never happens (Fig. 3, see below).

Highly asymmetric habitats

All aforementioned effects of resource choice accuracy disappear in highly asymmetric habitats (e.g. $h = 0.01$), or at least asymmetric habitats where the rare resource is particularly difficult to find (i.e. a low resource discovery rate δ is also needed, e.g. $h = 0.1$ but $\delta = 0.004$, or $h = 0.01$ as long as $\delta < 0.4$). In those conditions, the maximum trade-off still allowing branching is more-or-less constant with respect to resource choice (Fig. 3, S11). This is because the rare resource has become so rare or unavailable, that a higher choice accuracy no longer contributes to depleting it more (the previously mentioned phenomenon by which individuals choosing the alternative abundant resource become more advantaged). As a consequence, whether evolutionary branching occurs almost exclusively depends on the strength of the trade-off s in highly asymmetric habitats. If the trade-off is very strong, the new habitat is a demographic sink for all choice strategies: non-choosy individuals (low β) utilize the abundant resource but are too maladapted to it, and choosy individuals (high β) find it more advantageous to pick the rare resource, but it still yields so little, that the establishment of a viable local population (and therefore adaptation) is not possible either way. Once the trade-off becomes sufficiently weak, the abundant resource becomes advantageous over the rare one, and it ends up being picked by choosy individuals (high β, by active choice) as well as by non-choosy individuals (low β, by passive exposure). Whether this results in local adaptation and (frequency-independent) branching then depends on whether that abundant resource yields a high-enough fitness to establish a viable local population, and this, again, depends on the strength of the trade-off which affects all resource choice strategies β in the same way (Fig. S11).

That said, there seems to be a very slight increase in the maximum trade-off allowing branching at high choice accuracy when resource discovery is very low and habitat symmetry is low but not too low ($h = 0.1$ and $\delta = 0.004$, Fig. 3, S12, S13). This is because as the trade-off becomes weak enough that it is advantageous for choosier individuals (higher β) to pick the more abundant resource, therefore utilizing resources in similar proportions to non-choosy individuals (which predominantly choose the abundant resource due to passive exposure), still some non-choosy individuals pick the rare resource a higher proportion of the time than choosier individuals. That proportion is dictated by the habitat symmetry parameter h (e.g. passive choosers still choose the rare resource 9% of the time when $h = 0.1$, 0.9% when $h = 0.01$, etc.). In contrast, in such conditions, the exposure of choosy individuals to the abundant resource tends to be slightly higher (as it is motivated by active choice), thus increasing the advantage to adapt to that resource, and allowing this adaptation to happen up to slightly stronger trade-offs. Because the increase in exposure from active choice is even more slight when habitat symmetry is lower (e.g. it can only be from 99.1% to 100% when $h = 0.01$), this weak pattern is more visible in more moderately asymmetric habitats (e.g. $h = 0.1$ instead of $h = 0.01$, Fig. S13). This phenomenon only applies when resource discovery is low (here, $\delta = 0.004$) because as resource discovery increases, the rare resource can now be depleted enough that frequency dependence kicks in and overrides this weak pattern (Fig. 3).

Finally, highly asymmetric habitats strongly select against generalists. Again, because of biased exposure to a locally abundant resource, the frequency-dependent advantage of generalists disappears, and divergent specialists evolve locally adapted to the more abundant resource in each habitat, even at very weak trade-offs as long as they are nonzero (when $s = 0$ genetic drift takes over and no divergence occurs between the habitats due to substantial migration, $m = 0.01$, Fig. 3, S14). The same phenomenon is separately predicted by the adaptive dynamics of the model without active choice ($\beta = 0$, Fig. S2B). Note that generalists may still be favored in asymmetric habitats if individuals could disperse between habitats multiple times in their lifetime, but we did not consider this option here. Resource choice accuracy β does not affect this pattern, as choosier individuals (high β) get exposed to the locally abundant resource just the same, albeit by choice (Fig. S14).

Effect of the resource discovery rate

Other than through interactions with the parameters explored above, the main effect of the resource discovery rate δ is to increase the range of trade-offs suitable for branching by allowing branching at stronger trade-offs (Fig. 3). When resource discovery increases, individuals can access more of the resource contained in a habitat, which tends to (1) increase the fitness of individuals specializing on a rare resource in asymmetric habitats (Fig. S15), and (2) contribute to resource depletion, and therefore frequency-dependent disruptive selection, in more symmetric habitats (thereby also making moderately asymmetric habitats more equivalent to symmetric habitats with respect to branching dynamics, and making resource choice accuracy β matter more in those cases, e.g. $h = 0.1$ in Fig. 3). Notably, the resource discovery rate has no effect on the minimum trade-off strength s needed for branching, as this depends entirely on the partitioned exposure to the two resources brought about by habitat asymmetry (low h) or active choice (high β), in conditions where generalists would otherwise be favored if resources were encountered equally often (under weak trade-offs, the discovery rate is not limiting the amount of resource utilized). The expansion of the range of trade-offs suitable for branching with higher resource discovery rate is separately predicted by the deterministic adaptive dynamics of the model under random choice ($\beta = 0$, Fig. S2).

Effect of resource compartmentalization

We studied a version of our model where resource encounter is independent of resource abundance, by setting the resource abundance weight parameter α to zero (see Methods). When $\alpha = 0$, non-choosy individuals ($\beta = 0$) encounter each resource half of the time, even if one is rare (i.e. regardless of h). This could correspond to a situation where resources are nested in compartments within the habitat (i.e. microhabitats) — e.g. fruits within host plants, preferred heights within trees, or host species of corals within coral reefs — with the constraint that the two microhabitats occupy the same area in the habitat. This may not be an accurate description of all ecosystems, but this extension of the model at least allows to explore the roles of stratification and compartmentalization of resources in the environment. The implementation is such that choosy individuals (higher β) are able to direct their foraging efforts more towards the microhabitat that yields the highest payoff (see Methods for details).

When resource encounter and abundance are fully decoupled, the microhabitat that hosts the rare resource in asymmetric habitats (low h) has a particularly low yield, but is still explored by non-choosy individuals. Exposure to the abundant resource in a habitat is therefore reduced, increasing the profitability that this resource must have in order to be advantageous to specialize on (i.e. to compensate for the cost of deviating from a phenotype specialized on the rare resource). Hence, compartmentalization of the resources through the decoupling between encounter and abundance decreases the maximum trade-off strength still allowing branching under random resource choice ($\beta = 0$, Fig. S16, S17, also visible in analyses of the adaptive dynamics of the model under random choice, Fig. S2C). Increasing the resource choice accuracy β makes the resource abundance weight α irrelevant, as highly choosy individuals (e.g. $\beta = 1$) direct their efforts purely based on expected payoff and target the most advantageous resource regardless of the rate of passive encounter. Therefore, the foraging and branching dynamics of $\beta = 1$ when $\alpha = 0$ are identical to when $\alpha = 1$ (all of the aforementioned Results). This produces patterns similar to the case without compartmentalization in the more symmetric habitats (high h): $\alpha = 0$ yields the same foraging dynamics as $\alpha = 1$ in fully symmetric habitats ($h = 1$), because then no resource is more rare than the other, irrespective of microhabitats. In asymmetric habitats (low h), however, this means that branching will occur under stronger trade-offs s at higher choice accuracies β, owing to choosier individuals wasting less energy foraging in microhabitats where the yield is low, and generally increasing fitness and the potential for local adaptation (Fig. S16).

Generalist starting point

When the population starts as a generalist ($x_0 = 0$), branching occurs up to much stronger trade-offs than when starting as a specialist (Fig. S18). This occurs for both symmetric and asymmetric habitats, albeit because of different reasons. In asymmetric habitats (low h), branching occurs up to stronger trade-offs s for a generalist, because a generalist population is exactly at the right starting point to readily respond to the two opposite regimes of directional selection operating within each habitat (i.e. selection towards specializing to the most locally abundant resource) — it does not need to de-specialize, unlike a specialist population which must overcome the cost of deviating from its well-adapted initial phenotype in order to successfully colonize the alternative habitat (Fig. S19). This is independent of resource choice strategy, and therefore, the maximum trade-off still suitable for branching remains relatively constant with respect to resource choice accuracy β (Fig. S18). The upper limit in trade-off strength still allowing branching is the point where directional evolution in the starting habitat occurs so fast relative to the colonization of the alternative habitat (owing to differences in habitat-specific population size) that the population only specializes on the resource most abundant in its environment (this is visible when the resource discovery rate is sufficiently low, e.g. $\delta = 0.004$ in Fig. S18, which reinforces the penalty suffered by migrants once the population starts to specialize). We note that under strong trade-offs, it is likely that a generalist population will go extinct before any adaptation can occur, as the population is not sufficiently adapted to either resource to start with (being a generalist), but this cannot happen in our model where the population size is fixed (here $N = 1\,000$).

In symmetric habitats (high h), the upper limit to the strength of the trade-off still allowing branching increases with resource choice accuracy β (Fig. S18). This is because active resource choice from a generalist reinforces the frequency-dependent processes responsible for branching in sympatry. In symmetric habitats, evolutionary branching under random choice ($\beta = 0$) is typically preceded by the evolution of a transient generalist phenotype (e.g. Fig. S3), because that phenotype is a branching point: an attractor of the adaptive dynamics which becomes unstable once reached (this can be visualized by performing an invasion analysis, see Fig. S2) — starting at the branching point therefore maximizes the chances of branching. As the strength s of the trade-off increases, specialists become increasingly fitter than generalists, and may tend to remain specialists, but this depends on the exact starting trait value. Indeed, phenotypes that are sufficiently close to the branching point ($x = 0$) may still fall within its basin of attraction, instead of evolving towards one of the two specialist equilibrium phenotypes ($x = \pm 1$). By exploring evolutionary endpoints of simulations across starting phenotypic values x_0, we find that the basin of attraction of the generalist branching point shrinks faster with increasing trade-off strength s under active resource choice than under random choice (Fig. 5), but that the branching point itself remains a branching point up to higher trade-off strengths, thus explaining the more widespread branching observed at higher resource choice accuracy β. Upon closer inspection, we find that this robustness of the branching point to stronger trade-offs stems from active resource choice keeping the profitability of the two resources in check with respect to one another — every time a resource is used slightly more, the alternative resource automatically becomes more advantageous to generalists, and the next individual in the queue chooses it (Fig. S20), thus creating frequency dependence that maintains the generalist phenotype as an evolutionary attractor. This breaks down when s reaches very high values, at which point the basin of attraction of the generalist equilibrium shrinks to zero and this equilibrium becomes a repellor, i.e. the junction between the basins of attractions of the two remaining stable equilibria (the specialist phenotypes $x = \pm 1$). Then, an initial generalist typically falls on one side or the other (depending on the stochasticity of drift and mutations) and undergoes purely directional selection towards specialization on a single resource (e.g. Fig. S20).

We note that the lower end of trade-off values s suitable for branching are not affected by the starting phenotype (Fig. S18). In asymmetric habitats, weak nonzero trade-offs always favor ecological divergence regardless of resource choice (see previous sections). In symmetric habitats, weak trade-offs select for a single generalist as stable endpoint of evolution (Fig. S4), and so starting there does not affect these dynamics. Besides, and for the same reasons as mentioned before, the resource discovery rate δ expands the range of trade-off values suitable for branching in generalist starting populations as well (Fig. S18), by reducing the penalty suffered by less-well-adapted individuals when the population starts to deviate from the central phenotype $x = 0$.

Discussion

In this study we explored the eco-evolutionary dynamics of an individual-based model of adaptive diversification under various degrees of resource choice behavior. We find the following. (1) Choosiness promotes ecological specialization and resource conservatism (i.e. prevents adaptation to other resources present in the environment), selecting against generalists as long as the population does not start off as a generalist. (2) This resource conservatism reduces the scope for within-habitat frequency-dependent diversification (in the form of evolutionary branching) when the population starts as a specialist. (3) While higher choosiness favors conservatism in specialists, the generalist strategy remains a branching point for stronger trade-offs for those strategies starting sufficiently close to it. (4) The effect of resource choice is negligible when the resources are highly spatially partitioned. (5) The scope for branching is maximized at intermediate choosiness when resources are moderately partitioned spatially.

Previous models of diet and habitat choice have identified the phenomenon whereby increased choosiness tends to select for specialists and against generalists (Rueffler et al., 2007; Ravigné et al., 2009). Ravigné et al. (2009) highlighted that this "raises the bar" for evolutionary explanations of ecological generalism, which must then include factors such as fluctuating environments (Kisdi, 2002; Egas et al., 2004), selection for dispersal (Kisdi, 2002; Ronce, 2007; Edelaar et al., 2017) or suboptimal decision making due to incomplete information (Egas et al., 2004; Rueffler et al., 2007). This stands in stark contrast with models lacking diet or habitat choice, which predict that generalists are favored when the shape of the utilization trade-off curve between resources is convex (equivalent to our trade-off strength parameter s being below the threshold value of $s = 0.5$; Levins, 1962; Rueffler et al., 2006). By biasing exposure to any preferred resource, choosiness increases how profitable the alternative resource must be for there to be a frequency-dependent advantage to utilize it. Selection favors adaptation to the resources that are already disproportionately used (as already noted in Rueffler et al., 2007). In turn, this directs evolution towards niche conservatism, and hinders adaptive diversification of specialists in sympatry, for a species that is already somewhat specialized on a given resource.

For an initial generalist, however, frequency-dependent diversification within a habitat can occur up to stronger trade-offs under active (i.e. more accurate) resource choice than under random choice. With active choice, a population of generalists will keep the profitability of two initially equally abundant resources in check with respect to each other, by systematically alternating foraging efforts towards the slightly less depleted resource. This makes the generalist phenotype a convergent attractor of the evolutionary dynamics despite strong ecological trade-offs, maintaining the population under disruptive selection where random choice would have pushed the system towards specialization on a single resource as soon as a stochastic utilization bias emerges. Rueffler et al. (2007) found that diet choice reduces the chances to approach a branching point when not starting as a generalist, but did not comment on the robustness of the convergence stability of the generalist branching point under strong trade-offs. To our knowledge, this phenomenon has not been described before, and suggests that active choice may actually facilitate adaptive diversification when the initial population is an ecological generalist. We note, however, that this relies on the resources being in similar abundance and availability in the environment: if one resource becomes utilized in sufficiently greater proportion, active choice will promote specialization for that resource. Hence, this phenomenon may be more readily observed (if at all) in natural systems where resources are relatively abundant and easy to find. On the one hand, this could be the case for *pursuer* species of foragers (sensu MacArthur and Pianka, 1966), which are not limited by resource scarcity and instead invest in optimizing handling time (MacArthur & Pianka, 1966; Norberg, 1977; Stephens & Krebs, 1986; Norberg, 2021). Hummingbirds and honeyeaters are usually cited as belonging to that category (Norberg, 2021). On the other hand, *searcher* species (limited by long search times) have been proposed to be more often generalists than pursuer species (MacArthur & Pianka, 1966; Brown, 1990). Alternatively, this phenomenon could also apply to species whose resource encounter is high enough that they can afford “laziness” most of the time, such as short-tailed shrews *Blarina brevicauda* (Martinsen, 1969; Herbers, 1981), or sit-and-wait predators such as *Anolis* lizards (Andrews, 1971).

The effect of resource choice on diversification dynamics disappears as resources become highly spatially isolated. Hence, resource choice is predicted to play little role in colonization-driven, frequency-independent speciation. This, however, is not true for moderately spatially partitioned resources. Rather, we show that active resource choice brings frequency-dependent selection back into spatially heterogeneous habitats where it would have been negligible under random choice. Intermediate resource partitioning may be a hallmark of common settings for ecological speciation, such as ecological gradients (Endler, 1977; Doebeli & Dieckmann, 2003; Nosil, 2012), parapatric biogeography (Gavrilets et al., 2000; Mallet, 2005) and hybrid zones (Endler, 1977; Barton & Hewitt, 1989; Abbott, 2017). In fact, Doebeli and Dieckmann (2003) found that a spatial ecological gradient in resource availability must be steep, but not too steep, to maximize disruptive frequency-dependent selection and speciation in a parapatric setting. Our results suggest that active resource choice may be another way to reinforce this frequency-dependent process of competition in spatially heterogeneous landscapes.

Rettelbach et al. (2013) showed that disruptive frequency-dependent selection driven by competition within habitats could interact with between-habitat, frequency-independent divergent selection to produce a third type of scenario beyond the more *competitive* (within-habitat and through frequency-dependent selection) and the more *ecological* (between-habitat and through local adaptation) modes of adaptive speciation (Dieckmann et al., 2004; Nosil, 2012; Rettelbach et al., 2013). In their model, assortative mating and sexual reproduction are key to this third mode of speciation. Although our results do not necessarily qualify as a new mode of speciation, here we show that frequency-dependent and spatially divergent selection also interact in an asexual model, independent of assortative mating, when resource choice behavior is taken into account. Evidence for both frequency-dependent disruptive selection and divergent local adaptation acting in concert has been documented in relation to speciation in three-spine sticklebacks *Gasterosteus aculeatus* (Schluter, 2003; Bolnick, 2004; Hendry et al., 2009; Bolnick & Stutz, 2017).

Under moderate spatial partitioning of the resources, the scope for evolutionary branching of an initial specialist is maximized at intermediate resource choice accuracy (i.e. choosiness) — enough to promote resource depletion, but not so high as to promote resource conservatism. We note that in our model the capacity for resource choice does not evolve, i.e. the assessment accuracy is fixed (similar to matching habitat choice in Ravigné et al., 2004). Models of resource choice have traditionally analyzed the evolution or coexistence of ecological morphs once optimal behavioral preference has been achieved, that is, assuming that behavior has evolved, and done so rapidly (e.g. Stenseth, 1984; Brown, 1990; Vincent et al., 1996; borrowing from optimal foraging theory, Stephens and Krebs, 1986). In contrast, it may be argued that neural mechanisms that are critical for optimal decision making during foraging evolve slowly, compared to ecological and/or morphological adaptations related to niche use (Pyke, 1984; Bernays, 1998; Railsback, 2022). Suboptimal foraging and incomplete information about the environment may be the rule more than the exception, due to the various biological functions trading-off with energetically demanding cognitive abilities (Mayhew, 1997; Morris, 2003). Hence, we consider it important to not only look at purely adaptive behavior, but to explore the continuum of possibilities between random choice and fully accurate decision making (e.g. as in Rueffler et al., 2007). Doing so allowed us, for example, to find that the scope for evolutionary branching is maximized at intermediate resource choice accuracy in moderately asymmetric habitats, which may be highly relevant in systems where resource choice behavior is not optimal.

We also find that resource choice may matter more for diversification when resources are spatially heterogeneous but compartmentalized in microhabitats within habitats (e.g. fruits within trees within a locality, if this is the scale at which resource exploitation is relevant, Morris, 1987). We consider the case where microhabitats are in similar propensity but of different profitability in different localities. When this type of resource structure is considered, more adaptive resource choice allows to direct efforts towards the most profitable microhabitat, which facilitates between-habitat divergence through local adaptation. This highlights the negative effect that resource compartmentalization has on adaptive divergence across habitats in the absence of active choice, as it causes non-choosy organisms to waste energy by foraging in unprofitable microhabitats, a phenomenon connected to incomplete information about the environment and documented, for example, in phytophagous insects (Mayhew, 1997).

Previous studies have highlighted the role of the scale of competition and density regulation in habitat selection models (reviewed in Ravigné et al., 2009). Under soft selection, density is regulated within habitats and the number of individuals produced in each habitat, i.e. habitat output, is constant (Levene, 1953). Under hard selection, density regulation via competition is global, and habitat output is variable (Dempster, 1955). Protected polymorphism (i.e. diversity of coexisting morphs) is typically only allowed in population genetics models of soft selection, as in hard selection models the fittest genotype overtakes the entire population (Levene, 1953; Kisdi, 2001; Ravigné et al., 2004). In a hybrid model with local density regulation but variable habitat output (which would normally behave like a hard selection model in the absence of habitat choice), Ravigné et al. (2004) showed that matching habitat choice makes selection softer by expanding the impact of local density regulation on the maintenance of a polymorphism. Considering habitat choice analogous to resource choice (as in many classical models of matching habitat choice, the choice affects which habitat to migrate into based on the profitability of the local resources, reviewed in Ravigné et al., 2009), we find the opposite pattern (and so do Rueffler et al., 2007). This is because the model by Ravigné et al. (2004) is a population genetics model with haploid genetics, where extreme phenotypes are within a single mutational step from each other. Instead, a continuously varying (possibly polygenic) specialization trait leads to a bistable system where both extremes are stable and may well coexist (Rueffler et al., 2007), but directional selection will typically direct within-habitat trait evolution one way or the other in the absence of frequency-dependent selection (as in Rueffler et al., 2007; Ravigné et al., 2009).

While our model has a fixed consumer population size and technically does not follow the usual classification of soft versus hard selection models, habitat output is variable and our model is technically closer to a hard selection one. Nevertheless, we can tune the dynamics between softer-selection outcomes and harder-selection outcomes with our resource discovery parameter δ. With high δ, foragers share all of the resource in a habitat (proportionately to their utilization efficiency), allowing poor consumers of a local resource to nevertheless enjoy a high fitness in the absence of competition; migrants can easily establish and evolve to specialize on the local resource (this is essentially soft selection favoring protected polymorphism). With low δ, the amount of resource obtained is constrained by utilization efficiency, and a poor consumer of a local resource will typically not establish, regardless of the absence of competition (this is hard selection). Consistent with that, higher resource discovery generally broaden the range of trade-off strengths suitable for evolutionary branching when resources are asymmetrically distributed, and we propose that such an approach could be a useful implementation linking the two types of density regulation through a continuum (as proposed e.g. by Débarre and Gandon, 2011), rather than having to consider only the two ends of the spectrum.

Like any model, ours makes several simplifying assumptions which may have affected our results. First, we did not consider continuous resource and consumer population dynamics, or any specific kind of functional response of the consumer (e.g. Holling's disc equation as in Stenseth, 1984; Brown, 1990, 1996; Vincent et al., 1996; Rueffler et al., 2007). This is because our model is not based on a demographic model. However, the resources can still be depleted and give rise to frequency-dependent selection, and the resource discovery rate allows us to approximate different types of density regulation. Different patterns may emerge under different kinds of population dynamical aspects such as predator-prey fluctuations (Matsuda & Namba, 1989; Abrams, 1999; Abrams & Matsuda, 2003, 2004; Abrams, 2006) and/or more realistic sensory and movement strategies (e.g. Netz et al., 2022). Second, we did not consider separate trade-offs for various additional aspects of the foraging process such as search time or handling time (unlike models based on optimal foraging theory, e.g. Vincent et al., 1996; Rueffler et al., 2007). However, Rueffler et al. (2007) found that a suitable trade-off in one of these dimensions usually leads to diversification even if selection does not promote diversification in others, and so this may have little influence on the validity of our conclusions. Third, we focused on the diversification rather than on the coexistence of different morphs, the latter sometimes being permitted under broader conditions. For example, while diversification only produced distinct specialists with exclusive diets in the model by Rueffler et al. (2007), evolutionarily stable coexistence was allowed between specialists and generalists, and between specialists and some intermediate types (neither fully specialists nor generalists). Broader conditions for coexistence than diversification are also supported by Ravigné et al. (2009) and models with more morphs (Brown, 1996; Egas et al., 2004). Such coexistence without in situ diversification may arise, for example, from migration or large mutational steps (but see Rueffler et al., 2007 for polymorphisms arising without branching points and yet through small mutational steps). Finally, we studied an asexual model without the possibility for assortative mating to evolve, although assortative mating is a key ingredient for speciation (Weissing et al., 2011). Extensions of our study that allow sexual reproduction should shed light on the reproductive aspect of adaptive diversification under behavioral resource choice. We expect resource choice and mate choice to reinforce each other at least in some conditions if, for example, resource choice biases the encounter of potential mates assortatively (Servedio et al., 2011).

Acknowledgments

We thank the Center for Information Technology of the University of Groningen for their support and for providing access to the high-performance computing cluster Hábrók. RS was funded by an Adaptive Life PhD scholarship from the University of Groningen, the Netherlands (no. 190181604).

Author Contributions

RS conceived and designed the study, wrote final simulation code, produced and analyzed simulation data, and wrote the manuscript draft. JD wrote initial simulation code, generated preliminary data and results used for exploratory purposes, and provided feedback on the manuscript. GSvD developed initial simulation code and conceptualized the model, provided supervision and critical feedback on analyses and the manuscript. RSE provided supervision and critical feedback on study design, model implementation, analyses and on the manuscript.

770 # Tables

Table 1: Overview of model parameters and default values.

Symbol	Name	Default
h	Habitat symmetry	1
s	Trade-off strength	1
x_i^{opt}	Optimal trait value for resource i	±1
δ	Resource discovery rate	0.04
β	Resource assessment accuracy	0
α	Resource abundance weight	1
m	Migration rate	0.01
μ	Mutation rate	0.01
σ_x	Mutational standard deviation	0.02
N	Population size	1 000
n_{R}	Number of rounds per feeding season	10
T_{max}	Simulation time	100 000
x_0	Starting trait value	-0.9

Figures

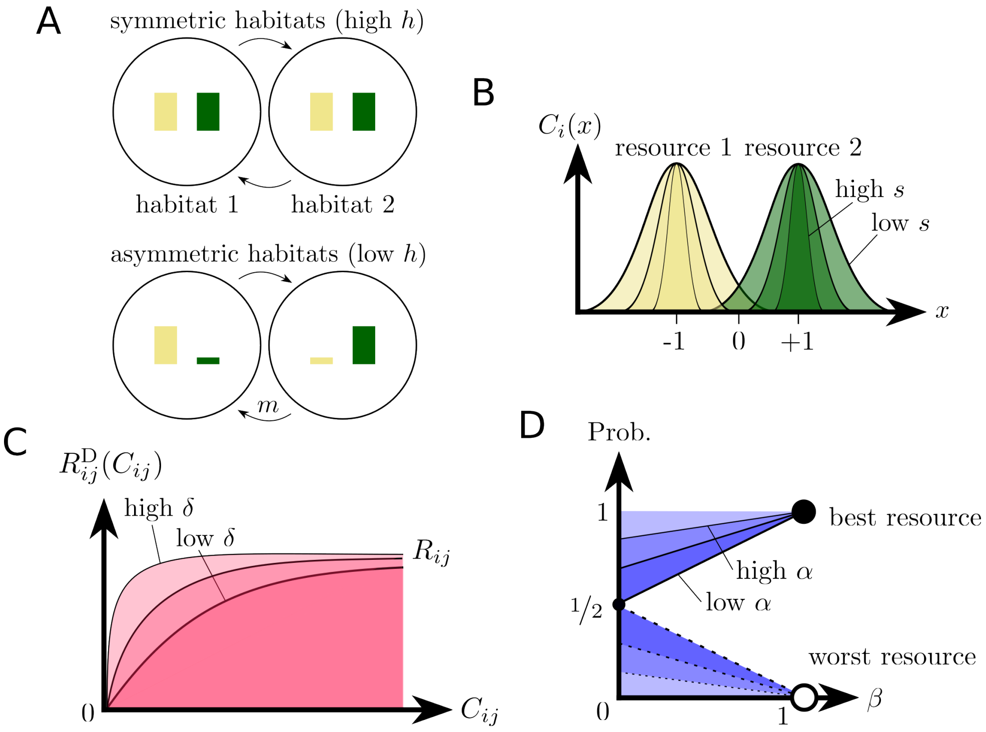

Figure 1: Model overview. (A) Symmetric versus asymmetric partitioning of the resources between habitats depending on the habitat symmetry parameter h. Migration occurs between habitats at per capita rate m per generation. (B) Consumption rates on either resource follow two Gaussian curves whose widths are controlled by the trade-off parameter s. (C) The amount of resource discovered by a population of feeders having chosen resource i in habitat j is a saturating function of their combined consumption rates, with initial slope parameter δ, the rate of resource discovery. (D) After payoffs have been estimated, the probability of choosing the best (and conversely, the worst) resource depends on the resource choice parameter β. The resource abundance weight α controls the baseline probability of choosing either resource in the absence of choice. This baseline probability approaches the relative proportion of each resource as α goes up (in this example the local concentration of the best resource is 1, while that of the worst resource is 0).

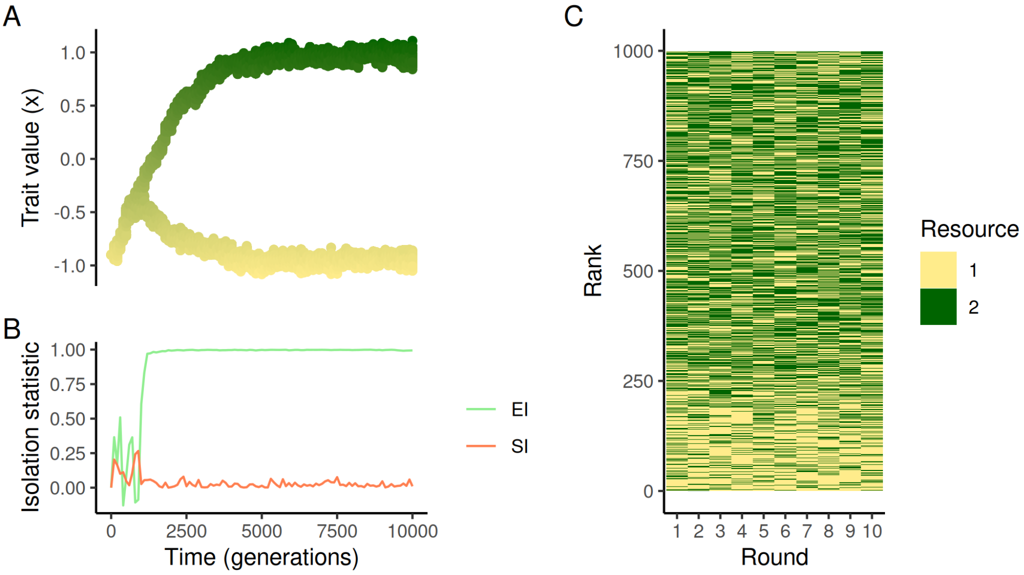

Figure 2: Example simulation in symmetric habitats ($h = 1$) with intermediate assessment accuracy ($\beta = 0.5$). (A) Individual trait values through time. (B) Isolation statistics through time. EI, ecological isolation; SI; spatial isolation (see Methods). Here, evolutionary branching occurs early and in relative spatial isolation due to the level of habitat asymmetry. (C) Overview of the resources chosen by each individual in each feeding round in generation 1 000, when the population is still mostly adapted to resource 1. Due to active resource choice, resource 1 tends to be chosen early on in the feeding queue, until it is no longer more advantageous and resource 2 ends up being chosen just as often. Parameters: $h = 1$, $\beta = 0.5$, $s = 0.8$, $\delta = 0.04$, $m = 0.01$. Other parameters as per Table 1.

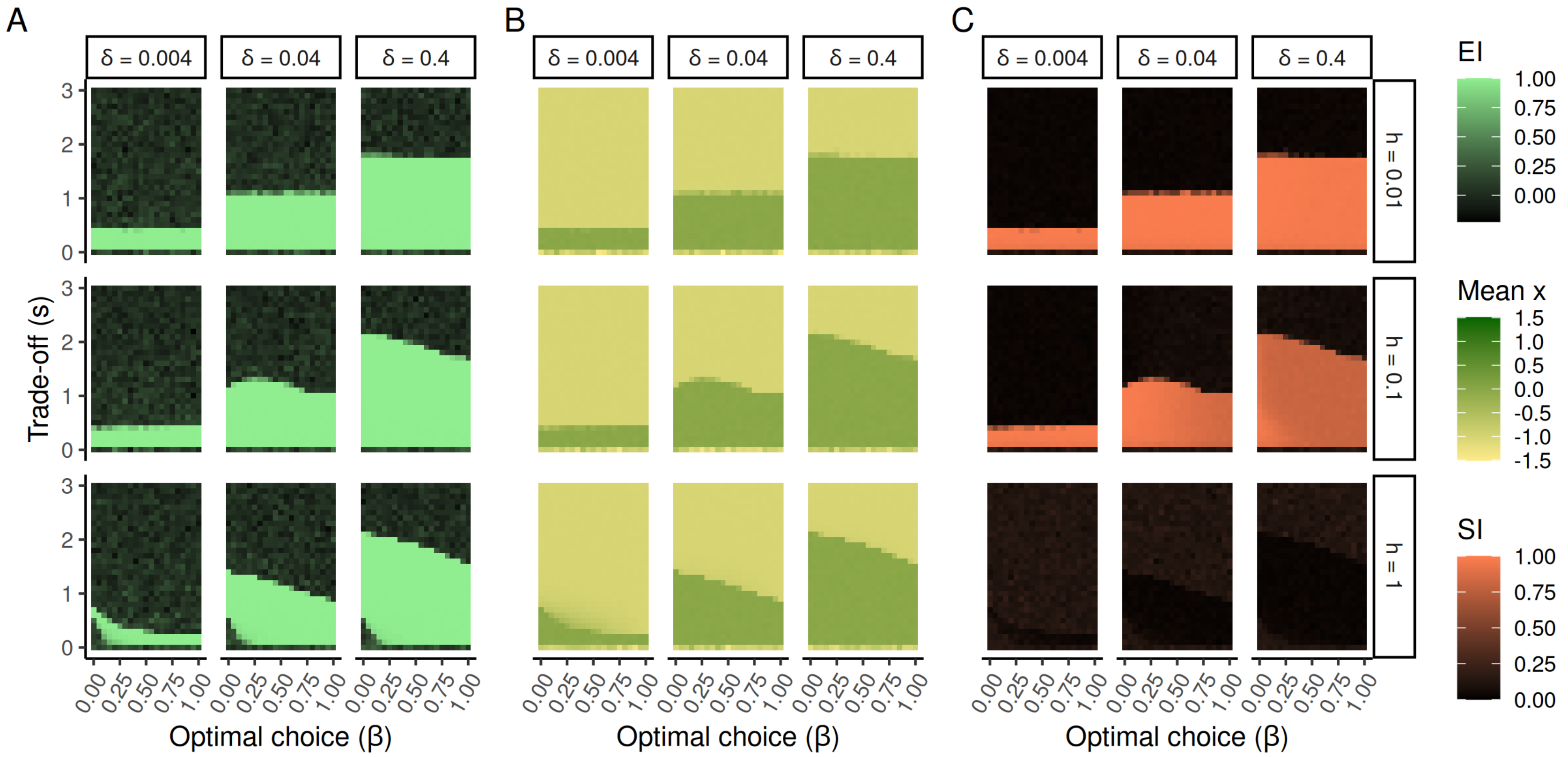

Figure 3: Outcomes of simulations across values of resource assessment accuracy β, trade-off strength s, resource discovery rate δ and habitat symmetry h. Each cell shows the mean final value after 100 000 generations of (A) the ecological isolation statistic EI, (B) the average trait value in the population ("mean x"), or (C) the spatial isolation statistic SI (see Methods), across 10 replicate simulations per parameter combination. Other parameters as per the default values in Table 1. Regions of parameter space where mean $x \approx -1$ correspond to a single specialist outcome (of resource 1), regions where mean $x \approx 0$ and EI is low correspond a single generalist, and regions where mean $x \approx 0$ and EI is high correspond to two specialists (one of each resource, see Fig. 4 for examples).

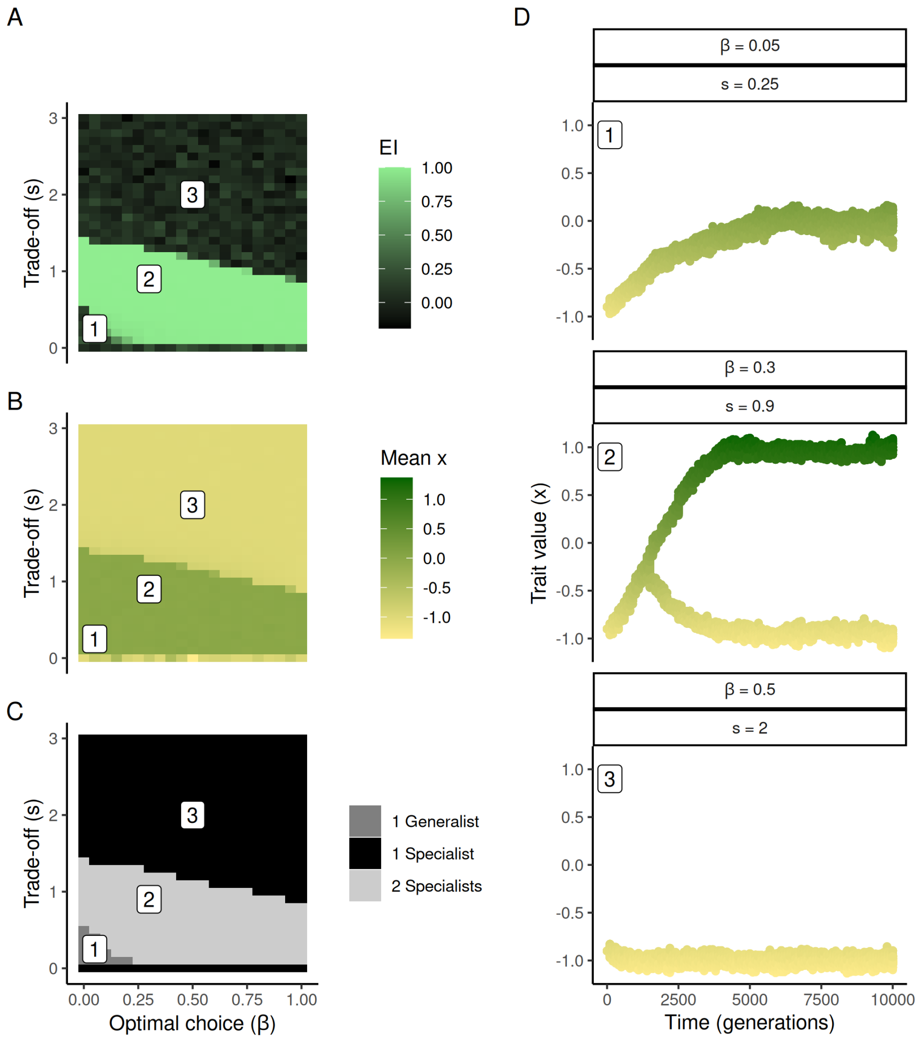

Figure 4: Types of outcomes. (A) Mean final ecological isolation (EI) across parameter space (restricted to the panel with $h = 1$ and $\delta = 0.04$ in Fig. 3A). (B) Same for the mean trait value at the end of the simulations (Fig. 3B). (C) Aggregate of A and B summarizing where the outcome is a single generalist (mean $x \approx 0$, low EI), a single specialist (mean $x \approx -1$, low EI) or two specialists (mean $x \approx 0$, high EI). (D) Example simulations illustrating these three outcomes. Numbered labels in A through C show where these simulations are located in parameter space.

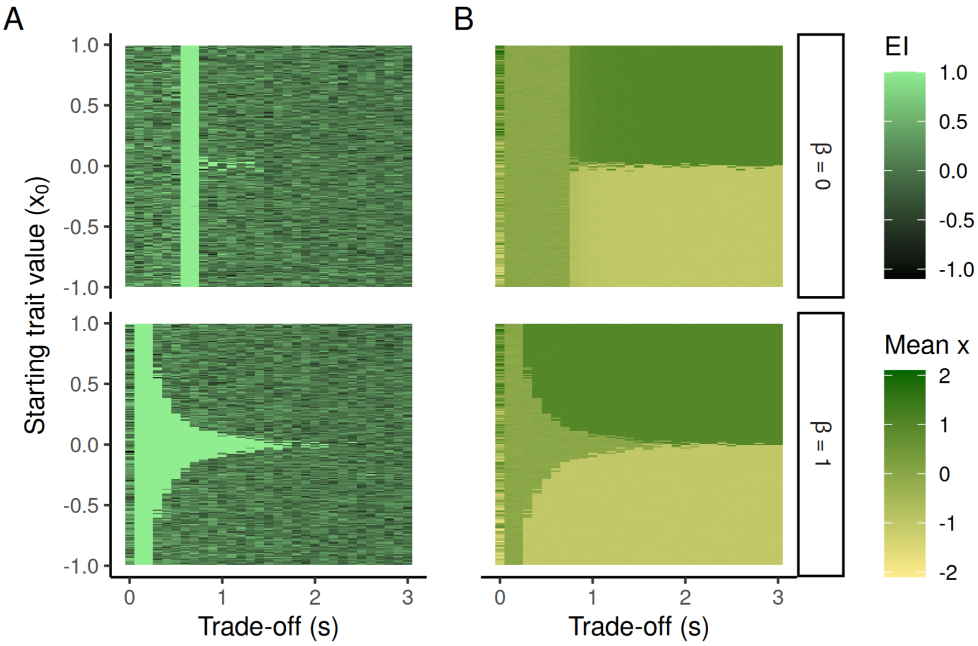

Figure 5: Basin of attraction of the generalist branching point ($x = 0$) across a transect of trade-off strengths s, at two extreme levels of resource assessment accuracy ($\beta = 0$ and $\beta = 1$). One simulation was run for each combination of parameter values. For each combination, we show (A) the value of the ecological isolation statistic EI and (B) the mean ecological trait value in the population, at the last generation of the simulation. The simulations resulting in evolutionary divergence (high EI) are the ones where the population is attracted to the branching point at the center of ecological trait space ($x = 0$). With increasing trade-off strength s the basin of attraction of this branching point becomes more narrow (and conversely those of the two specialist equilibrium phenotypes at $x = \pm 1$ expand). Note that with high choice accuracy ($\beta = 1$), the basin of attraction of the branching point starts to decay at lower trade-off strength s compared to random choice ($\beta = 0$), but the equilibrium remains a branching point up to higher values of s.

Supplementary Figures

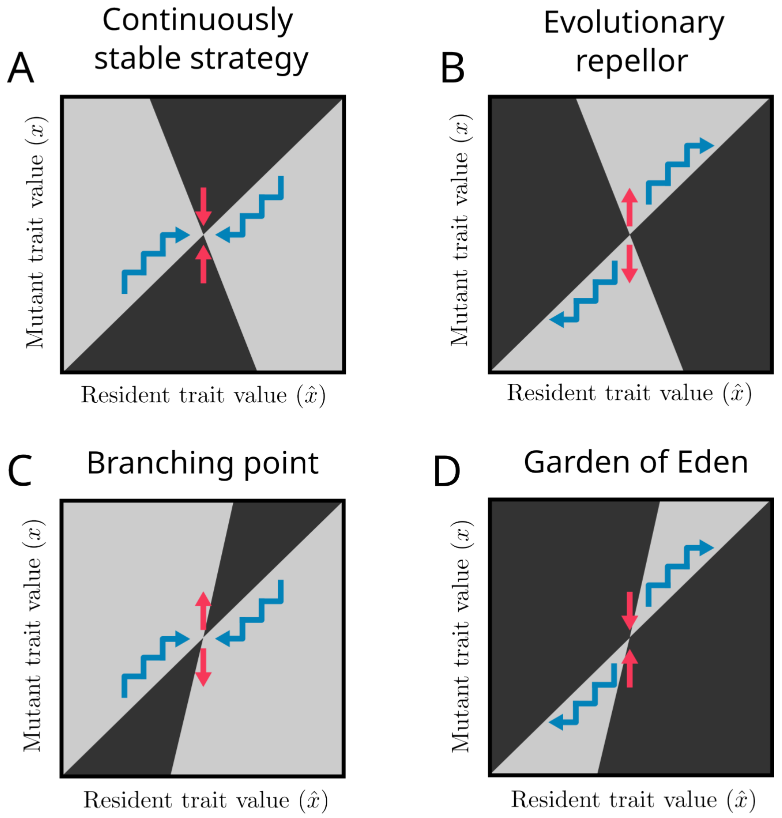

Figure S1: A pairwise invasibility plot (PIP) is a phase plot showing, for each possible value of a trait fixed in a theoretical (monomorphic) *resident* population (here $\hat{x}$), the range of other values of the same trait that a rare *mutant* arising in a population of residents could have, and what the relative fitness of said mutant (here x) would be, compared to the resident. This relative *invasion fitness* determines whether a mutant can invade, and replace, a given resident. A PIP shows, in two different colors, all pairs of mutant and resident strategies where the mutant can invade (light gray here), and all pairs where the mutant cannot (dark gray). The graphical depiction predicts the dynamics of evolution through successive invasions (of mutants becoming the new residents, and so on, blue arrows). Eventually, a so-called *equilibrium* (or *singular*) strategy may be reached, where the direction of evolution changes (i.e. where the *isoclines* delimiting the invasion boundaries cross). Singularities that evolution by selection leads to (blue arrows) are *convergence stable*, but need not be endpoints of the evolutionary dynamics, as once reached they may be *evolutionarily stable* or not (red arrows).(A) Equilibrium strategies that are both convergence and evolutionarily stable are called continuously stable strategies (CSS) — they are stable endpoints of evolution.(B) Repellors are equilibria which are both convergence and evolutionarily unstable — selection leads away from them. (C) Branching points are convergence-stable attractors that are evolutionarily unstable once reached — they promote diversification into two morphs, each with their own trait value. (D) Gardens of Eden are repellors that would be evolutionarily stable if reached but in practice never are. For more information, see Geritz et al. (1998) and Otto and Day (2007).

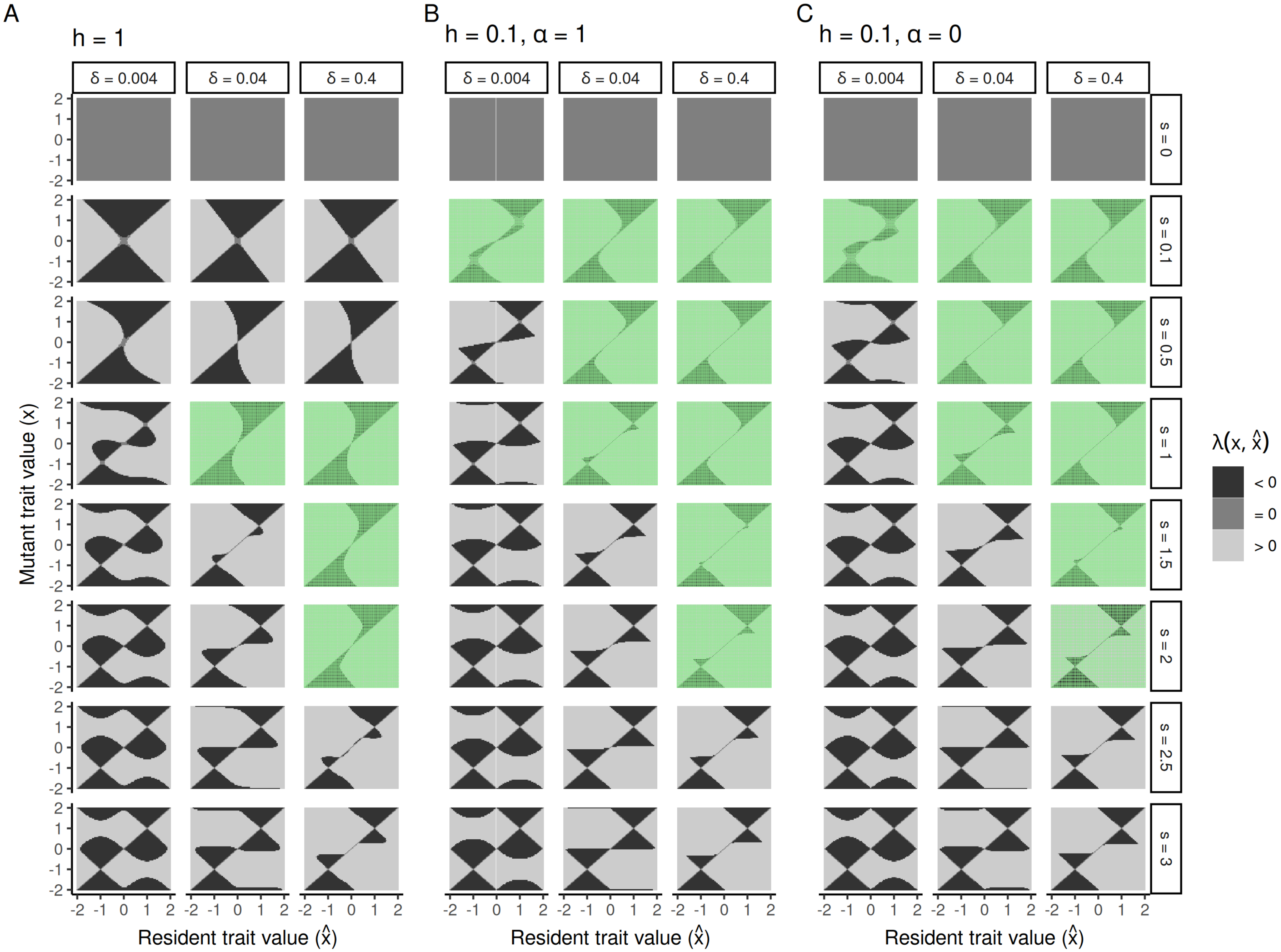

Figure S2: (See next page.)

Figure S2 (continued): Pairwise invasibility plots (PIP) across various parameter combinations explored in our simulations (see Fig. 3 for $h = 1$ and $\alpha = 1$, and Fig. S16 for $\alpha = 0$) when resource choice is random ($\beta = 0$). Note that α is irrelevant when $h = 1$ (see Methods). $\lambda(x, \hat{x})$, invasion fitness of a mutant with trait value x in a resident population with trait value $\hat{x}$ — the mutant invades if $\lambda(x, \hat{x}) > 0$. Green overlays symbolize parameter combinations for which individual-based simulations resulted in successful evolutionary branching of ecological strategies (reaching at least EI = 0.9 in ecological isolation at the end of a simulation, on average across replicates in Fig. 3 and S16). These combinations largely match the parameter sets where the generalist strategy ($x = 0$) can be graphically identified as a branching point in the PIP. See Appendix for details and Figure S1 for how to interpret PIPs.

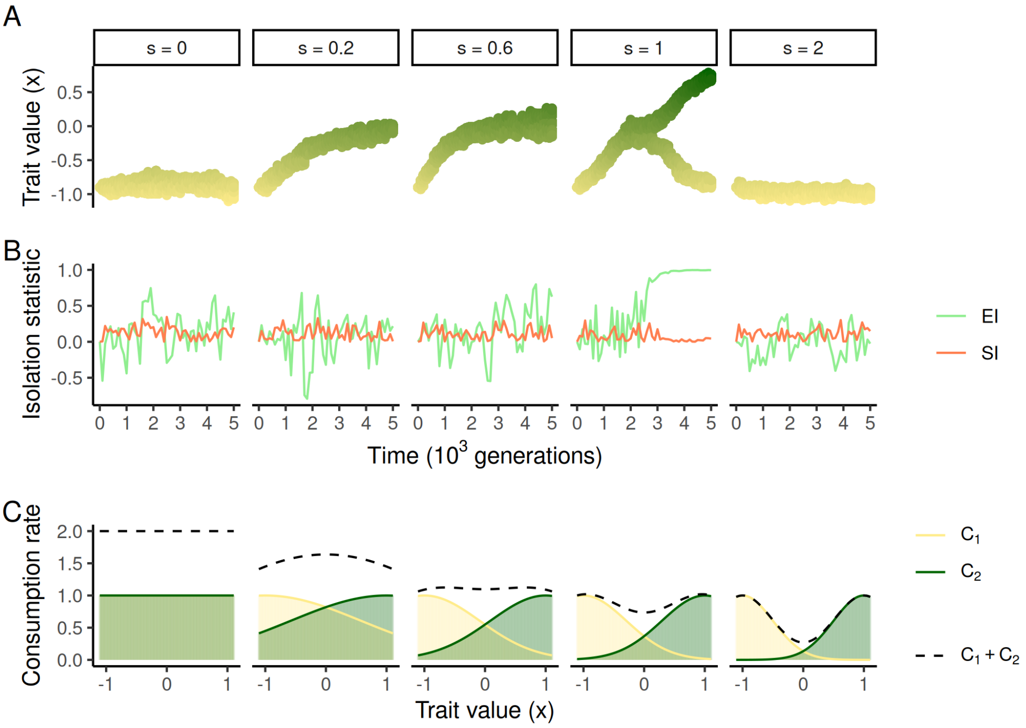

Figure S3: Simulations across trade-off strengths s in symmetric habitats ($h = 1$) and under random choice ($\beta = 0$). Other parameters as per Table 1. (A) Individual traits through time. Evolutionary branching occurs within a specific range of trade-off strengths — a generalist ($x \approx 0$) evolves if s is too low, or the population remains as a single specialist ($x \approx -1$) if s is too high (when $s = 0$ the trait drifts randomly). When branching occurs, it is driven by frequency-dependent selection (i.e. advantage to utilize the less depleted resource) and first goes through a generalist phase. (B) Isolation statistics through time, showing that divergence (whenever EI is high) occurs in sympatry (SI remains low) under these parameter values. EI, ecological isolation; SI, spatial isolation. (C) Consumption curves for both resources (full lines) and sum of both consumption rates (dashed lines). Generalists are favored when $s < 0.5$ as then the cumulative consumption curve peaks at $x = 0$.

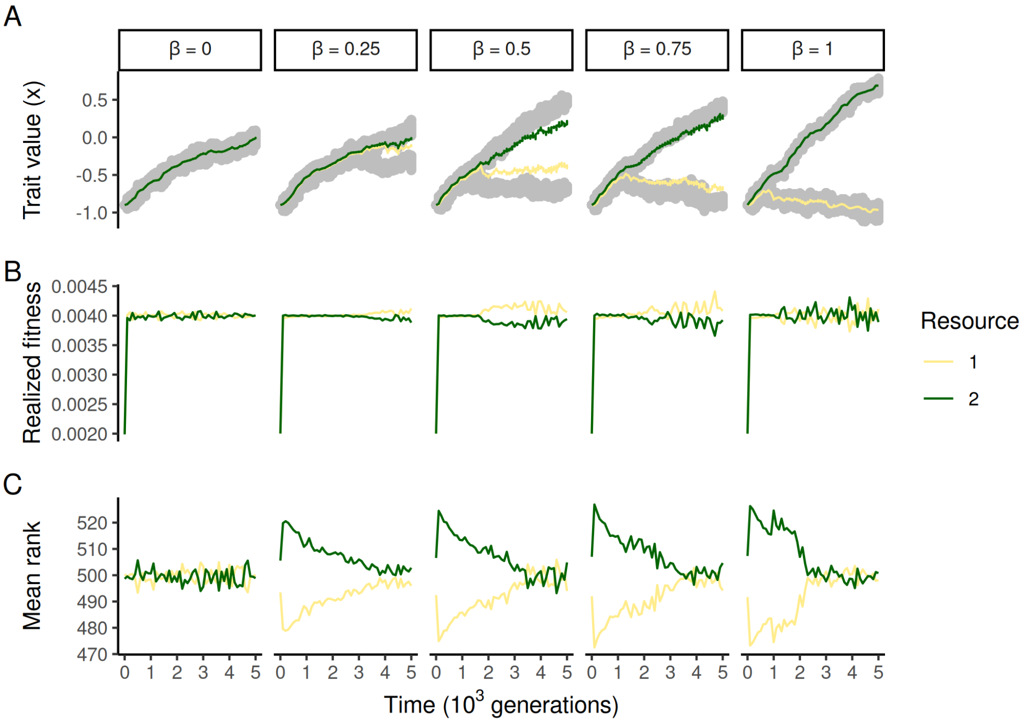

Figure S4: Simulations across resource assessment accuracies β in symmetric habitats ($h = 1$) when the trade-off is weak ($s = 0.2$). Other parameters as per Table 1. (A) Individual trait values through time. Colored lines represent the mean trait value of individuals choosing each resource at each generation. As choosiness β increases, individuals choosing different resources become more phenotypically segregated, and this can be seen already before branching. (B) Mean fitness gain from feeding on each resource at every generation. (Differences in fitness between the resources are negligible and due to imperfect choice in diverging specialists.) (C) Average rank in the queue of individuals choosing each resource, at each generation. At high β, and before branching, resource 2 tends to be chosen later in the queue, when resource 1 has been depleted — a pattern indicating frequency dependence.

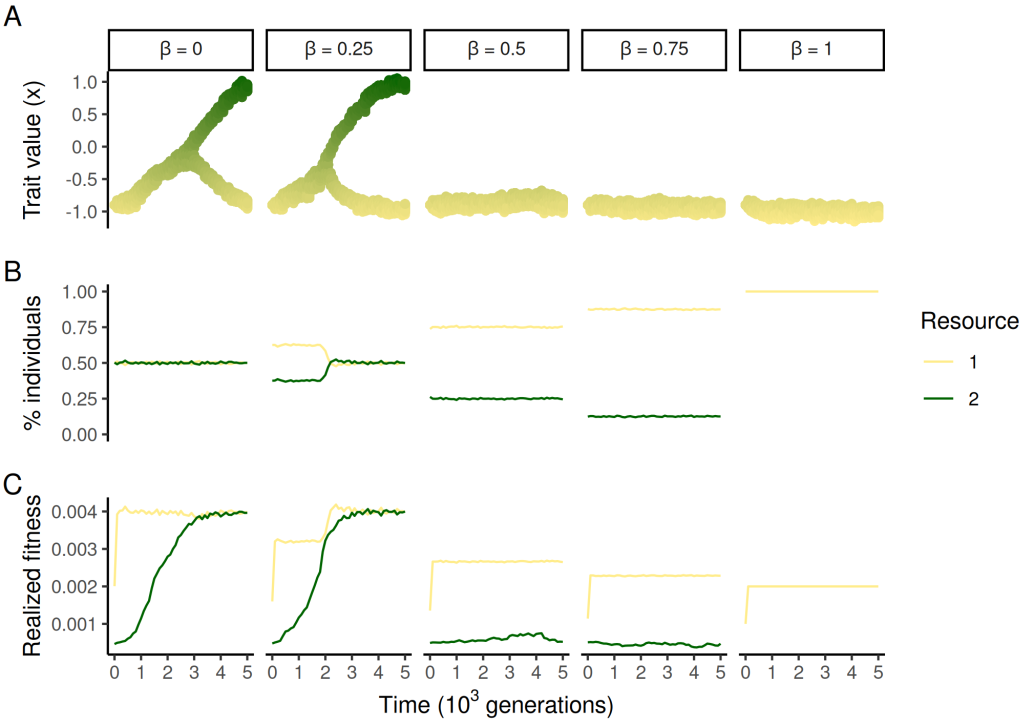

Figure S5: Simulations across resource assessment accuracies β in symmetric habitats ($h = 1$) under a strong trade-off ($s = 1.2$). Other parameters as per Table 1. (A) Individual trait values through time, showing that branching is lost as choosiness increases. (B) Proportion of individuals choosing each resource at each generation. With increased choosiness, more individuals choose resource 1 over resource 2. (C) Mean fitness gain from utilizing each resource at each generation, showing that under a strong trade-off, resource 1 is more advantageous than resource 2 despite being depleted. By biasing choice towards resource 1, this reduces exposure to resource 2 and prevents branching.

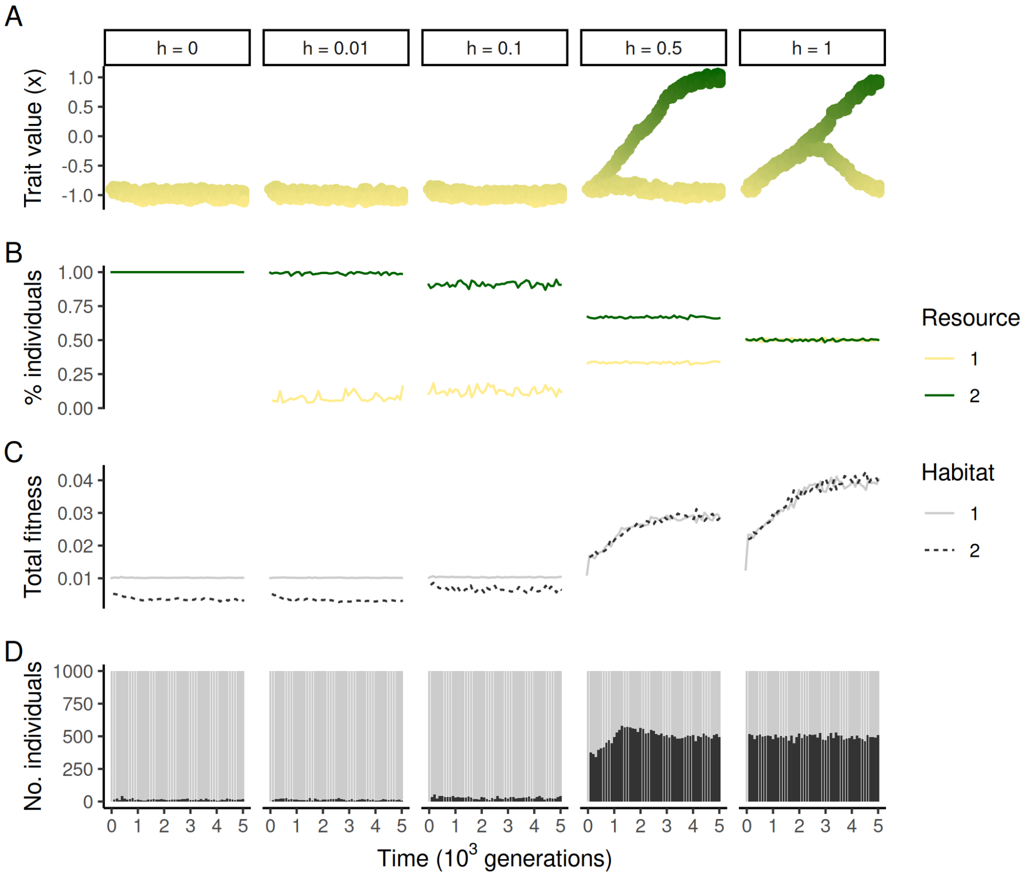

Figure S6: Simulations across habitat symmetry levels h, under a strong trade-off ($s = 1.2$) and random choice ($\beta = 0$). Other parameters as per Table 1. (A) Trait values through time. Branching is lost as habitat symmetry h decreases (right to left), because more asymmetric habitats require a weaker trade-off to be conducive to evolutionary branching. (B) Proportion of individuals choosing each resource at each generation in habitat 2. In more asymmetric habitats, individuals (which, under these parameters, are not choosy) utilize the more abundant resource more, even though they are not well-adapted to it. (C) Mean fitness after all feeding rounds in both habitats, showing that this choice of the maladaptive but abundant resource results in a lower fitness in habitat 2 when habitat asymmetry is high (low h). (D) Population density across habitats and through time. When h is low, individuals from habitat 2 fail at establishing a stable population because their fitness on resource 2 is too low.

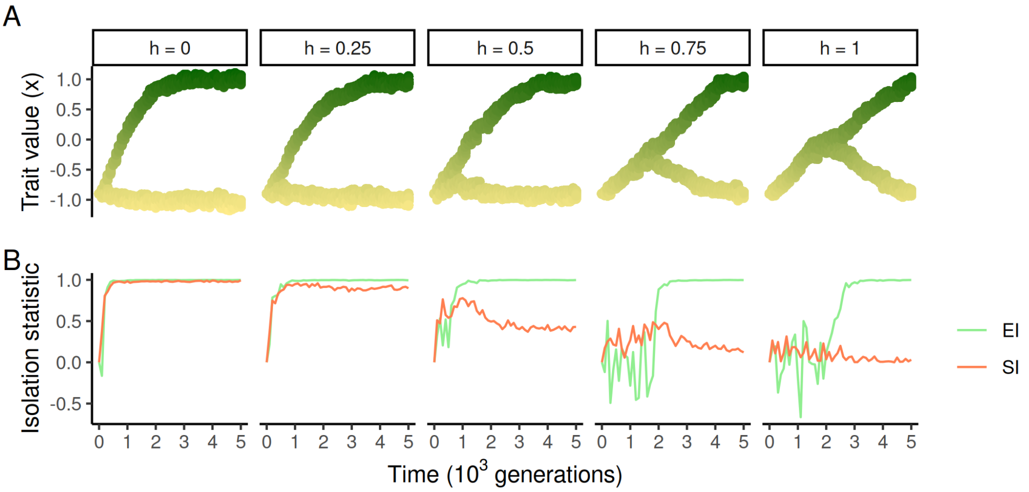

Figure S7: Simulations across habitat symmetry levels h, under moderate trade-off strength ($s = 1$) and random choice ($\beta = 0$). Other parameters as per Table 1. (A) Individual trait values through time. As habitat asymmetry increases (h decreases, right to left), branching becomes more and more driven by local adaptation to the most abundant resource, and less by frequency dependence. (B) Isolation statistics showing that divergence occurs concurrently with spatial isolation when habitat asymmetry is high. EI, ecological isolation; SI, spatial isolation.

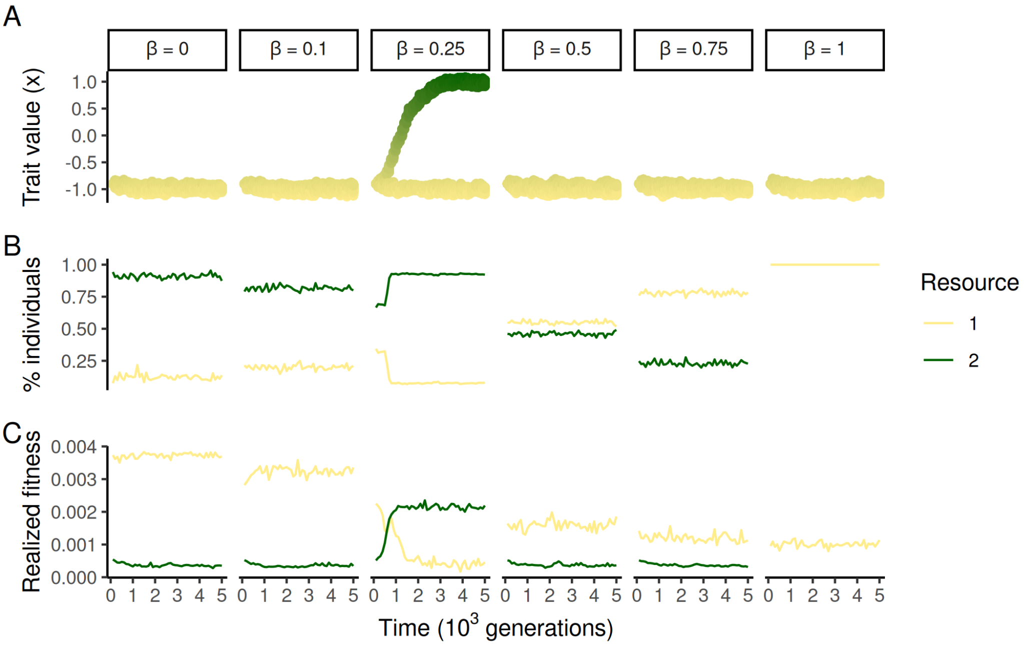

Figure S8: Simulations across resource assessment accuracies β, in asymmetric habitats ($h = 0.1$) and under a strong trade-off ($s = 1.2$). Other parameters as per Table 1. (A) Trait values through time. Under moderate resource asymmetry (i.e. with high-enough resource discovery, $\delta = 0.04$), branching occurs at intermediate choosiness (here, $\beta = 0.25$). (B) Proportion of individuals choosing each resource at each generation in habitat 2. As choosiness increases, the rare resource 1 is chosen more often in habitat 2. (C) Mean fitness gain from choosing each resource through time, in habitat 2, showing that resource 1 is still the most advantageous despite being rare. For branching and adaptation to the maladaptive resource 2 to occur, resource 1 must be chosen often enough that a viable population with sufficient fitness can be established in habitat 2, but not so often that individuals are no longer exposed to resource 2.

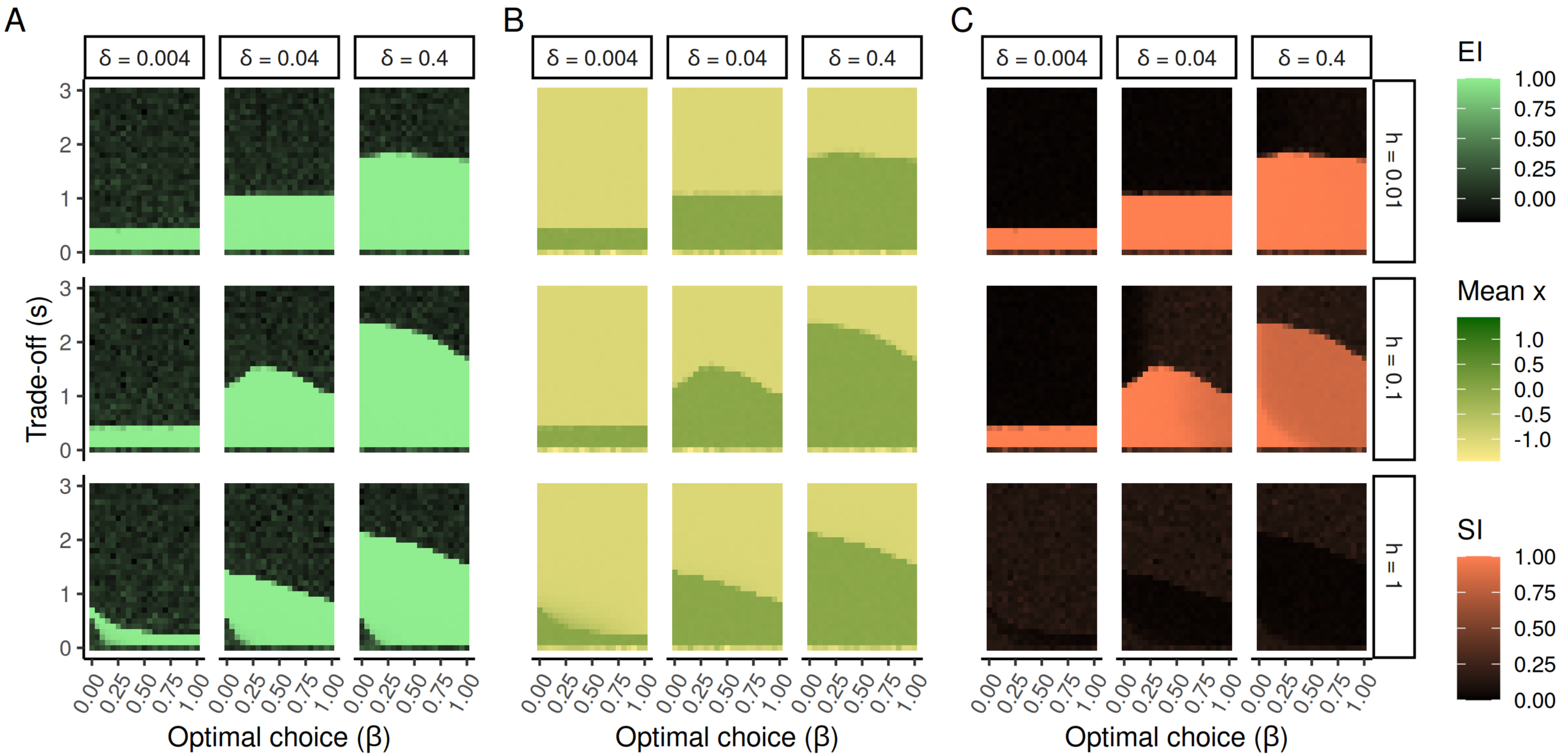

Figure S9: Simulation outcomes across the same parameter space as in Figure 3, but with a lower migration rate ($m = 0.001$). Legend as per Figure 3. All simulations are run under $m = 0.001$ except those under $h = 1$, which are the same as those in Figure 3 (i.e. $m = 0.01$), and are here for comparison, because lowering the migration rate was not expected to cause any difference when habitats are symmetric ($h = 1$) and eco-evolutionary dynamics are driven by within-habitat processes in both habitats simultaneously, rather than by colonization-limited processes (as in asymmetric habitats with low h).

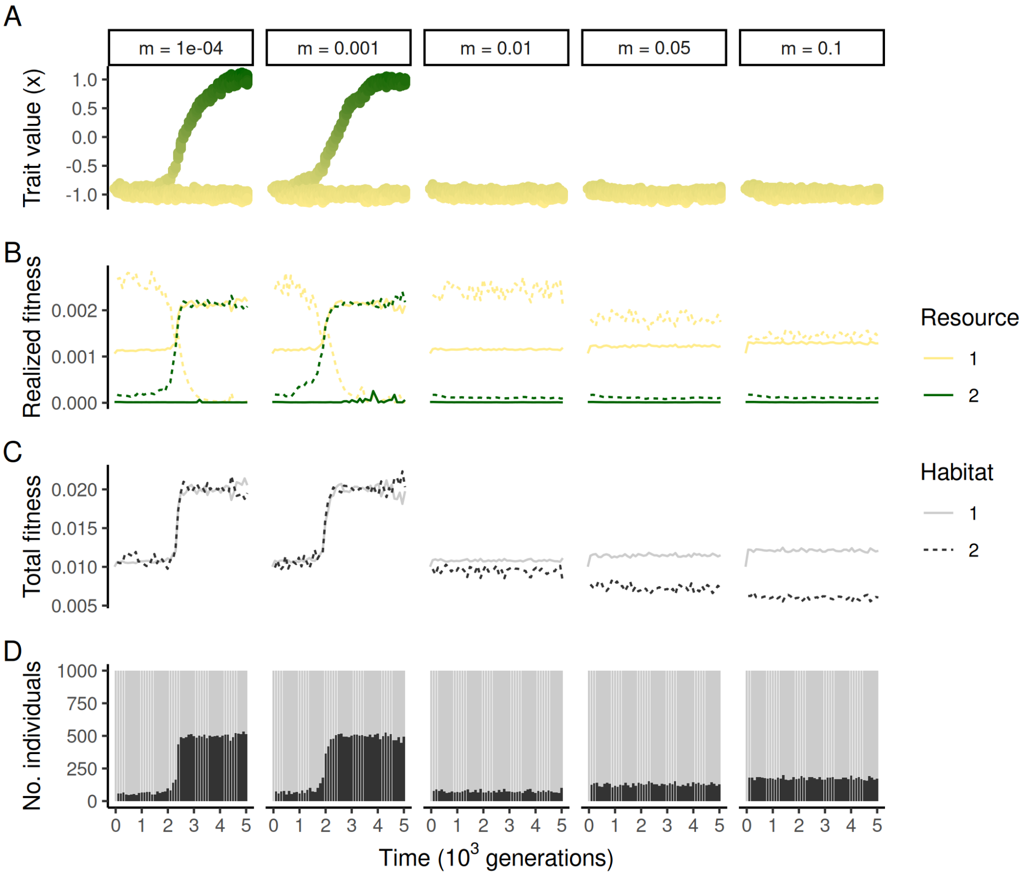

Figure S10: Simulations across migration rates m in asymmetric habitats ($h = 0.1$), under a strong trade-off ($s = 1.5$) and at intermediate resource assessment accuracy ($\beta = 0.3$). Other parameters as per Table 1. (A) Traits through time. Intermediate choosiness maximizes the chances for branching in moderately asymmetric habitats when migration is low — if migration increases, branching is lost. (B) As migration goes down, the rare resource 1 becomes more profitable in habitat 2 (less competition from immigrants), and slightly less so in habitat 1 (more competition with individuals that would have otherwise migrated). (C) Mean fitness of individuals after all feeding rounds in each habitat, where reduced migration increases fitness in habitat 2 relative to habitat 1 — until a viable population can establish and adapt to resource 2 in habitat 2. (D) Population densities across habitats.

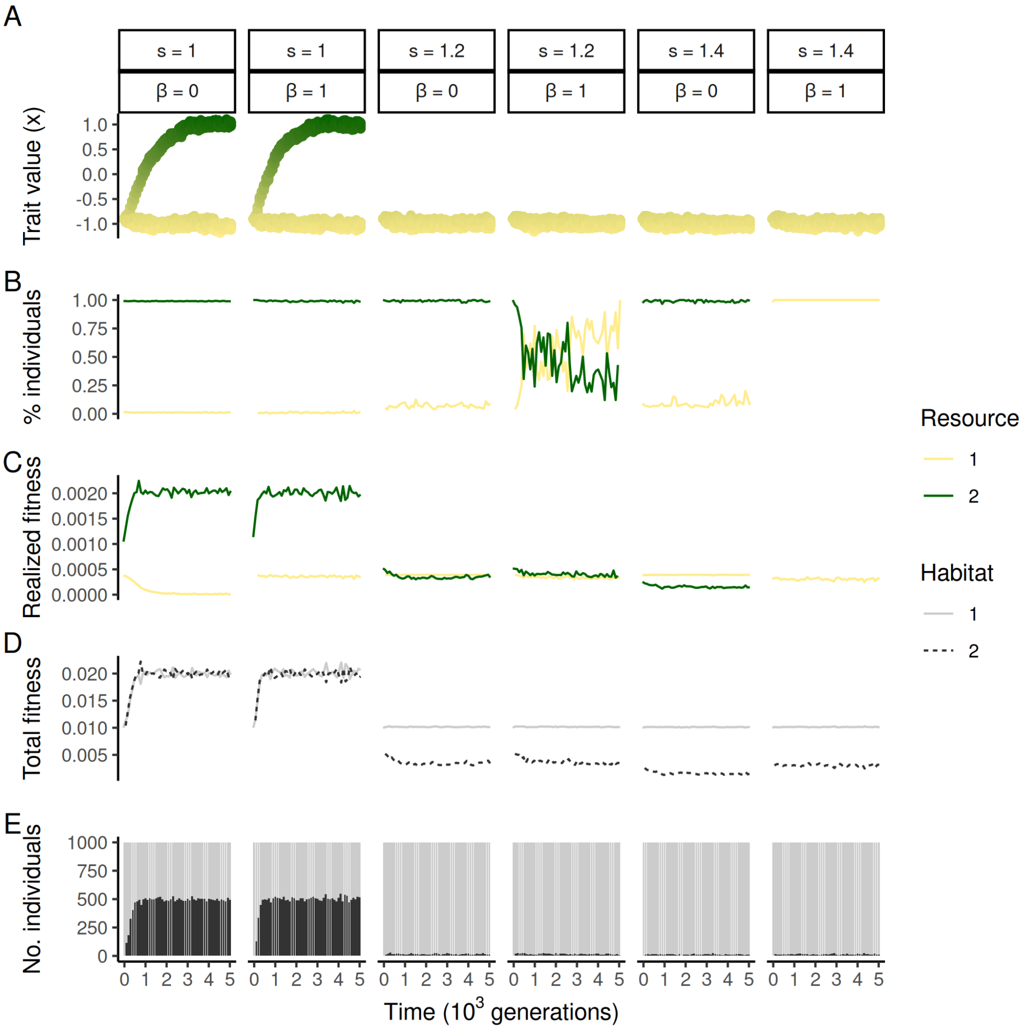

Figure S11: Simulations across trade-off strength s at two levels of choosiness ($\beta = 0$ and $\beta = 1$), in highly asymmetric habitats ($h = 0.01$). Other parameters as per Table 1. (A) Traits through time. Trade-off strength affects both ends of the choosiness spectrum in a similar way — branching occurs if the trade-off is not too strong. (B) Proportion of individuals choosing each resource at each generation in habitat 2. Both choosy ($\beta = 1$) and non-choosy ($\beta = 0$) individuals pick the same resource (the abundant resource 2) when the trade-off is weak enough. (C) Mean fitness gain from choosing each resource in habitat 2, showing that the abundant resource becomes the most profitable as the trade-off weakens. (D) Mean fitness after all feeding rounds in both habitats. A population can establish in habitat 2 once the trade-off is sufficiently weak, at which point choosy and non-choosy individuals are already utilizing the same resource. (E) Population densities across habitats.

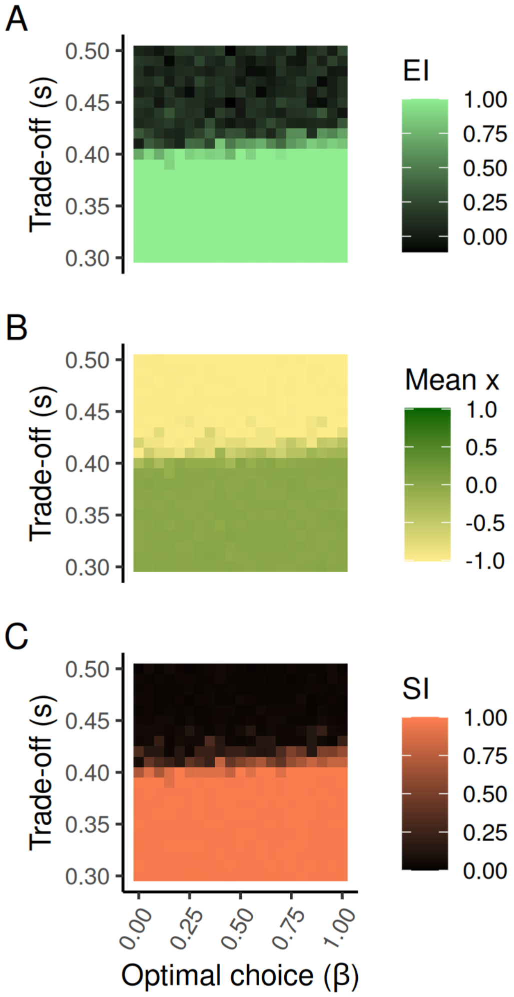

Figure S12: Zoom-in on a particular range of trade-off strengths s in the parameter space explored in Figure 3, when $h = 0.1$ and $\delta = 0.004$. Legend as per Figure 3.

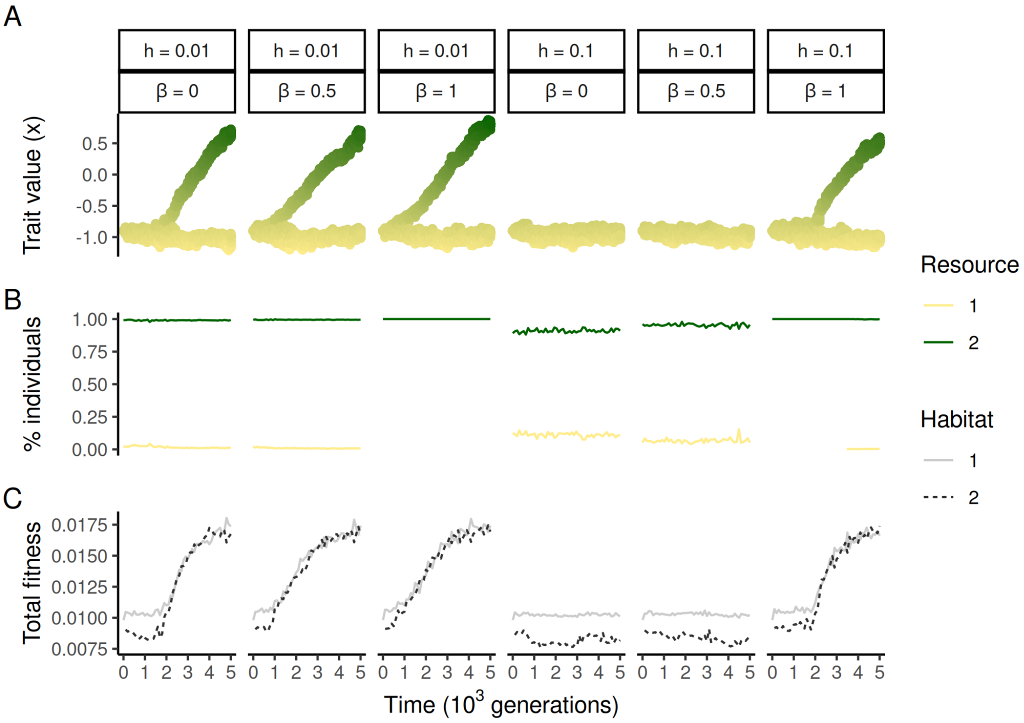

Figure S13: Simulations across levels of habitat symmetry h and resource assessment accuracies β under a weak trade-off ($s = 0.4$) and at low resource discovery rate ($\delta = 0.004$). Other parameters as per Table 1. (A) Traits through time. When resource discovery is low, branching becomes slightly more likely with higher choosiness β when habitats are not too asymmetric ($h = 0.1$) — a pattern that disappears when asymmetry is very high ($h = 0.01$). (B) Proportion of individuals choosing each resource in habitat 2. When habitat symmetry is not too low ($h = 0.1$), noticeably fewer non-choosy individuals (low β) pick resource 2 than choosy individuals (high β), as non-choosy individuals encounter resources purely based on exposure. (C) Mean fitness after all feeding rounds in both habitats. The establishment of a viable population in habitat 2 is rendered more difficult when (non-choosy) individuals pick the rarer resource 1 by passive exposure (a problem that does not present itself when resource 1 is sufficiently rare, $h = 0.01$).

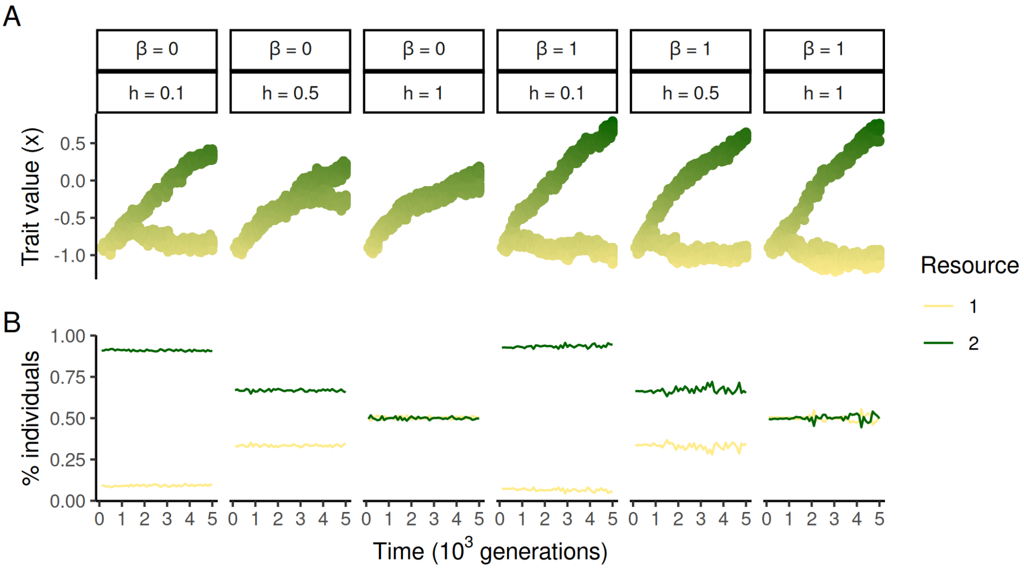

Figure S14: Simulations across levels of habitat symmetry h and resource assessment accuracies β under a weak trade-off ($s = 0.2$). Other parameters as per Table 1. (A) Traits through time. Under random choice ($\beta = 0$) a high habitat asymmetry (low h) is needed for branching when the trade-off would normally favor generalists, while high choosiness promotes branching at all levels of habitat symmetry. (B) Proportion of individuals choosing each resource in habitat 2. Habitat asymmetry introduces a bias in exposure which selects against generalists in non-choosy individuals ($\beta = 0$). This effect is not visible in choosy individuals ($\beta = 1$) because they are already biased in their exposure (even in symmetric habitats) due to active choice.

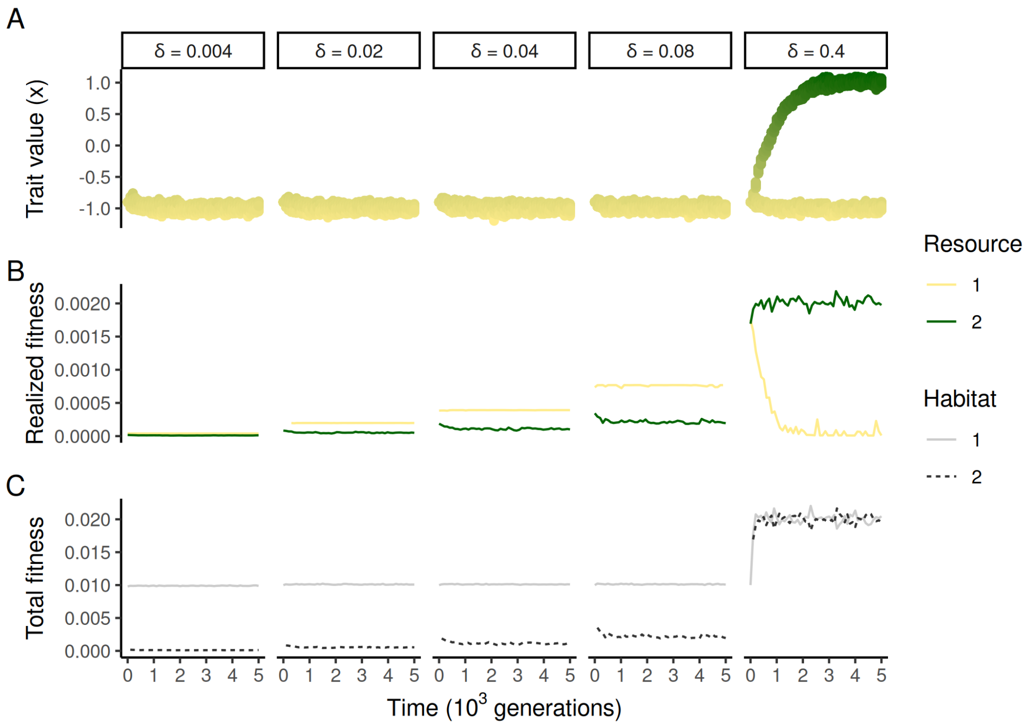

Figure S15: Simulations across resource discovery rates δ in highly asymmetric habitats ($h = 0.01$), under a strong trade-off ($s = 1.5$) and random choice ($\beta = 0$). Other parameters as per Table 1. (A) Traits through time. Generally, resource discovery facilitates branching by alleviating limiting conditions such as strong trade-offs or low resource concentrations. (B) Mean fitness gain from feeding on each resource at each generation in habitat 2. (C) Mean fitness after all feeding rounds in both habitats. By making a rare resource more available, resource discovery is critical in establishing a sufficiently high fitness for a viable colonizing population to be maintained in asymmetric habitats.

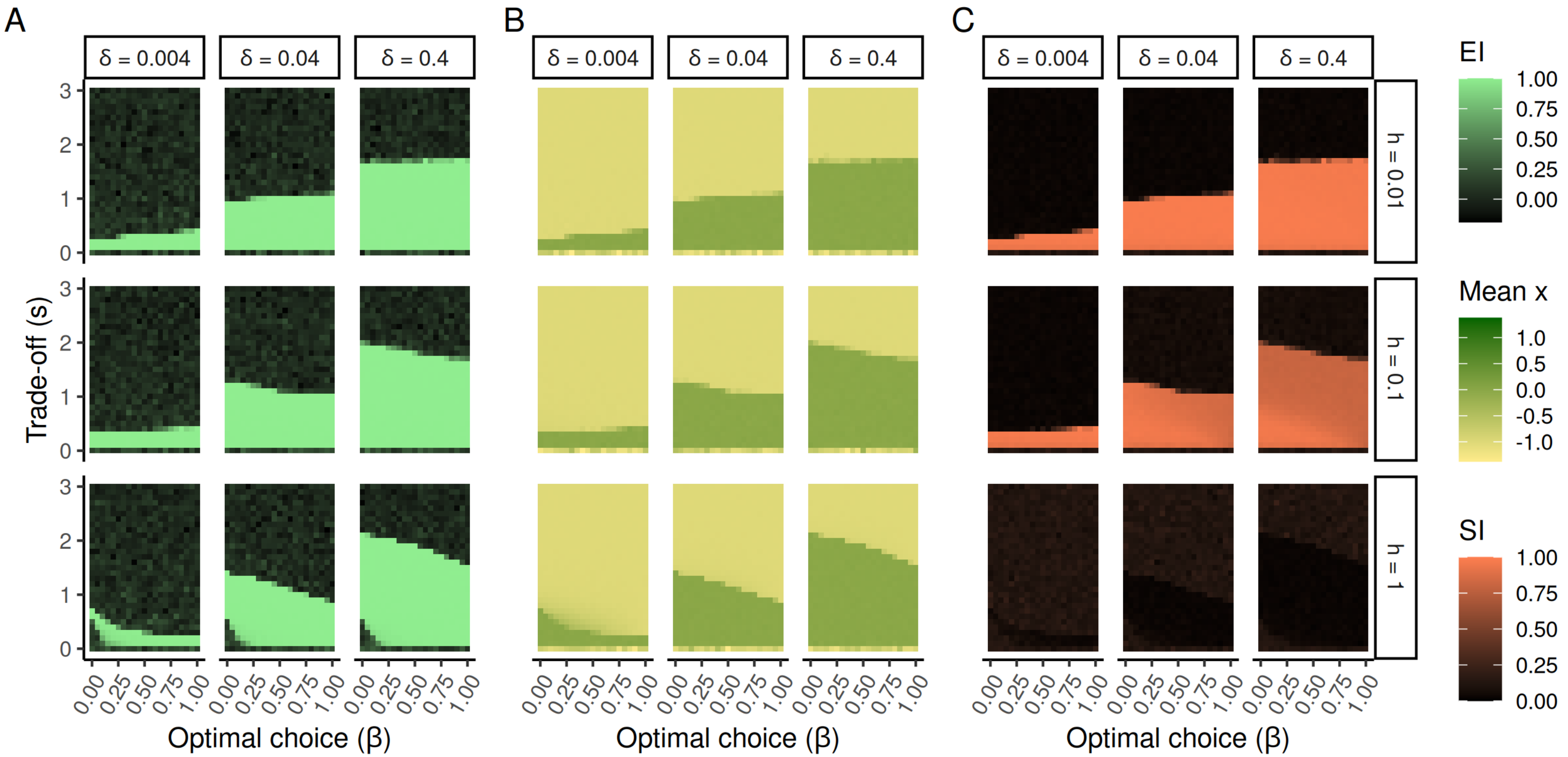

Figure S16: Simulation outcomes across the same parameter space as in Figure 3 but with low resource abundance weight ($\alpha = 0$). Legend as per Figure 3. Note that simulations with $h = 1$ shown here are the same as in Figure 3 (i.e. $\alpha = 1$) because by construction the model under $\alpha = 0$ is equivalent to $\alpha = 1$ when $h = 1$ (resource are equally abundant in both habitats, see Methods).

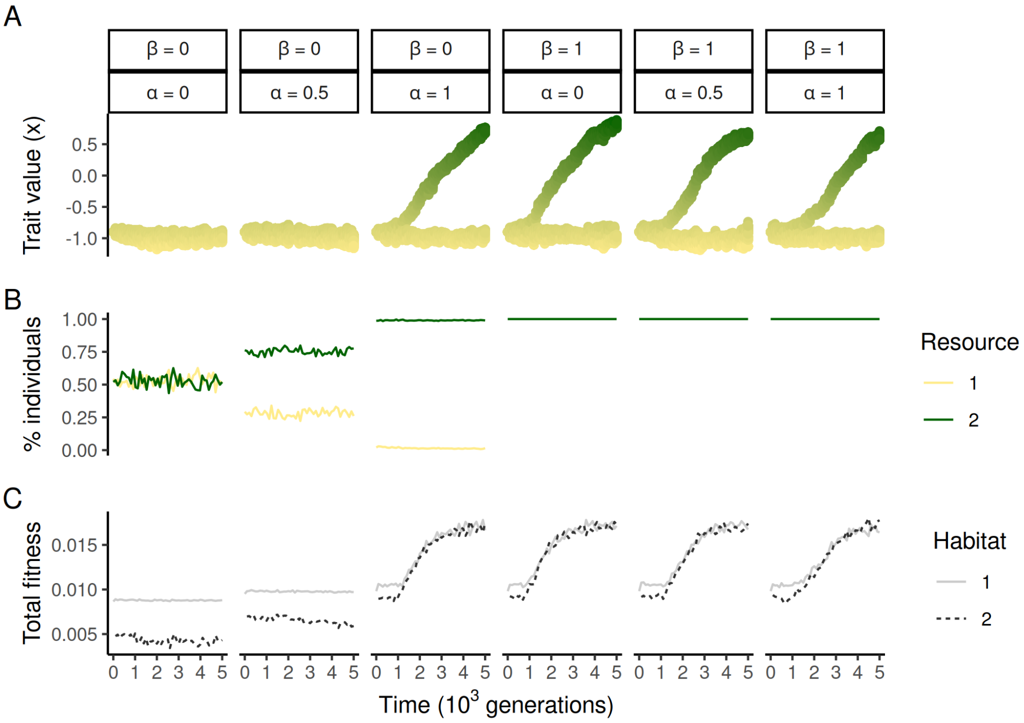

Figure S17: Simulations across resource abundance weights α at two levels of resource assessment accuracy ($\beta = 0$ and $\beta = 1$), in highly asymmetric habitats ($h = 0.01$), at a low resource discovery rate ($\delta = 0.004$) and under a weak trade-off ($s = 0.4$). Other parameters as per Table 1. (A) Traits through time. Decoupling resource abundance and encounter (lower α) reduces the probability of branching in less choosy individuals (low β). (B) Proportion of individuals feeding on each resource at each generation in habitat 2. Lowering the resource abundance weight α forces non-choosy individuals ($\beta = 0$) to pick resource 1 close to half of the time even when it is nearly absent, thus reducing exposure to the more abundant resource 2. (C) Mean fitness after all feeding rounds in both habitats, showing that high exposure to a nearly absent resource is accompanied by a reduction in fitness in habitat 2, hindering the potential of the population to settle and adapt in this habitat. By construction, resource abundance weight has no effect when $\beta = 1$ (see Methods).

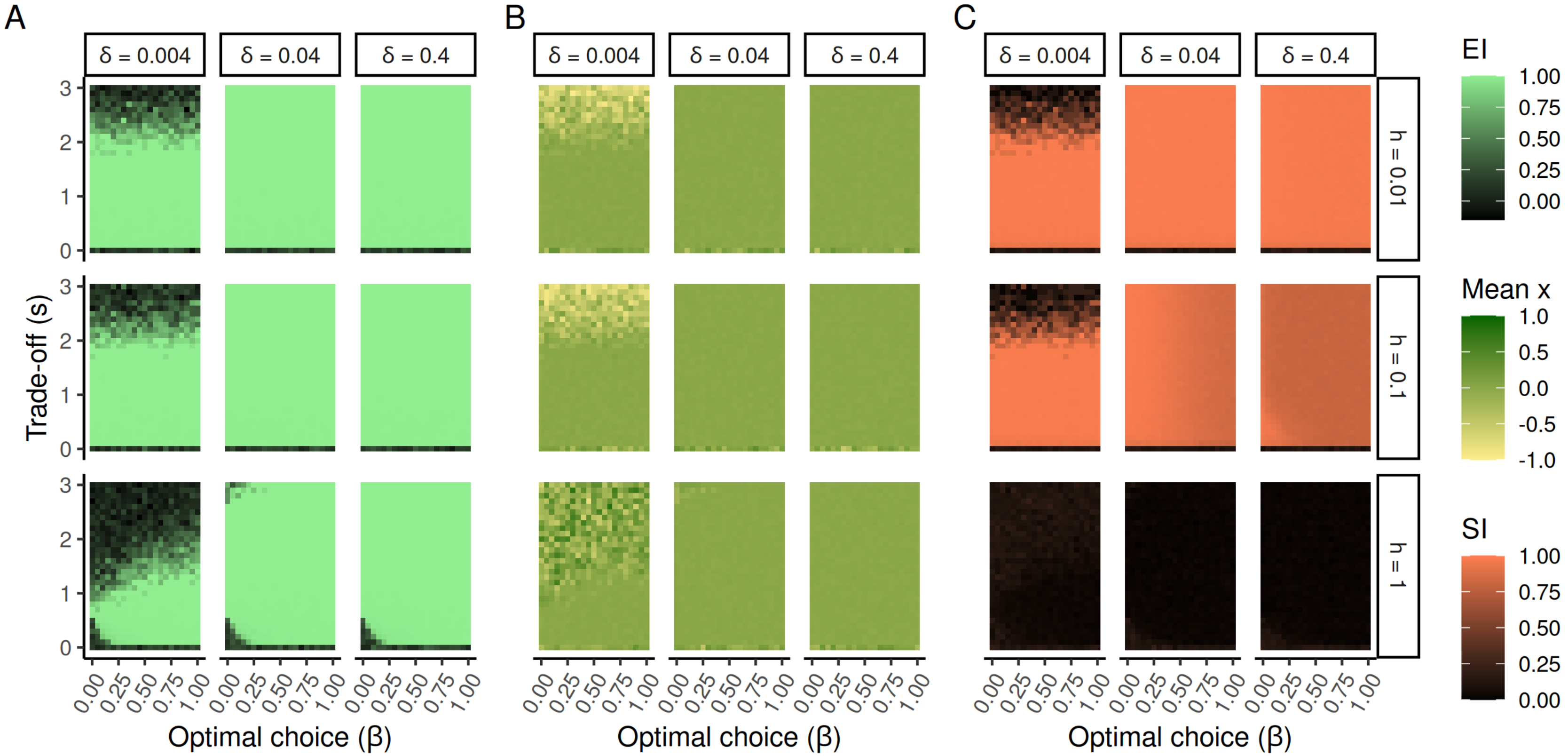

Figure S18: Simulation outcomes across the same parameter space as in Figure 3, but where the population starts as a generalist ($x_0 = 0$). Legend as per Figure 3.

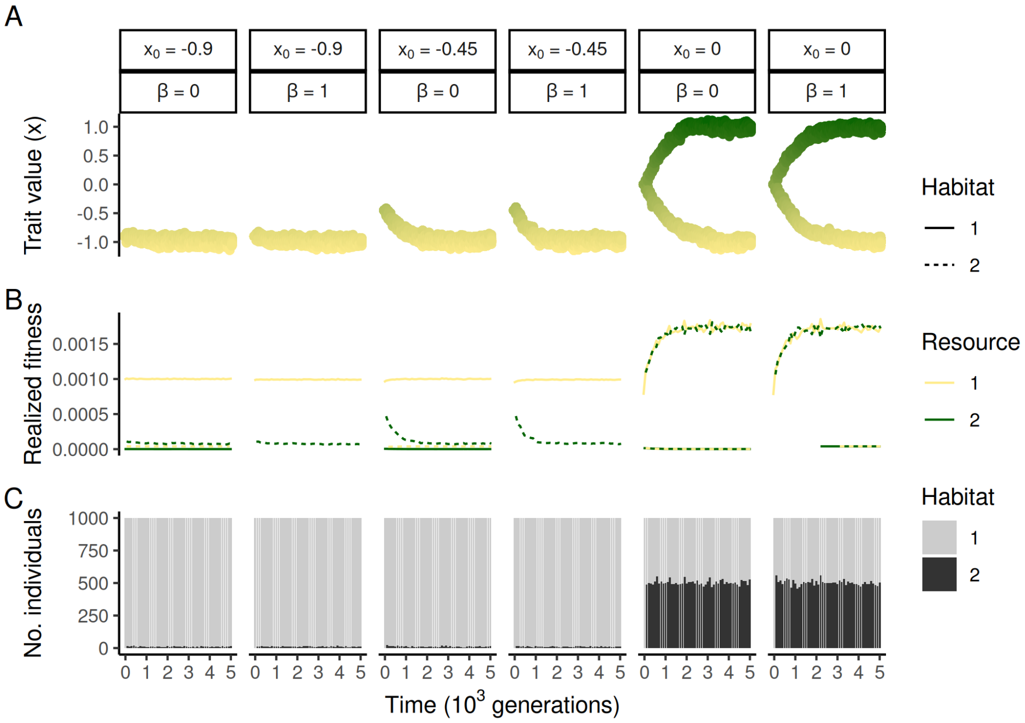

Figure S19: Simulations across starting points x_0 at two resource assessment accuracies ($\beta = 0$ and $\beta = 1$), in highly asymmetric habitats ($h = 0.01$), at a low resource discovery rate ($\delta = 0.004$) and under a moderate trade-off ($s = 1$). Other parameters as per Table 1. (A) Traits through time, showing that branching in asymmetric habitats can still occur under stronger trade-offs if the population starts closer to the generalist strategy $x = 0$. (B) Mean fitness gain from feeding on each resource in both habitats. Adaptation to resource 2 in habitat 2 proceeds once the starting trait value is close enough to zero as to give a sufficiently high fitness to individuals utilizing that resource, which can then respond to directional selection for increased adaptation without having to overcome the cost of deviating from some initial, specialized phenotype. (C) Population densities in both habitats.

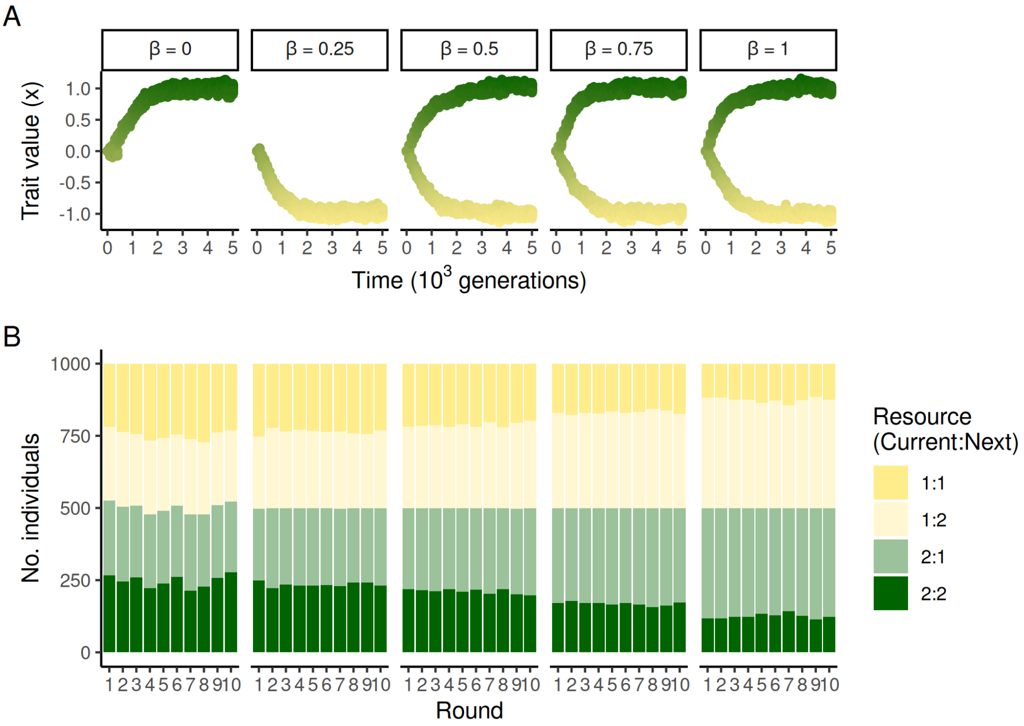

Figure S20: Simulations across resource assessment accuracies β when the population starts off as a generalist ($x_0 = 0$), in symmetric habitats ($h = 1$), at a low resource discovery rate ($\delta = 0.004$) and under a strong trade-off ($s = 1.5$). Other parameters as per Table 1. (A) Traits through time. When starting as a generalist, higher choosiness promotes branching where non-choosy individuals (low β) would have specialized on either resource (at random depending on stochastic fluctuations). (B) Numbers of individuals in each combination of resource chosen by the focal individual ("current") and resource chosen by the next individual in the queue (in the same habitat, "next") at generation 0. As choosiness β increases, individuals in the feeding queue are more likely to choose the opposite resource to their predecessor, indicating strong frequency dependence and an advantage to pick the resource that is slightly less depleted (in symmetric habitats where both resources start in equal amount).

Appendix

Here we introduce a deterministic version of our model, which was used for adaptive dynamics analysis (Metz et al., 1996; Geritz et al., 1998). Adaptive dynamics theory is a body of conceptual tools allowing the analysis of the outcome of evolution by selection using evolutionary invasion analysis. In this study, we used some of those tools to predict the expected outcome of our stochastic model in the absence of resource choice based on perceived payoff ($\beta = 0$, see Methods). We could not derive equations for $\beta > 0$ because the choice then depends on the order in which individuals are taken throughout feeding rounds. The present analysis is therefore used as benchmark against which to compare and validate the findings from individual-based simulations in a simplified scenario.

Demographic model Let there be a mutant with trait value x in a monomorphic resident population with trait value $\hat{x}$. The demographic dynamics of a rare mutant are given by

$$\overrightarrow{N}_{t+1} = \mathbf{\Lambda}(x, \hat{x})\, \overrightarrow{N}_t \tag{10}$$

where $\overrightarrow{N}_t$ is the vector of densities of the mutant across habitat patches at time t, itself given by

$$\overrightarrow{N}_t = \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}_t \tag{11}$$

where N_j is the density of mutants in habitat patch j. $\mathbf{\Lambda}$ is the demographic transition matrix from one generation to the next, given by

$$\mathbf{\Lambda}(x, \hat{x}) = \boldsymbol{M}\, \boldsymbol{Q}(x, \hat{x}) \tag{12}$$

where $\boldsymbol{M}$ is the migration matrix, given by

$$\boldsymbol{M} = \begin{pmatrix} 1 - m & m \\ m & 1 - m \end{pmatrix}, \tag{13}$$

in which m is the migration rate between the two patches, and where $\boldsymbol{Q}$ is the reproduction matrix, given by

$$\boldsymbol{Q}(x, \hat{x}) = \begin{pmatrix} W_1(x, \hat{x}) & 0 \\ 0 & W_2(x, \hat{x}) \end{pmatrix} \tag{14}$$

in which $W_j(x, \hat{x})$ is the per capita growth rate of the mutant in habitat patch j.

The per capita growth rate $W_j(x, \hat{x})$ in a given habitat is equivalent to the probability of an individual being picked as parent of a new offspring in the weighted lottery of reproduction, and is directly proportional to the accumulated amount of resources over multiple feeding rounds (see Methods), which is itself proportional to the average amount of resource obtained in a round. The resource obtained by an individual in a round depends on (1) the resource chosen, and (2) which other individuals chose the same resource. In the absence of payoff-based choice ($\beta = 0$), these two events are independent. Hence, over many feeding rounds,

$$W_j(x, \hat{x}) \propto \sum_{i=1}^{2} P_{ij} \sum_{n=0}^{\hat{N}_j} W_{ij}\big(x, \hat{x}, n\big)\, \mathbb{P}\big(\hat{N}_{ij} = n\big) \tag{15}$$

where $W_{ij}(x, \hat{x}, n)$ is the amount of resource i accumulated in habitat j by a mutant with trait x, in a resident population with trait $\hat{x}$ where n individuals have also chosen resource i, P_{ij} is the baseline probability of choosing resource i at random, and $\mathbb{P}(\hat{N}_{ij} = n)$ is the probability that the number $\hat{N}_{ij}$ of resident individuals having chosen resource i in habitat j is n.

The probability P_{ij} of choosing a given resource i in habitat j is given by

$$P_{ij} = {}^1\!/\!_2\,(1 - \alpha) + \alpha\, R_{ij} \big/ R_j^{\text{tot}} \tag{16}$$

where R_{ij} is the (untouched) total amount of resource i in habitat j (either 1 or h, the habitat symmetry parameter, see Methods), $R_j^{\text{tot}} = R_{1j} + R_{2j}$ is the total amount of resources in habitat j, and α is the resource abundance weight parameter, tuning how important relative resource abundances are for encounter rates (if $\alpha = 0$ the encounter probability is $1/2$ regardless of resource abundance, see Methods).

Since every individual chooses randomly ($\beta = 0$), the number $\hat{N}_{ij}$ of (resident) individuals having chosen resource i in habitat j in a given round follows the binomial distribution

$$\hat{N}_{ij} \sim \text{Binom}\big(\hat{N}_j, P_{ij}\big) \tag{17}$$

where $\hat{N}_j$ is the total number of resident individuals in habitat j. This means that the probability of any given number n of individuals having chosen resource i in habitat j is given by the binomial formula

$$\mathbb{P}\big(\hat{N}_{ij} = n\big) = \binom{\hat{N}_j}{n} P_{ij}^n \left(1 - P_{ij}\right)^{\hat{N}_j - n}. \tag{18}$$

In turn, the amount of resource i obtained by a mutant with trait value x in habitat j amidst a resident population with trait $\hat{x}$, of which n have chosen resource i, is given by

$$W_{ij}(x, \hat{x}, n) = \begin{cases} R_{ij}^{\text{D}}(\hat{x}, n)\, C_i(x) \Big/ C_{ij}(\hat{x}, n) & \text{if } C_{ij}(\hat{x}, n) > 0 \\ 0 & \text{otherwise,} \end{cases} \tag{19}$$

where $R_{ij}^{\text{D}}(\hat{x}, n)$ is the amount of resource i discovered in habitat j by a population of n feeders with trait value $\hat{x}$, $C_i(x)$ is the consumption rate of a mutant with trait value x on resource i, and $C_{ij}(\hat{x}, n)$ is the cumulative consumption rate on resource i of all n residents having also chosen resource i (here we assume the impact of the rare mutant to be negligible on the amount of resource discovered). The amount of resources discovered by those individuals is given by

$$R_{ij}^{\mathrm{D}}(\hat{x}, n) = R_{ij} \left(1 - \exp\big(-\delta\, C_{ij}(\hat{x}, n)\big)\right) \tag{20}$$

where δ is the resource discovery rate (see Methods). For a given resource i, and since the resident population is monomorphic with trait $\hat{x}$, the cumulative consumption rate on all n residents having also chosen that resource is given by

$$C_{ij}(\hat{x}, n) = n\, C_i(\hat{x}) \ . \tag{21}$$

In the numerical computations, we further assumed individuals to be equally distributed between the two habitats, owing to the fixed total population size and the symmetrical migration matrix (Eq. 13), that is, $\hat{N}_1 = \hat{N}_2 = N/2$.

Invasion fitness Following Otto and Day (2007), the population growth rate of a mutant across both habitat patches is given by the leading eigenvalue of the transition matrix $\boldsymbol{\Lambda}$ (Eq. 12). Here, it is

$$r(x, \hat{x}) = \frac{1}{2}\Bigg((1-m)\,(W_1(x,\hat{x}) + W_2(x,\hat{x})) \tag{22}$$

$$+ \sqrt{\Big((m-1)\,(W_1(x,\hat{x}) + W_2(x,\hat{x}))\Big)^2 - 4\,W_1(x,\hat{x})\,W_2(x,\hat{x})\big(1-2\,m\big)}\Bigg) \ . \tag{23}$$

This growth rate can then be compared with that of the resident, $r(\hat{x}, \hat{x})$, to know if any given mutant can invade and become the new resident, or not, in the form of an *invasion fitness* function,

$$\lambda(x, \hat{x}) = r(x, \hat{x}) - r(\hat{x}, \hat{x}) \ . \tag{24}$$

In adaptive dynamics analysis, a mutant can invade if $\lambda(x, \hat{x}) > 0$. Otherwise, it goes extinct and the resident remains. Mapping the value of the invasion fitness across many combinations of mutants and residents results in a pairwise invasibility plot (PIP), which graphically summarizes the expected evolutionary dynamics. See Figure S1 for how to interpret PIPs.

References

Abbott, R. J. (2017). Plant speciation across environmental gradients and the occurrence and nature of hybrid zones. *Journal of Systematics and Evolution*, *55*(4), 238–258. https://doi.org/10.1111/jse.12267

Abrams, P. A. (1999). The adaptive dynamics of consumer choice. *The American Naturalist*, *153*(1), 83–97. https://doi.org/10.1086/303154

Abrams, P. A. (2006). The prerequisites for and likelihood of generalist-specialist coexistence. *The American Naturalist*, *167*(3), 329–342. https://doi.org/10.1086/499382

Abrams, P. A., & Matsuda, H. (2003). Population dynamical consequences of reduced predator switching at low total prey densities. *Population Ecology*, *45*(3), 175–185. https://doi.org/10.1007/s10144-003-0159-3

Abrams, P. A., & Matsuda, H. (2004). Consequences of behavioral dynamics for the population dynamics of predator-prey systems with switching. *Population Ecology*, *46*(1), 13–25. https://doi.org/10.1007/s10144-003-0168-2

Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

Andrews, R. M. (1971). Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology*, *52*(2), 262–270. https://doi.org/10.2307/1934584

Barton, N. H., & Hewitt, G. M. (1989). Adaptation, speciation and hybrid zones. *Nature*, *341*(6242), 497–503. https://doi.org/10.1038/341497a0

Bernays, E. A. (1998). The value of being a resource specialist: Behavioral support for a neural hypothesis. *The American Naturalist*, *151*(5), 451–464. https://doi.org/10.1086/286132

Bolnick, D. I. (2004). Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, *58*(3), 608–618. https://doi.org/10.1111/j.0014-3820.2004.tb01683.x

Bolnick, D. I., & Otto, S. P. (2013). The magnitude of local adaptation under genotype-dependent dispersal. *Ecology and Evolution*, *3*(14), 4722–4735. https://doi.org/10.1002/ece3.850

Bolnick, D. I., & Stutz, W. E. (2017). Frequency dependence limits divergent evolution by favouring rare immigrants over residents. *Nature*, *546*(7657), 285–288. https://doi.org/10.1038/nature22351

Bravo, H., Dromard, C. R., van der Meer, M. T. J., Schleimer, A., & van der Meij, S. E. T. (2024). Dining on corals: Stable isotope evidence for close trophic connection between gall crabs (Cryptochiridae) and their stony coral hosts. *Symbiosis*. https://doi.org/10.1007/s13199-023-00968-y

Brown, J. S. (1990). Habitat selection as an evolutionary game. *Evolution*, *44*(3), 732–746. https://doi.org/10.1111/j.1558-5646.1990.tb05951.x

Brown, J. S. (1996). Coevolution and community organization in three habitats. *Oikos*, *75*(2), 193. https://doi.org/10.2307/3546243

Débarre, F., & Gandon, S. (2011). Evolution in heterogeneous environments: Between soft and hard selection. *The American Naturalist*, *177*(3), E84–E97. https://doi.org/10.1086/658178

Del Campo, M. L., Via, S., & Caillaud, M. C. (2003). Recognition of host-specific chemical stimulants in two sympatric host races of the pea aphid *Acyrthosiphon pisum*. *Ecological Entomology*, *28*(4), 405–412. https://doi.org/10.1046/j.1365-2311.2003.00524.x

Dempster, E. R. (1955). Maintenance of heterogeneity. *Cold Spring Harbor Symposia on Quantitative Biology*, *20*, 25–32.

Dieckmann, U., & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, *400*(6742), 354–357. https://doi.org/10.1038/22521

Dieckmann, U., Doebeli, M., Metz, J. A. J., & Tautz, D. (Eds.). (2004). *Adaptive speciation*. Cambridge University Press. https://doi.org/10.1017/CBO9781139342179

Doebeli, M., & Dieckmann, U. (2003). Speciation along environmental gradients. *Nature*. https://doi.org/10.1038/nature01274

Edelaar, P., & Bolnick, D. I. (2012). Non-random gene flow: An underappreciated force in evolution and ecology. *Trends in Ecology & Evolution*, *27*(12), 659–665. https://doi.org/10.1016/j.tree.2012.07.009

Edelaar, P., Jovani, R., & Gomez-Mestre, I. (2017). Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. *The American Naturalist*, *190*(4), 506–520. https://doi.org/10.1086/693345

Edelaar, P., Siepielski, A. M., & Clobert, J. (2008). Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution*, *62*(10), 2462–2472. https://doi.org/10.1111/j.1558-5646.2008.00459.x

Egas, M., Dieckmann, U., & Sabelis, M. W. (2004). Evolution restricts the coexistence of specialists and generalists: The role of trade-off structure. *The American Naturalist*, *163*(4), 518–531. https://doi.org/10.1086/382599

Endler, J. A. (1977). *Geographic variation, speciation, and clines*. Princeton University Press.

Fukasawa, Y., & Ishii, K. (2023). Foraging strategies of fungal mycelial networks: Responses to quantity and distance of new resources. *Frontiers in Cell and Developmental Biology*, *11*. https://doi.org/10.3389/fcell.2023.1244673

Gavrilets, S., Li, H., & Vose, M. D. (2000). Patterns of parapatric speciation. *Evolution*, *54*(4), 1126–1134. https://doi.org/10.1111/j.0014-3820.2000.tb00548.x

Geritz, S. A. H., Kisdi, É., Meszéna, G., & Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, *12*(1), 35–57. https://doi.org/10.1023/A:1006554906681

Hendry, A. P., Bolnick, D. I., Berner, D., & Peichel, C. L. (2009). Along the speciation continuum in sticklebacks. *Journal of Fish Biology*, *75*(8), 2000–2036. https://doi.org/10.1111/j.1095-8649.2009.02419.x

Herbers, J. M. (1981). Time resources and laziness in animals. *Oecologia*, *49*(2), 252–262. https://doi.org/10.1007/BF00349198

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, *93*(870), 145–159. https://doi.org/10.1086/282070

Kelly, C. K. (1992). Resource choice in *Cuscuta europaea*. *Proceedings of the National Academy of Sciences*, *89*(24), 12194–12197. https://doi.org/10.1073/pnas.89.24.12194

Kisdi, É. (2001). Long-term adaptive diversity in Levene-type models. *Evolutionary Ecology Research*, *3*, 721–727.

Kisdi, É. (2002). Dispersal: Risk spreading versus local adaptation. *The American Naturalist*, *159*(6), 579–596. https://doi.org/10.1086/339989

Kondrashov, A. S., & Kondrashov, F. A. (1999). Interactions among quantitative traits in the course of sympatric speciation. *Nature*, *400*(6742), 351–354. https://doi.org/10.1038/22514

Levene, H. (1953). Genetic equilibrium when more than one ecological niche is available. *The American Naturalist*, *87*(836), 331–333. https://doi.org/10.1086/281792

Levins, R. (1962). Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *The American Naturalist*, *96*(891), 361–373. https://doi.org/10.1086/282245

Lewinsohn, T. M., & Roslin, T. (2008). Four ways towards tropical herbivore megadiversity. *Ecology Letters*, *11*(4), 398–416. https://doi.org/10.1111/j.1461-0248.2008.01155.x

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609. https://doi.org/10.1086/282454

Mallet, J. (2005). Speciation in the 21st century. *Heredity*, *95*(1), 105–109. https://doi.org/10.1038/sj.hdy.6800686

Martinsen, D. L. (1969). Energetics and activity patterns of short-tailed shrews (*Blarina*) on restricted diets. *Ecology*, *50*(3), 505–510. https://doi.org/10.2307/1933910

Matsuda, H., & Namba, T. (1989). Co-evolutionarily stable community structure in a patchy environment. *Journal of Theoretical Biology*, *136*(2), 229–243. https://doi.org/10.1016/S0022-5193(89)80228-0

Mayhew, P. J. (1997). Adaptive patterns of host-plant selection by phytophagous insects. *Oikos*, *79*(3), 417–428. https://doi.org/10.2307/3546884

Metz, J. A. J., Geritz, S. A. H., Meszena, G., Jacobs, F. J. A., & van Heerwaarden, J. S. (1996). Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In S. J. van Strien & S. M. Verduyn Lunel (Eds.), *Stochastic and spatial structures of dynamical systems* (pp. 183–231).

Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, *7*(6), 198–202. https://doi.org/10.1016/0169-5347(92)90073-K

Moreno-Gámez, S. (2022). How bacteria navigate varying environments. *Science*, *378*(6622), 845–845. https://doi.org/10.1126/science.adf4444

Morris, D. W. (1987). Ecological scale and habitat use. *Ecology*, *68*(2), 362–369. https://doi.org/10.2307/1939267

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*(1), 1–13. https://doi.org/10.1007/s00442-003-1241-4

Netz, C., Hildenbrandt, H., & Weissing, F. J. (2022). Complex eco-evolutionary dynamics induced by the coevolution of predator–prey movement strategies. *Evolutionary Ecology*, *36*(1), 1–17. https://doi.org/10.1007/s10682-021-10140-x

Norberg, R. Å. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology*, *46*(2), 511–529. https://doi.org/10.2307/3827

Norberg, R. Å. (2021). To minimize foraging time, use high-efficiency, energy-expensive search and capture methods when food is abundant but low-efficiency, low-cost methods during food shortages. *Ecology and Evolution*, *11*(23), 16537–16546. https://doi.org/10.1002/ece3.8204

Nosil, P. (2012). *Ecological speciation*. Oxford University Press.

Otto, S. P., & Day, T. (2007). Evolutionary invasion analysis. In *A biologist's guide to mathematical modeling in ecology and evolution* (pp. 454–512). Princeton University Press.

Parent, C. E., Agashe, D., & Bolnick, D. I. (2014). Intraspecific competition reduces niche width in experimental populations. *Ecology and Evolution*, *4*(20), 3978–3990. https://doi.org/10.1002/ece3.1254

Pyke, G. H. (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics*, *15*, 523–575.

R Core Team. (2025). R: A language and environment for statistical computing.

Railsback, S. F. (2022). Suboptimal foraging theory: How inaccurate predictions and approximations can make better models of adaptive behavior. *Ecology*, *103*(8), e3721. https://doi.org/10.1002/ecy.3721

Ravigné, V., Dieckmann, U., & Olivieri, I. (2009). Live where you thrive: Joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *The American Naturalist*, *174*(4), E141–E169. https://doi.org/10.1086/605369

Ravigné, V., Olivieri, I., & Dieckmann, U. (2004). Implications of habitat choice for protected polymorphisms. *Evolutionary Ecology Research*, *6*(1), 125–145.

Rettelbach, A., Kopp, M., Dieckmann, U., & Hermisson, J. (2013). Three modes of adaptive speciation in spatially structured populations. *The American Naturalist*, *182*(6), E215–E234. https://doi.org/10.1086/673488

Reynolds, R. G., & Fitzpatrick, B. M. (2007). Assortative mating in poison-dart frogs based on an ecologically important trait. *Evolution*, *61*(9), 2253–2259. https://doi.org/10.1111/j.1558-5646.2007.00174.x

Reznick, D. (2016). Hard and soft selection revisited: How evolution by natural selection works in the real world. *Journal of Heredity*, *107*(1), 3–14. https://doi.org/10.1093/jhered/esv076

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 231–253. https://doi.org/10.1146/annurev.ecolsys.38.091206.095611

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, *62*(2), 327–335. https://doi.org/10.2307/1936707

Rueffler, C., Van Dooren, T. J. M., & Metz, J. A. J. (2007). The interplay between behavior and morphology in the evolutionary dynamics of resource specialization. *The American Naturalist*, *169*(2), E34–E52. https://doi.org/10.1086/510635

Rueffler, C., van Dooren, T. J. M., & Metz, J. A. J. (2006). The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. *The American Naturalist*, *167*(1), 81–93. https://doi.org/10.1086/498275

Schluter, D. (2000). *The ecology of adaptive radiation.* Oxford University Press.

Schluter, D. (2003). Frequency dependent natural selection during character displacement in sticklebacks. *Evolution*, *57*(5), 1142–1150. https://doi.org/10.1111/j.0014-3820.2003.tb00323.x

Servedio, M. R., Doorn, G. S. V., Kopp, M., Frame, A. M., & Nosil, P. (2011). Magic traits in speciation: 'magic' but not rare? *Trends in Ecology & Evolution*, *26*(8), 389–397. https://doi.org/10.1016/j.tree.2011.04.005

Stenseth, N. C. (1984). Evolutionarily stable strategies in food selection models with fitness sets. *Journal of Theoretical Biology*, *109*(4), 489–499. https://doi.org/10.1016/S0022-5193(84)80154-X

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton University Press.

Svanbäck, R., & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: An optimal diet theory method. *Evolutionary Ecology Research*, *7*(7), 993–1012.

Tilman, D. (1982). *Resource competition and community structure.* Princeton University Press.

Tinoco, B. A., Graham, C. H., Aguilar, J. M., & Schleuning, M. (2017). Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, *126*(1), 52–60. https://doi.org/10.1111/oik.02998

Turelli, M., Coyne, J. A., & Prout, T. (1984). Resource choice in orchard populations of *Drosophila*. *Biological Journal of the Linnean Society*, *22*(2), 95–106. https://doi.org/10.1111/j.1095-8312.1984.tb01672.x

Vincent, T. L. S., Scheel, D., Brown, J. S., & Vincent, T. L. (1996). Trade-offs and coexistence in consumer-resource models: It all depends on what and where you eat. *The American Naturalist*, *148*(6), 1038–1058. https://doi.org/10.1086/285970

Weissing, F. J., Edelaar, P., & van Doorn, G. S. (2011). Adaptive speciation theory: A conceptual review. *Behavioral Ecology and Sociobiology*, *65*(3), 461–480. https://doi.org/10.1007/s00265-010-1125-7