Diversification of predators in multi-trophic communities: A trait-based theoretical approach

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Abstract

One of the main challenges in ecology and evolutionary biology is to understand how biodiversity emerges and is maintained, given the complexity of ecological and evolutionary processes combined. Understanding how multi-trophic interactions occur from a theoretical perspective is highly relevant for our understanding of diversification in complex ecosystems. Here, I explore how the diversification of predators is driven by predator-prey interactions in an eco-evolutionary context. I evaluate the effect of ecological and reproductive characteristics of predators on their diversification by using a trait-based and individual-based model. In terms of predator ecological characteristics, I find that higher feeding efficiency and intermediate predator niche widths facilitate diversification through higher population sizes and ecological opportunity respectively. In terms of reproduction, asexual reproduction facilitates predator diversification when compared to sexual reproduction, while the latter can hinder diversification unless assortative mating is high. Finally, high predator mutation rates allow for diversification, but only in combination with the characteristics mentioned before. The model thus improves our mechanistic understanding of the diversification of trophic communities, and it enables us to further study how eco-evolutionary interactions can allow biodiversity to arise.

Introduction

The interplay between ecology and evolution

Understanding how biodiversity arises is one of the main goals in biology. Among the biggest sources of biodiversity on Earth are radiations, the explosive diversification of a lineage from a single species[1], a topic that has inspired both theoretical and empirical biodiversity research [2–4]. Such diversifications are now known to be the result of multiple interacting processes such as geographical isolation, sexual selection, and local adaptation[2]. In particular, the role of ecological interactions (e.g. competition, predation) has been known to be a key component of evolution and thus diversification since the time of Darwin and Wallace[5,6]. On this note, the rapid evolution of ecological and phenotypic diversity is described by adaptive radiations[7]. This process involves the diversification of traits triggered by ecological opportunity, ecological interactions such as competition, and evolutionary-driven key innovations (e.g. trait evolution). For adaptive radiations to happen, evolution needs to act on functional traits, in which there's a direct interaction between phenotypic traits and their abiotic and biotic environment. There is also substantial empirical evidence for such a trait based connection between for example competition, niche availability, and trait evolution, as is illustrated by, for example, the radiation of the Galapagos finches[8], and the diversification of *Anolis* lizards in America[9].

Only recently it's been recognized that ecological interactions not only drive evolution, but evolutionary changes also affect ecological interactions over a relatively few number of generations, producing eco-evolutionary feedbacks[10]. Studies of these interactions can focus on how some species have strong effects in their ecosystems (e.g. niche construction)[11,12], while other studies focus on how evolution in traits alters the population dynamics in ecological timescales[13]. Eco-evolutionary feedbacks require a strong influence of novel traits acting on and reshaping their environment. Subsequently, changes in an environment may cause selection on the populations that modified it[14] in a coinciding eco-evolutionary timescale. The importance of eco-evolutionary processes as a driver for adaptive radiations is clear, however, the mechanisms that give rise to these processes are still not completely understood, especially between trophic levels[15–17].

Trophic interactions and upward adaptive radiation cascades

Biological communities are often defined by the relation between species and their functional roles in determining the flow of energy across populations, known as trophic interactions[18]. Interactions between species also play a fundamental role in adaptive radiations, as is found in both mutualistic[19–21] and antagonistic organisms[22,23]. In particular, predation can be a strong force driving diversification through adaptive radiation[24]. The effect of predation on the diversification of prey can be either positive, exerting selective pressure which can lead to diversification of prey[25], or negative, reducing prey population sizes and thus, limiting evolution in a similar fashion to that of interspecific competition. The diversification of prey triggered by predators has thus been broadly studied empirically and theoretically. However, the study of the processes that drive the diversification of predators in a multi-trophic level community context is less studied. Only a few have addressed adaptive radiations in predators[26,27] and the terminology "Upwards adaptive radiation cascades" has been suggested. Upward adaptive radiation cascades have the following characteristics: 1) Phenotypic and evolutionary diversification of a lineage coexisting in a single ecosystem; 2) The cascade of evolutionary consequences as a result of the ecological interactions over two or more trophic levels; and 3) The upward, or bottom-up, effect that the ecological processes have on populations for diversification to happen[17]. An example of this phenomenon is observed in the diversification of insect parasitoids as a response to adaptive radiation of their specific hosts[28,29]. Another example is the American alewife *(Alosa pseudoharengus*) that diversified in response to the construction of a dam by humans, which in turn promoted the diversification of its predator, the chain pickerel (*Esox niger*)[30].

Adaptive traits and their role in speciation

In order to better explain how upward adaptive radiation cascades occur, their mechanisms and consequences, a better understanding of the diversification of functional traits is necessary. In the study of radiations in general, it is often the case that some traits are more prone to induce diversification than others. In adaptive radiations, these relevant traits correspond to ecological traits that are adaptive to different niches. For example, body size is commonly viewed as a functional trait of high relevance as it often relates to multiple aspects of an organism's niche including resource utilization, interactions with other organisms, and habitat utilization[18].

Resource niches, also known as α-niches, dictate specifically the local resource availability and thus also potential organismal resource utilization[31]. Given such a focus on diversification in traits that are related to resource utilization in the α-niche dimension, particular aspects of diversification also come into play. For example, sympatric speciation, the emergence of new species from a population without spatial isolation[32], needs consideration. Furthermore, sympatric speciation is caused by different mechanisms including competition, and assortative mating (the tendency to choose similar mates), which can lead to reproductive isolation.

Sympatric speciation is often described either in terms of reproductive isolation by sexual selection and genetic incompatibilities (although these are not the only mechanisms that lead to reproductive isolation), or by how populations experience divergent selection for use of separate niches. Studies often focus on either the role of sexual or divergent selection separately, but there is a shortcoming when considering both processes together due to their complexity. In some cases, however, fitness (defined as the ecological and/or reproductive success of an individual or population) is influenced by assortative mating on ecological traits. Such correlation is referred to as pleiotropy, the phenomenon when a single gene influences more than one trait[34]. In theoretical models, these correlated traits are referred to as "magic traits", defined as single traits that describe assortative mating, and are also under ecological selection[32]. Empirical examples include studies on the threespine stickleback species complex (*Gasterosteus aculeatus*)[35], butterflies of the genus *Heliconius*[36], and seahorses of the family Syngnathidae[37]. Equally, some theoretical models also make use of magic traits as shown by Moore[38], Slatkin[39], and Kirkpatrick and Nuismer[40], to name a few. To fully understand adaptive radiations in trophic communities such mechanisms needs to be explored both empirically and theoretically.

Individual-based models for eco-evolutionary dynamics

Studying upward adaptive radiations is a difficult task due to the complexity of the eco-evolutionary feedbacks and the involved mechanisms mentioned above. As a result, many different approaches have been developed to model the dynamics of life, with an increase in detail and complexity. From the exponential growth model of Malthus in the late 18th century to the contemporary adaptive dynamics framework for modelling adaptive trait dynamics[41], models have helped us develop theory and thus the understanding of such complexity. A majority of models rely on deterministic approaches that while crucial for our understanding of theoretical eco-evolutionary dynamics, can miss the complexity of individual variation. To address this problem, individual-based models (IBM) allow simulating populations in terms of discrete agents with individual characteristics[42]. This discretization of organisms and processes allows to study more closely some characteristics of life that otherwise can become difficult to incorporate into alternative methods. Incorporating elements such as genetics, different mating systems, and recombination in reproduction represents an advantage since it allows for the so-called individual variation[43]. Another important characteristic of IBMs is stochasticity, which allows to include random events in simulations, that are important to consider in ecological and evolutionary mechanisms and processes such as predation, mutation, and survival. Making use of different approaches like IBMs can, if implemented properly, aid in the study of evolution by enabling different approaches in different levels of complexity and relevance, in line with emerging research.

Motivation and goals

While there is growing literature that shows evidence of upward adaptive radiation cascades in nature, there remains a gap regarding the theoretical support of the eco-evolutionary processes and mechanisms that drive such radiations in predator-prey systems. For example, Pontarp[44] shows the effects of predator niche width, evolvability and predator feeding efficiency for predator and prey diversification. However, one of the assumptions of this study is asexual reproduction, which can affect how diversification occurs[45,46]. In this project, I investigate from a theoretical perspective how ecological factors (predator niche width and feeding efficiency), mutation rate, type of reproduction, and mate choice determine how predators diversify with coevolving prey. For this, I implement an individual-based model built on a trait-based approach for ecological interactions with explicit genetics**.** The model shows the ecological and evolutionary dynamics of populations in one (prey-resource) and two (predator-prey-resource) trophic levels. I analyse the diversification of predators by measuring the number of predator morphs at the end of the simulation, population sizes, and their speciation events. This allows to further explain how ecological and evolutionary factors influence predator diversification.

Methods

Model

The model presented here simulates adaptive radiations driven by ecological interactions in a predator-prey system using a Lotka-Volterra model as a basis, expanded to include trait dependant interactions and eco-evolutionary dynamics[44]. The model is designed in the context of an α-niche framework. The organisms thus interact locally in one habitat, and I explicitly model three distinct non-evolving types of resources, which are consumed by prey that in turn is consumed by predators. Trait-dependent interactions imply that resource utilization, predation, competition, and mating interactions are dictated by the matching of a continuous one-dimensional evolving trait. Although generally formulated in the model (i.e. an abstraction of any functional trait) such a trait may, for example, be body size, a trait that controls both the niche position of an individual and its niche width (i.e. degree of specialization). It follows that organisms consume more efficiently resources with a similar trait to theirs (e.g. a predator bigger in size consuming bigger prey), while also competing more strongly with other organisms in their trophic level with similar traits. The niche width represents the range of the resource that an organism can consume. A narrow niche width represents individuals that are specialized in one resource type and that consume other resources inefficiently; in contrast, a wide niche width represents generalist individuals that can consume other resources more efficiently at the expense of higher competition with individuals well adapted to these resources.

The implementation of my model is inspired by previous work by Ripa[47,48]. This is done by using an individual-based approach, where prey and predator populations are modelled by individual entities with their traits coded by explicit genetics in an additive way (trait value is given by the sum of effects from each locus). Resources are defined deterministically based on consumption (see resources section below). Reproduction occurs in two possible ways depending on simulation scenarios, either asexually, where the offspring is a clone of its parent; or sexually (only modelled in predators), where organisms choose a mate and reproduce, giving offspring their recombined genes. In each discrete generation of a simulation, individuals consume resources, choose a mate (in the sexual reproduction scenario), reproduce, and the offspring survives based on its fitness, which depends on its consumption rate of resources and predation. At the end of each generation, the offspring replaces the current population, resulting in non-overlapping generations. The following sections further explain each of these components, which are illustrated in Fig. 1.

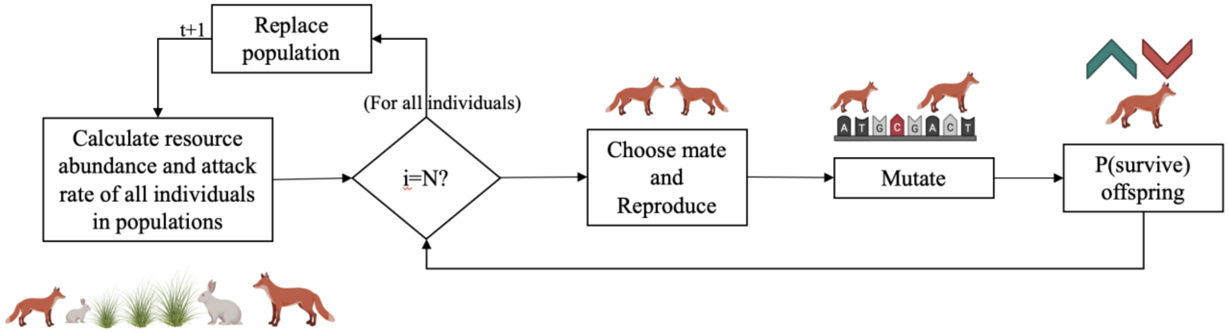

Fig. 1: Flowchart of steps followed in each generation. First, resource abundances and consumption are calculated. Then, all individuals from each population choose a mate (when reproducing sexually), reproduce, their offspring can mutate, and survives based on their fitness. Finally, the offspring population replaces the parent population for the next generation.

Survival and fitness

Fitness in this model determines the survival of a given individual's offspring. Fitness of prey depends on their consumption of resources, and the predation that acts upon them:

$$f_i = \sum_j a_{ij} R_j^* - b_{max} \sum_l b_{li} \tag{1}$$

Where a_{ij} is the attack rate of resource *j*; R_j^* is the equilibrium abundance of resource *j*; b_{max} is the maximum predation rate; and b_{li} is the attack rate from the predators on the individual *i*. Similarly, fitness of a predator *l* is given by:

$$f_l = g b_{max} \sum_i b_{li} \tag{2}$$

Where g is the predator feeding efficiency, and b_{li} is the attack rate of predator *l* on the prey.

Individuals that survive to the next generation are assumed to reach sexual maturity and produce $F = 2$ offspring (and if they find a mate, in the sexual reproduction scenario). Survival of an offspring i depends on their fitness, and since fitness is the product of survival and fecundity F, survival can be expressed as follows:

$$S_i = \frac{f_i}{F} \tag{3}$$

The probability of survival of an individual offspring is then compared against a sample from a uniform distribution between 0 and 1, which determines if the individual offspring survives.

Resource dynamics

Resources (R_j) are discretely defined in one habitat and take equally distant values between 1 and 3. Resources follow chemostat dynamics, that is, resources grow on a fast timescale and are at a constant abundance within each generation. Additionally, resources have a type I response from its consumers (i.e. prey), assuming that the resource dynamics is faster than the prey dynamics[47], they can be described by:

$$\frac{dR_j}{d\tau} = K - R_j - \sum\nolimits_i \frac{a_{ij} R_j}{F} \tag{1}$$

Where τ denotes the time on a fast timescale, K is the system size, and the sum denotes the total consumption of resource j from the prey, rescaled by the fecundity F, in a way that the abundance depends on the adult populations of prey after survival independent of F. By solving this equation, it is possible to obtain the equilibrium abundance of a resource R_j^* in every generation, given by:

$$R_j^* = \frac{K}{1 + \sum_i a_{ij} / F} \tag{2}$$

Ecological traits and consumption

The ecological trait α from a consumer i interacts with the ecological trait β from a resource j according to the following expression[44]:

$$e^{-\frac{(\alpha_i - \beta_j)^2}{2\sigma_\alpha^2}} \tag{3}$$

Where α_i corresponds to the trait value in the consumer and β_j corresponds to the trait value of the resource. Since resources are discretely defined, their trait values also correspond to the number of resources, such that $j = \beta_j \in \{1,2,3\}$. Consumption of a resource j is then maximized when $\alpha_i = \beta_j$. In prey, a difference of one unit in trait value represents a shift from one resource type to the other (Fig. 2, mid and bottom panels); while in predators, a shift in prey type depends on the distribution of traits of available prey. The niche width of the consumer is given by σ_α, and interacts as described above. Subsequently, the consumption a_{ij} of a resource j done by a consumer (prey) i is given by:

$$a_{ij} = \frac{a_0}{K} e^{-\frac{(\alpha_i - \beta_j)^2}{2\sigma_\alpha^2}} \tag{4}$$

Where a_0 corresponds to the base attack rate of the prey, therefore $\frac{a_0}{K}$ is the attack rate of the prey on one unit of the resource.

Similarly, consumption b_{li} of a predator l on prey i is given by:

$$b_{li} = b_0 e^{-\frac{(\gamma_l - \alpha_i)^2}{2\sigma_\gamma^2}} \tag{5}$$

Where b_0 is the base attack rate of the predator, γ_l is its trait value, and σ_γ is its niche width. The resource, prey, and predator interactions are illustrated in Fig. 2.

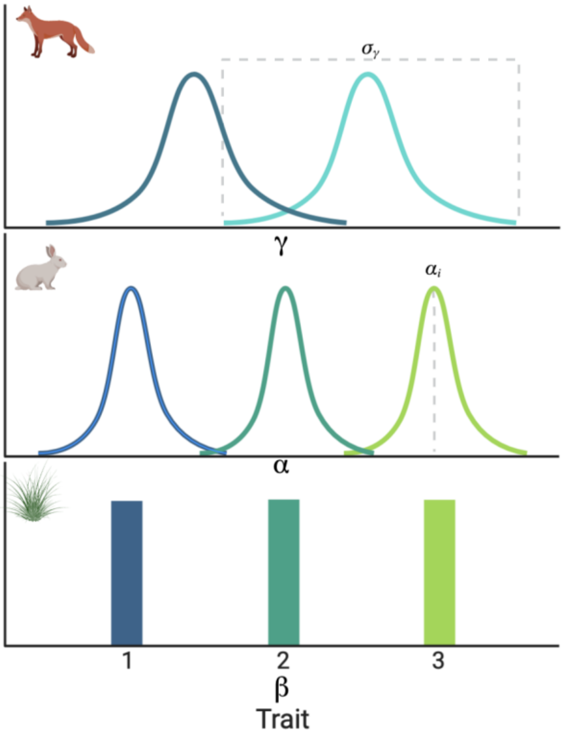

Fig. 2: Illustration of niche interactions between resources, prey, and predators. Resources take discrete values between 1 and 3 (bottom panel). Each prey and predator have an optimal trait value (illustrated as α_i for the prey in the middle panel) that dictates what resources they consume with the maximum attack rate. Niche width (illustrated as σ_γ for the predator in the top panel) determines the amount of resources in a lower trophic level that an individual can consume.

Mate choice and reproduction

The implementation counts with two models: one with clonal reproduction (no mating), and one with sexual reproduction of predators. For the sexual reproduction scenario, each individual chooses randomly from a list of up to 1000 individuals (or the population size -1 if it's lower) without replacement and excluding itself. The individual iterates through the sample until it accepts a mate, and in case it doesn't find any, it doesn't reproduce. An individual *i* can accept a mate *j* based on their trait γ with a probability $P_\gamma(i,j)$ as follows:

$$P_\gamma(i,j) = \begin{cases} e^{-c_{\gamma,i}(\gamma_j-\gamma_i)^2}, & c_{\gamma,i} \geq 0 \\ \min\left(1, e^{-c_{\gamma,i}(\gamma_j-\gamma_i)^2-1}\right), & c_{\gamma,i} < 0 \end{cases} \qquad (6)$$

Where $c_{\gamma,i}$ is a choosiness parameter of an individual *i* on trait γ, such that the higher the value of $c_{\gamma,i}$, the higher the preference for individuals with similar trait values γ. Therefore, a high value of $c_{\gamma,i}$ represents strong assortative mating (i.e. individuals preferring similar mates), a negative value represents disassortative mating (i.e. individuals preferring distinct mates), and a value of 0 represents random mating.

Once a mate is chosen, individuals produce *F = 2* offspring, each having the recombined genes of their parents. Individuals are hermaphroditic and non-monogamous; this means that mates are not differentiated between male and female and can be chosen many times by different individuals as long as they fulfil the condition. The choice of hermaphroditic and non-monogamous individuals was done merely to reduce computational time, implementing a model with either of these two assumptions should produce comparable results. For the clonal reproduction scenario, all individuals produce *F = 2* offspring and there is no recombination. After reproduction is completed, the offspring replaces the entire population, producing non-overlapping generations.

Genetics model

Each individual has an evolving ecological trait (α for prey, and γ for predators) coded by 16 diallelic loci for prey, and 32 diallelic loci for predators. While the model can be expanded for other parameters, evolution only acts on the ecological traits. The genetic model of the trait is additive, and each allele can take a value of 0 or 1 with an effect size of ±1/2 which is added and converted to its phenotypic trait value. During reproduction, each allele can mutate independently to its alternative allele with a probability μ, allowing evolution to occur.

The genotypic value is rescaled to a value between 0 and 4, which allows the phenotype to go beyond the extreme niche values of 1 and 3 dictated by the resources. Conversion from genotype to a phenotype α can be expressed with the following expression:

$$\alpha = count(genotype, 1) * \frac{max(\alpha) - min(\alpha)}{2 * loci} \tag{7}$$

Where $count(1, genotype)$ refers to the number of alleles that take the value of 1, $max(\alpha)$ is the maximum trait value (i.e., 4), $min(\alpha)$ is the minimum trait value (i.e., 0), and $loci$ is the number of loci that code the trait. This means that for prey, the effect of each allele corresponds to 0.125, and the effect of each allele for a predator is 0.0625. A prey would need 8 substitutions to the alternative allele in order to shift resources by 1 unit, while a predator would need 16 substitutions to shift to a prey 1 trait unit away.

Morph clustering definition

The number of morphs at any given generation is defined based on a population's ecological trait values. Since trait values are defined continuously, it's necessary to cluster them by similar values. The algorithm created to define the number of morphs in a population goes as follows: The initial step is to calculate the kernel density estimate (KDE) of the population at a given generation *t* based on the distribution of traits weighted by the number of individuals for each trait value. This estimation is done with Silverman's method[49] smoothed using a Gaussian kernel with a bandwidth *h = 0.4*. This method gives a multimodal KDE, where each cluster is defined as the region between two local minima (valleys). The second step is to filter out clusters where the density of the peak is lower than 0.2 the density at the maximum peak in the kernel; this step allows to filter out trait values with very low population sizes, which are the product of noise. The third and final step is to merge clusters where the distance between their peaks is less than 5 times the mutational step, in which cases the distance can be explained by multiple mutations in a few generations. While the first step is based on a mathematical basis, the second and third steps are done based on biological relevance and the model design.

Model implementation

The model described above was implemented in MATLAB (*ver. R2021b*)[50], with the exception of the morph analysis component. The model has the following modules:

- **Resource.m:** Class that contains different resources. Its attributes are trait value, habitat* in which the resource is, system size, and resource abundance. Methods include a constructor, and a function to calculate equilibrium abundance, as described in (5).
- **Individual.m**: Contains the base class that defines an individual. Attributes include an ecological resource trait (termed alpha), habitat* (termed beta), display*, preference*, and choosiness traits. It also includes an ecological resource and habitat* niche width, probability of mutation attributes, and objects of the class Genetics for the alpha, beta*, display*, and preference* traits. Calculated values include an attack rate matrix and fitness value. Methods include a constructor, consumption, fitness, and dispersal*. (Note: Attributes marked with * are implemented, however, they are not used, since their use goes beyond the scope of this project)
- **Prey.m and Predator.m:** Classes that inherit from the Individual class, and contain overridden methods for consumption, as described in (7) and (8), and fitness, as described in (1) and (2). The predator class also includes feeding efficiency as an attribute.
- **Population.m:** Class that contains an array of individuals of type predator or prey. This class also contains array attributes for the trait distribution of the population, fitness values, and attack rates.
- **Genetics.m:** Class that contains the logic for any trait coded as a gene. Attributes include type (i.e. diallelic), number of loci, genotype array, minimum and maximum trait values, and probability of mutation. Methods include a constructor, conversion from genotype to phenotype, from phenotype to genotype, mutation in one gene, and recombination between two genes.

- **reproduce.m:** Module that contains the necessary functions for reproduction of one individual in both the asexual and sexual case, and a function to calculate the probability of accepting a mate, as described in (9).
- **main_pred_prey.m:** Script that executes one simulation. Receives as parameters whether the simulation is run for prey only, or for a predator and prey system, ecological niche widths for both predator and prey, base attack rate of the predator, feeding efficiency, the initial number of prey morphs, mutation rate for predator and prey, a flag to define whether it's an asexual or sexual scenario, and a choosiness parameter. An execution goes as follows: First, populations are initialized according to parameters and an output file is generated. An output csv file contains data for generation number, trait values (both for predator and prey), number of individuals for each trait value, and average fitness. The output from each generation is written every 2 generations to reduce disk usage. For every generation, the attack rate of the prey on the resource is calculated, followed by the new resource equilibrium abundance, and the attack rate of the predator population on prey. Then, every individual in every population finds a mate (in the sexual case) and reproduces. Each of the offspring mutates according to its associated probability of mutation, then its fitness is calculated, and they live to the next generation based on their probability of survival, as described in (3). Finally, the offspring population replaces the parent population for the next generation. An illustration of what occurs in every generation is summarized in Fig. 1.

Execution and parametrization

Given that the focus of this project is on predator evolution, I first performed analysis on the diversification of prey with the goal of finding a set of parameters (i.e. mutation rate and prey niche width) that result in prey diversification into three final morphs, adapted to each of the resources. Then, during a second analysis, I identified a predator parameter space where one morph of predator and one morph of prey coexist until the end of the simulation. With this constrained parameter space, I ran simulations allowing mutations to happen in both predator and prey.

For all simulations, the following default parameters were used: Maximum number of generations = 10000, $K = 400$ (For each resource), $F = 2$, $\mu_{prey} = 1e-05$, $a_0 = 2$, Number of loci for prey ecological trait α = 16, Number of loci for predator ecological trait β = 32. The initial population size of the prey was declared as $N_{0\_prey} = K$, allowing the population size to stabilize based on competition, and the initial population size of the predator was declared as $N_{0\_predator} = K/20$, allowing it to grow in population size, while not going extinct in the first generations due to stochasticity.

After filtering, the final execution parameters are as follows: Prey niche width was set as $\sigma_\alpha = 0.45$, predator base attack $b_0 = 5.00E-03$, predator niche width $\sigma_\gamma \in \{0.30, 0.35, 0.40, 0.45, 0.50\}$, predator feeding efficiency $g \in \{0.55, 0.60, 0.65\}$. Predator mutation rate was set as $\mu_{pred} \in \{1e-5, 5e-5, 1e-4, 5e-4, 1e-3, 5e-3\}$ which correspond to 1, 5, 10, 50, 100 and 500 times the prey mutation rate ($1e-5$). Reproduction was allowed to occur sexually or asexually. For sexual reproduction, the choosiness parameter for different strengths of assortative mating was set as follows:: $c_\gamma = 0$, representing random mating; $\mathrm{c}_\gamma = -\ln(5.00\mathrm{E}-03) \approx 6.9078$, representing low choosiness with a probability of choosing a mate equal to 0.1% when they are 1 resource unit away; and $\mathrm{c}_\gamma = \frac{-\ln(0.5)}{0.125^2} \approx 44.3614$, representing high choosiness with a 50% of probability of choosing a mate when they are 2 mutational steps apart (0.125). For the asexual reproduction scenario, 90 simulations were run corresponding to all parameter combinations, and similarly, 270 simulations were run in the sexual reproduction scenario. The results from these simulations were then analysed to find the number of morphs, population sizes, and speciation events. Analysis of results was done using R *(Ver. 4.0.3)*[51], along with the dplyr (*Ver. 1.0.4*)[52] and ggplot2 (*Ver. 3.3.3*)[53] libraries for data manipulation and plotting respectively.

Code availability

The entirety of the code used, including the model implementation, command-line scripts, analysis, and plotting can be found at: https://github.com/julioaayala/pred-prey-ibm along with instructions for its execution.

Results

Prey-resource diversification

Simulations of the prey-resource scenario without predation were run to find the niche width that gives rise to three morphs, adapted to each of the resources. When niche width takes a value of $\sigma_\alpha = 0.45$ and the mutation rate is $\mu_{prey} = 1e-05$, the prey diversifies into three stable morphs over 10000 generations (Fig. 3). When niche width is narrow ($\sigma_\alpha = 0.35$), prey doesn't diversify at all (Appendix, figure S1a) since intermediate mutants have inferior fitness and they can't transition to a different niche (Appendix, figure S2). Alternatively, a wide niche width ($\sigma_\alpha = 0.55$) diversifies into two morphs that sit in the middle of two resources (Appendix, figure S1b). The parameters used for a radiation resulting in three morphs ($\sigma_\alpha = 0.45$) were used as a baseline for the simulations including predation.

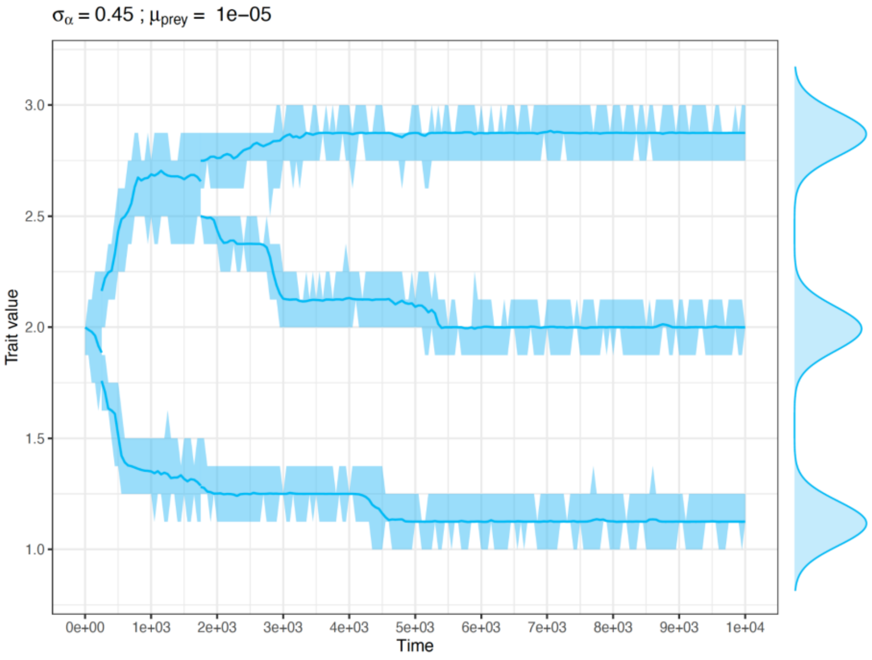

Fig. 3: Radiation of prey well adapted to three resources with a niche width $\sigma_\alpha = 0.45$ *and a mutation rate* $\mu_{prey} = 1e-05$ *over 10000 generations. The x-axis on the left panel represents time in generations, and the y-axis represents the trait value. A dark line represents the mean value of the morph cluster during 50 generations and shading represents the minimum and maximum values for the trait in the same timeframe. The right panel represents the distribution of traits in the last generation.*

Predator-prey diversification

Diversification of predators was analysed for all simulations, represented as the final number of morphs in the population (Fig. 4a). Simulations of predator-prey interactions can result in a set of different outcomes for the predator(s). Predators may follow extinctions or survive by adapting with coevolving prey without diversifying. Alternatively, predator diversification into two or three final morphs may occur (Appendix, table S1). For asexually reproducing predators, extinctions occurred in 32/90 of the scenarios (35.6%). For sexually reproducing predators with random mating and low choosiness ($c_\gamma = 6.9078$) extinctions occurred in 40/90 (44.4%) of the scenarios (Appendix, table S2,S3). In contrast, for high choosiness ($c_\gamma = 44.3614$) extinctions occurred in 48/90 (53.3%) of the scenarios (Appendix, table S4). Extinctions are portrayed in Fig. 4a as white cells.

For surviving communities, a higher niche width facilitates predator diversification. However, only when the niche width is intermediate ($\sigma_\alpha = 0.35 \text{ to } 0.45$), predators can diversify into three final morphs. Higher mutation rates also promote survival and diversification of predators, which is necessary to adapt with coevolving prey. Higher predator efficiency also promotes diversification mainly due to higher population sizes (Fig. 6b).

Sexual reproduction overall hinders the diversification of predators compared to asexual reproduction. Mutant alleles are lost twice as fast in sexually reproducing individuals due to recombination since only one of the two alleles is randomly passed on to the offspring generation. When no partner choice is set and mating is random ($c_\gamma = 0$), only in one scenario do predators diversify, resulting in two final morphs ($\mu_{\text{pred}} = 5\text{e}-03, \sigma_\alpha = 0.35, g = 0.65$) (Appendix, Table S2). Accordingly, low choosiness ($c_\gamma = 6.9078$) only results in diversification when mutation rate is the highest ($\mu_{\text{pred}} = 5\text{e}-03$) (Appendix, Table S3). Only when feeding efficiency is high and the niche width is intermediate ($\mu_{\text{pred}} = 5\text{e}-03, \sigma_\alpha = 0.35, g = 0.65$), do predators diversify into three final morphs. In contrast, A higher degree of assortative mating, represented as a high choosiness value ($c_\gamma = 44.3614$) promotes predator diversification in more scenarios when mutation rate is high ($\mu_{\text{pred}} \geq 1\text{e}-03$) (Appendix, Table S4)

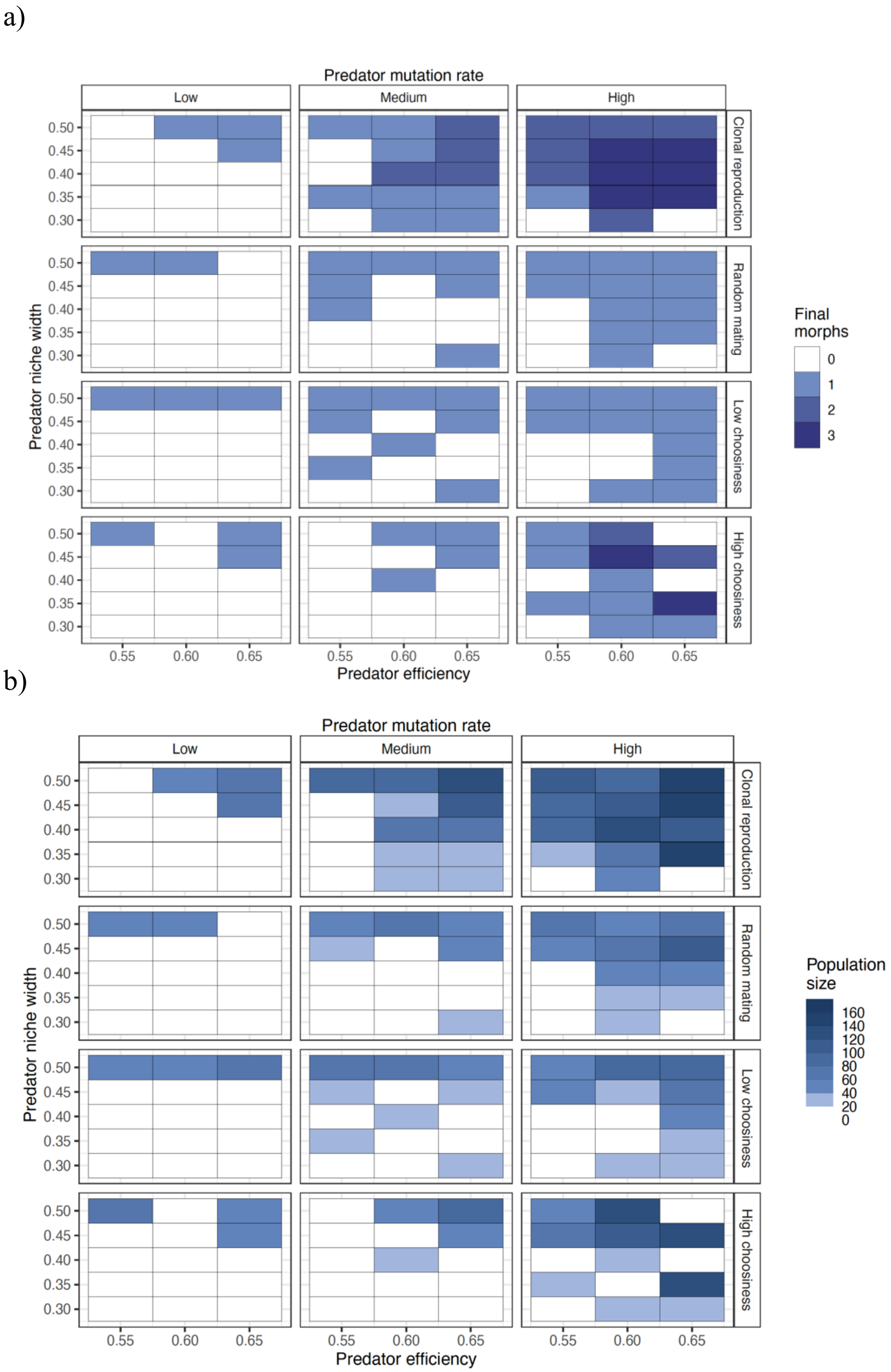

Fig. 4: Comparison between simulations at t = 10000 for a) final number of predator morphs (where 0 morphs represent extinctions), and b) final population size. The x axis represents predator efficiency, the y axis represents predator niche width, vertical panels represent low (1e-05), medium (1e-04) and high (1e-03) predator mutation rates, and horizontal panels represent asexual (clonal) reproduction, random mating ($c_\gamma = 0$), low ($c_\gamma = 6.9078$) and high ($c_\gamma = 44.3614$) choosiness.

Predator-prey co-radiations

The temporal dynamics for all simulation scenarios are different, however, general patterns can be observed. Predators can go extinct by not evolving fast enough with coevolving prey. Predators can also adapt, without diversifying, with coevolving prey, resulting in directional selection (Fig. 5a). Alternatively, when the mutation rate is high, predators can adapt to prey by shifting niches also without diversifying, which is a case observed only in sexual reproduction scenarios (e.g. Fig. 6a). Finally, predators can radiate with coevolving prey (Fig. 5b and c; Fig. 6b and c) resulting in two or three distinct morphs. For radiating predators reproducing asexually, the first speciation event occurs around the 1500th generation as the median (mean = 2176 ± 1944) (Appendix, table S5), and the second speciation event occurs around the 4000th generation as the median (mean = 4562 ± 2228) (Appendix, table S6). The first speciation event for sexually reproducing predators occurs on the 1500th generation as the median (mean = 2521± 2218) (Appendix, table S7), and the second speciation event occurs on the 4000th generation as the median (mean = 4600 ± 2665) (Appendix, table S8). Speciation events have no specific pattern in relation to niche width, mutation rate, or feeding efficiency.

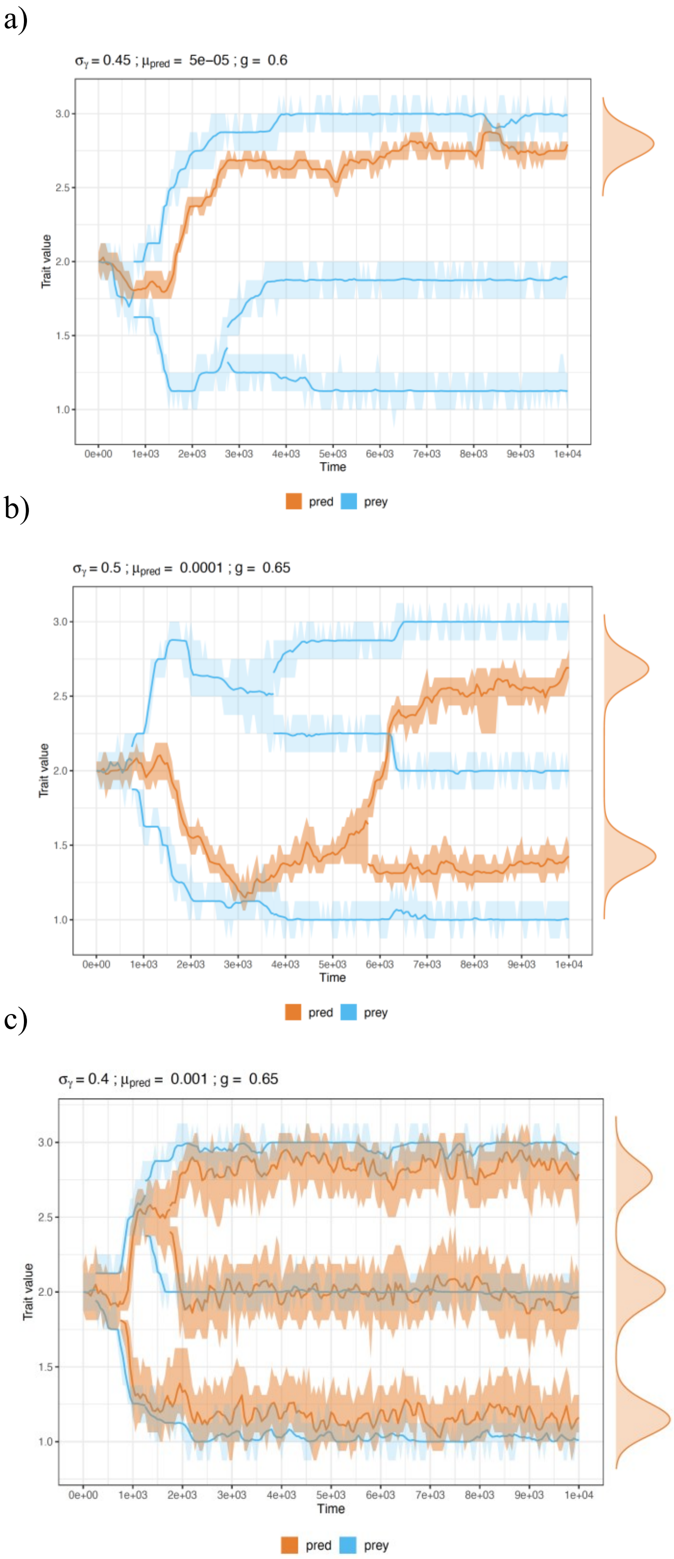

Fig. 5: Predator-prey radiation examples for clonal individuals concluding with a) 1 final morph when $\sigma_\gamma = 0.45$, $\mu_{pred} = 5e-05$, *and* $g = 0.6$ *b) 2 final morphs when* $\sigma_\gamma = 0.5$, $\mu_{pred} = 1e-04$, *and* $g = 0.65$ *, and c) 3 final morphs when* $\sigma_\gamma = 0.4$, $\mu_{pred} = 1e-03$, *and* $g = 0.65$. *Left panels represent distribution of traits*

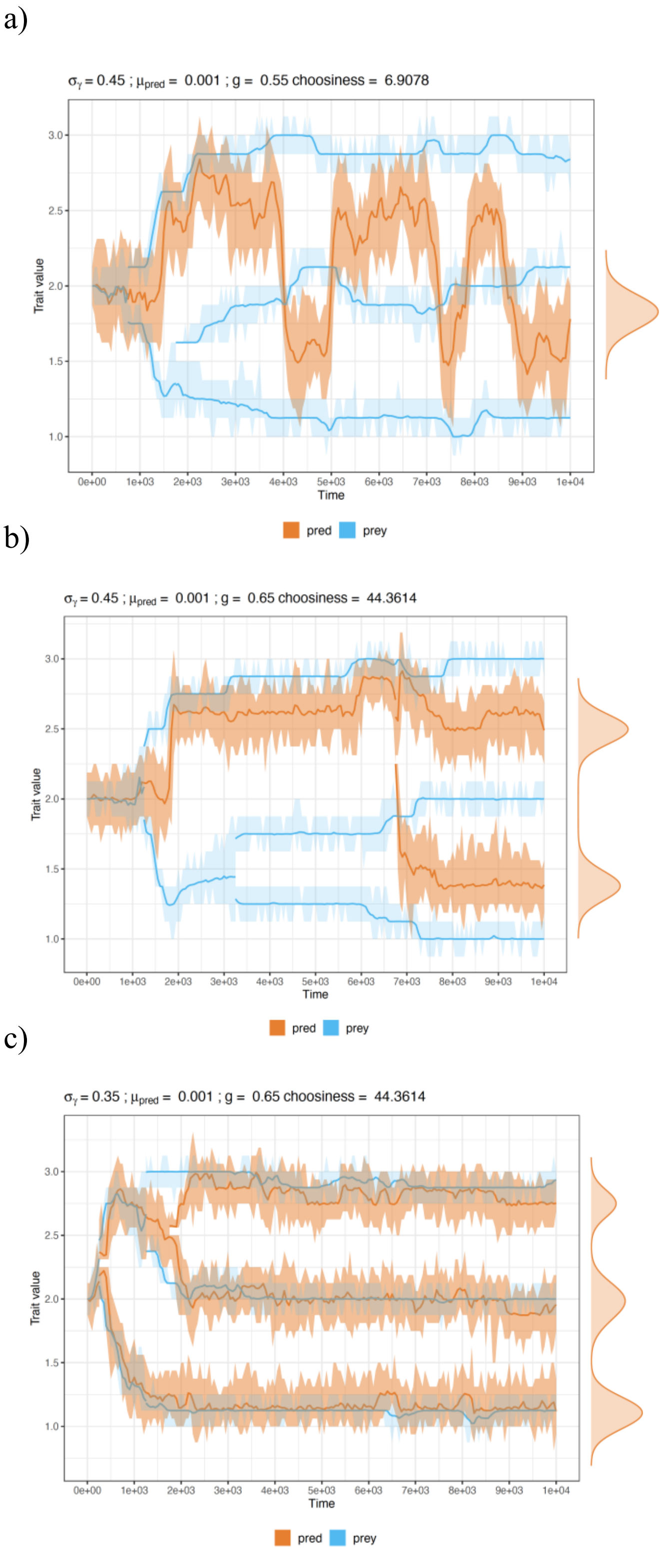

Fig. 6: Predator-prey radiation examples for predators with sexual reproduction concluding in a) 1 final morph when $\sigma_\gamma = 0.45$, $\mu_{pred} = 1e-03$, $g = 0.55$ *and* $c_\gamma = 6.9078$*; b) 2 final morphs when* $\sigma_\gamma = 0.45$, $\mu_{pred} = 1e-03$, $g = 0.65$ *and* $c_\gamma = 44.3614$*; and c) 3 final morphs when* $\sigma_\gamma = 0.35$, $\mu_{pred} = 1e-03$, $g = 0.65$ *and* $c_\gamma = 44.3614$. *Left panels represent radiations and right panels represent the distribution of traits*

Discussion

Identifying upward radiation cascades is difficult. One of the characteristics of upwards adaptive radiation cascades is the eco-evolutionary interactions between predators and prey around their time of diversification. However, not all predator radiations are upward radiation cascades, specifically when a lineage of predators meet an already diverse lineage of prey, where predator radiations can occur in response to novel opportunity[17]. Such is the case of killer whales (*Orcinus orca*), which have radiated into sympatric ecotypes with different prey preferences, morphology, and behaviour that diverged from around 150,000 to 700,000 years ago[54], in response to available diverse prey. Thus, it's important to differentiate between classic adaptive radiations and upward adaptive radiation cascades as part of our understanding of different biodiversity drivers.

Here, I try to better understand the diversification of predators by evaluating how their characteristics result in a different number of predator morphs, as well as how they diversify. Through modelling, I conclude that high predator feeding efficiency and intermediate predator niche widths facilitate diversification. Asexual reproduction facilitates predator diversification when compared to sexual reproduction, which often hinders diversification unless assortative mating is high. Finally, high predator mutation rates allow for diversification, but only in combination with the characteristics mentioned before. Such results are corroborated also in the literature. For example, despite model differences, the results obtained through my simulations are in line with the ones found by Pontarp[55] in terms of predator niche width and feeding efficiency, where I found that predator diversity is proportional to feeding efficiency and the radiation of predators occurs with intermediate niche widths. Feeding efficiency directly affects predator population sizes, which in turn increases evolutionary potential. I find the same effect with higher predator mutation rates, which when increased promote predator diversification. However, contrary to Pontarp[55] and Pontarp and Petchey[44], I don't find a disruption of diversification when mutation rate and efficiency is too high. This can be caused by the nature of the model, since I use explicit and discrete resources, whereas the previously mentioned studies model resources in an implicit, continuous way. Alternatively, another cause for this difference can be my choice of parameters, where I excluded values of efficiency that wouldn't lead to the coexistence of predator and prey in a non-evolving scenario, which would lead predators to go extinct due to depletion of prey.

In terms of predator niche width, results also align with adaptive dynamics radiation theory[41], where I find that intermediate predator niche width allows for diversification to occur: A too wide niche width results in generalists that don't benefit much from mutations, or end up in intermediate niches where they consume two types of prey as efficiently (e.g. Fig. 6b). On the other hand, a too narrow niche doesn't allow for diversification to occur since mutants with intermediate trait values have lower fitness and can't shift from one prey species to the other. This however also depends on mutation parameters: A higher mutation rate increases the probability of mutations not only to occur in more individuals in the population but also in multiple positions in their genome given that mutations occur independently in each locus, allowing for more than one mutation to happen in an individual per generation, resulting in bigger size of effects (i.e. the contribution of mutations) on its phenotypic value.

By including explicit genetics and sexual reproduction I explore how the mode of reproduction also influences diversification. Under conditions of sexual reproduction, recombination acts randomly on all loci, therefore, only half of mutations on individual alleles can randomly be passed on to the next generation, which slows down evolution. Sexual reproduction, however, does not prevent diversification from occurring. Traits have both an ecological and assortative mating function, individuals will prefer mates with similar ecological trait values. This preference, given by the choosiness parameter c_γ, determine how strong assortative mating is. Predator diversification in a sexual reproduction scenario is possible, but only when assortative mating and mutation rates are high (Fig. 6a., Appendix table S4). This pattern is observed due to the link between mating preferences and ecological niche, concordant with Boughman and Svanbäck[56] . The model presented here however, uses one single trait that fulfils both ecological and mate preference functions, and reproductive isolation is given by the distance between the trait values of two individuals and a non-evolving choosiness attribute that all individuals share. A distinction needs to be made between ecological divergence and reproductive divergence, even when an assumption of correlation between ecological and mating traits are made. Based on the design of this model, ecological diversification due to niche filling results in reproductive isolation, but not the other way around. When diversification occurs, I don't find a difference in the timing for neither the first nor the second speciation events when comparing sexually and asexually reproducing predators, which can be caused by fast adaptation of predators to diversifying prey.

However, a more thorough analysis needs to be done, including the simulation of replicates, and a higher resolution in the timestep used to evaluate speciation events.

The results presented here thus provide support to previous theoretical studies on eco-evolutionary processes on predator-prey adaptive radiations[44,55]. As discussed above, in my individual-based model I find that ecological opportunity, competition, mode of reproduction, and reproductive isolation through assortative mating can drive diversification. Ecological (niche width and feeding efficiency), reproductive (mode of reproduction, mate choice), and evolutionary (mutation rate) characteristics interact and correlate with each other to determine diversification potential in predators. This said, despite the theoretical nature of my study my results also connect well with several empirical results. For example, much like the case of cichlids in the African great lakes, where diversifying prey has induced radiations in predators[17,57,58], my results suggest upward radiation cascades occurring in simulated predator-prey systems. Predator radiations always occur after prey diversification, since there would otherwise not be any ecological opportunity or advantage to diversify, prey evolution creates new or shifts existing niches which promotes selection on predators.

In conclusion, I corroborate known results with a detailed and novel model, ultimately indicating the consistency of my results as well as strengthening available theory on upward radiation cascades. I also expand our general and specific mechanistic understanding of previous literature on the topic through the details and realism (e.g. sexual reproducing predators) of my IBM. As always, there are many areas for improvement and expansion. For example, the exploration of separate ecological and preference-display traits to establish the possible link between traits without the assumption of correlation; replicated runs to increase the robustness of results; further analysis on prey diversification; and inclusion of a wider parameter space that could lead to interesting findings otherwise missed by the previous filtering. However, the proposed model here provides some insights to the understanding of how multi-trophic communities arise and diversify, as it allows for different questions to be answered and scenarios to be tested, which can be relevant for empirical and experimental studies. Additionally, its architecture allows for extensions such as spatial structure to be implemented without difficulty, which also enables for a wider scope of scientific questions to be answered.

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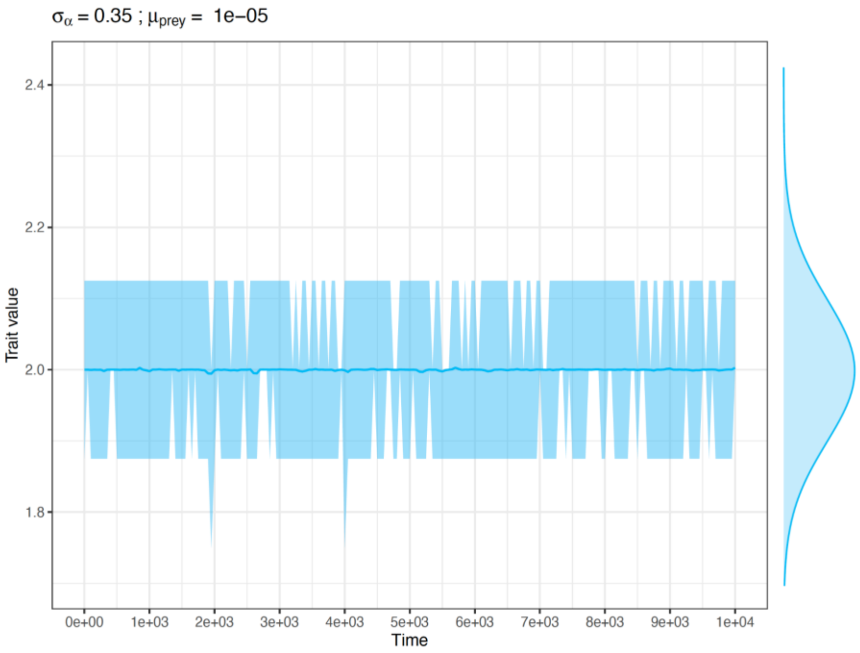
Appendix

a)



b)

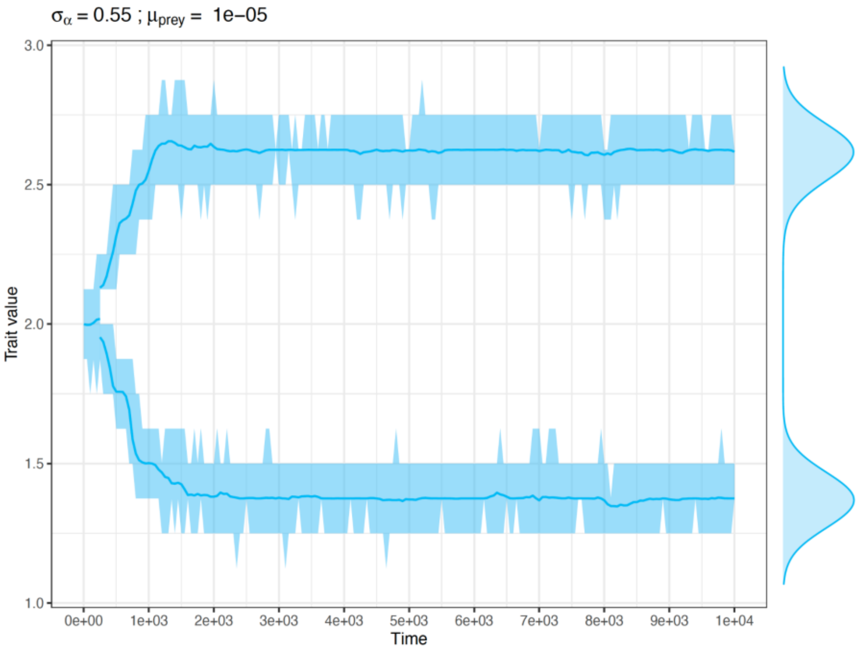


Fig. S1: Radiation of prey with mutation rate $\mu_{prey} = 1e-05$*, and niche width* $\sigma_\alpha = 0.35$ *(a) and* $\sigma_\alpha = 0.55$ *(b) over 10000 generations. The x axis on the left panel represents time in generations, and the y axis represents the trait value. A dark line represents the mean value of the morph cluster during 50 generations and shading represents minimum and maximum values for the trait in the same timeframe. The right panel represents the distribution of traits in the last generation.*

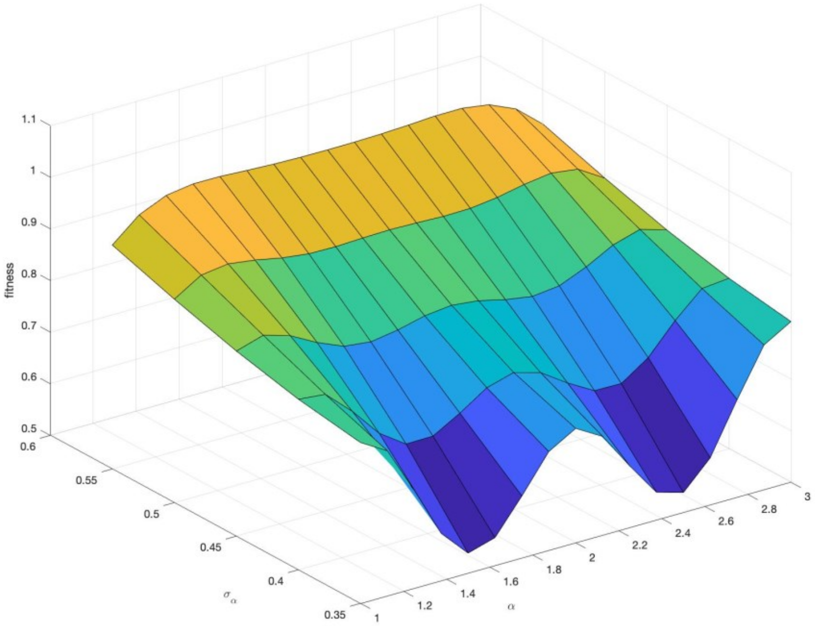


Fig. S2: Fitness landscape of coexisting prey without predation with different trait values (α) on the x axis, niche widths (σ_α) on the y axis, and fitness on the z axis.

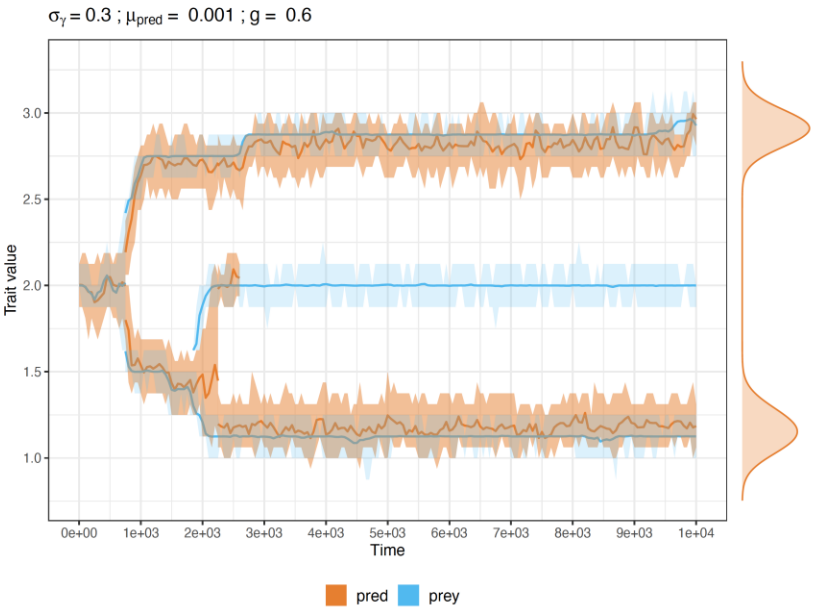


Fig S3: Radiation of asexual predator resulting in two morphs, with an extinction on an intermediate morph. Parameters are: mutation rate $\mu_{pred} = 1e-05$, *niche width* $\sigma_\alpha = 0.3$, *and* $g = 0.6$ *over 10000 generations.*

Table S1: Details on final generation for asexually reproducing predators

Predator niche width	*g*	*Predator mutation rate*	*Predator morphs*	*Prey morphs*	*Last generation*	*Predator population size*	*Extinction*
0.3	0.55	1.00E-04	0	0	1920	1	TRUE
0.3	0.55	5.00E-04	1	3	10000	24	FALSE
0.3	0.55	1.00E-03	0	0	4458	1	TRUE
0.3	0.55	5.00E-03	0	0	3558	3	TRUE
0.3	0.55	1.00E-05	0	0	720	2	TRUE
0.3	0.55	5.00E-05	0	0	674	2	TRUE
0.3	0.6	1.00E-04	1	3	10000	30	FALSE
0.3	0.6	5.00E-04	3	3	10000	111	FALSE
0.3	0.6	1.00E-03	2	3	10000	41	FALSE
0.3	0.6	5.00E-03	0	0	3840	1	TRUE
0.3	0.6	1.00E-05	0	0	4500	1	TRUE
0.3	0.6	5.00E-05	0	0	1012	2	TRUE
0.3	0.65	1.00E-04	1	3	10000	31	FALSE
0.3	0.65	5.00E-04	1	3	10000	30	FALSE
0.3	0.65	1.00E-03	0	0	794	3	TRUE
0.3	0.65	5.00E-03	0	0	762	22	TRUE
0.3	0.65	1.00E-05	0	0	1084	1	TRUE
0.3	0.65	5.00E-05	0	0	1464	2	TRUE
0.35	0.55	1.00E-04	1	3	10000	18	FALSE
0.35	0.55	5.00E-04	1	3	10000	35	FALSE
0.35	0.55	1.00E-03	1	3	10000	37	FALSE
0.35	0.55	5.00E-03	2	3	10000	49	FALSE
0.35	0.55	1.00E-05	0	0	3972	2	TRUE
0.35	0.55	5.00E-05	0	0	858	2	TRUE

0.35	0.6	1.00E-04	1	3	10000	36	FALSE
0.35	0.6	5.00E-04	3	3	10000	104	FALSE
0.35	0.6	1.00E-03	3	3	10000	71	FALSE
0.35	0.6	5.00E-03	0	0	3194	4	TRUE
0.35	0.6	1.00E-05	0	0	588	1	TRUE
0.35	0.6	5.00E-05	0	0	2120	2	TRUE
0.35	0.65	1.00E-04	1	3	10000	31	FALSE
0.35	0.65	5.00E-04	3	3	10000	113	FALSE
0.35	0.65	1.00E-03	3	3	10000	148	FALSE
0.35	0.65	5.00E-03	3	3	10000	115	FALSE
0.35	0.65	1.00E-05	0	0	3568	1	TRUE
0.35	0.65	5.00E-05	0	0	1452	1	TRUE
0.4	0.55	1.00E-04	0	0	2240	1	TRUE
0.4	0.55	5.00E-04	0	0	8052	1	TRUE
0.4	0.55	1.00E-03	2	3	10000	87	FALSE
0.4	0.55	5.00E-03	2	3	10000	51	FALSE
0.4	0.55	1.00E-05	0	0	3426	1	TRUE
0.4	0.55	5.00E-05	0	0	1112	2	TRUE
0.4	0.6	1.00E-04	2	3	10000	68	FALSE
0.4	0.6	5.00E-04	2	3	10000	82	FALSE
0.4	0.6	1.00E-03	3	3	10000	137	FALSE
0.4	0.6	5.00E-03	3	3	10000	88	FALSE
0.4	0.6	1.00E-05	0	0	3856	3	TRUE
0.4	0.6	5.00E-05	1	3	10000	34	FALSE
0.4	0.65	1.00E-04	2	3	10000	65	FALSE
0.4	0.65	5.00E-04	3	3	10000	162	FALSE
0.4	0.65	1.00E-03	3	3	10000	115	FALSE

0.4	0.65	5.00E-03	3	3	10000	151	FALSE
0.4	0.65	1.00E-05	0	0	3370	1	TRUE
0.4	0.65	5.00E-05	1	3	10000	62	FALSE
0.45	0.55	1.00E-04	0	0	7918	2	TRUE
0.45	0.55	5.00E-04	2	3	10000	85	FALSE
0.45	0.55	1.00E-03	2	3	10000	81	FALSE
0.45	0.55	5.00E-03	2	3	10000	69	FALSE
0.45	0.55	1.00E-05	0	0	2274	3	TRUE
0.45	0.55	5.00E-05	0	0	7556	1	TRUE
0.45	0.6	1.00E-04	1	3	10000	38	FALSE
0.45	0.6	5.00E-04	2	3	10000	118	FALSE
0.45	0.6	1.00E-03	3	3	10000	120	FALSE
0.45	0.6	5.00E-03	3	3	10000	115	FALSE
0.45	0.6	1.00E-05	0	0	2596	1	TRUE
0.45	0.6	5.00E-05	1	3	10000	54	FALSE
0.45	0.65	1.00E-04	2	3	10000	116	FALSE
0.45	0.65	5.00E-04	3	3	10000	127	FALSE
0.45	0.65	1.00E-03	3	3	10000	153	FALSE
0.45	0.65	5.00E-03	3	3	10000	136	FALSE
0.45	0.65	1.00E-05	1	3	10000	62	FALSE
0.45	0.65	5.00E-05	0	0	3770	1	TRUE
0.5	0.55	1.00E-04	1	3	10000	82	FALSE
0.5	0.55	5.00E-04	2	3	10000	128	FALSE
0.5	0.55	1.00E-03	2	3	10000	114	FALSE
0.5	0.55	5.00E-03	3	3	10000	119	FALSE
0.5	0.55	1.00E-05	0	0	3562	3	TRUE
0.5	0.55	5.00E-05	0	0	2230	1	TRUE

0.5	0.6	1.00E-04	1	3	10000	89	FALSE
0.5	0.6	5.00E-04	2	3	10000	116	FALSE
0.5	0.6	1.00E-03	2	3	10000	95	FALSE
0.5	0.6	5.00E-03	2	3	10000	117	FALSE
0.5	0.6	1.00E-05	1	3	10000	52	FALSE
0.5	0.6	5.00E-05	1	3	10000	53	FALSE
0.5	0.65	1.00E-04	2	3	10000	135	FALSE
0.5	0.65	5.00E-04	2	3	10000	126	FALSE
0.5	0.65	1.00E-03	2	3	10000	158	FALSE
0.5	0.65	5.00E-03	2	3	10000	166	FALSE
0.5	0.65	1.00E-05	1	2	10000	78	FALSE
0.5	0.65	5.00E-05	1	1	10000	104	FALSE

Table S2: Details on final generation for sexually reproducing predators with random mating

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Final predator morphs*	*Final prey morphs*	*Last generation*	*Final predator population size*	*Extinction*
0.3	0.55	1.00E-04	0	0	9238	3	TRUE
0.3	0.55	5.00E-04	0	0	2606	2	TRUE
0.3	0.55	5.00E-03	0	0	3712	3	TRUE
0.3	0.55	5.00E-03	0	0	3482	1	TRUE
0.3	0.55	1.00E-05	0	0	552	2	TRUE
0.3	0.55	5.00E-05	0	0	2456	2	TRUE
0.3	0.6	1.00E-04	0	0	680	3	TRUE
0.3	0.6	5.00E-04	1	3	10000	30	FALSE
0.3	0.6	5.00E-03	1	3	10000	33	FALSE
0.3	0.6	5.00E-03	0	0	5422	2	TRUE
0.3	0.6	1.00E-05	0	0	488	4	TRUE
0.3	0.6	5.00E-05	0	0	1730	1	TRUE
0.3	0.65	1.00E-04	1	3	10000	39	FALSE
0.3	0.65	5.00E-04	1	3	10000	43	FALSE
0.3	0.65	5.00E-03	0	0	3152	1	TRUE
0.3	0.65	5.00E-03	1	3	10000	47	FALSE
0.3	0.65	1.00E-05	0	0	432	1	TRUE
0.3	0.65	5.00E-05	0	0	2110	1	TRUE
0.35	0.55	1.00E-04	0	0	1258	2	TRUE
0.35	0.55	5.00E-04	1	3	10000	34	FALSE
0.35	0.55	5.00E-03	0	0	8638	1	TRUE
0.35	0.55	5.00E-03	0	0	2652	3	TRUE
0.35	0.55	1.00E-05	0	0	396	4	TRUE

0.35	0.55	5.00E-05	0	0	1458	5	TRUE
0.35	0.6	1.00E-04	0	0	5186	1	TRUE
0.35	0.6	5.00E-04	0	0	7124	2	TRUE
0.35	0.6	5.00E-03	1	3	10000	32	FALSE
0.35	0.6	5.00E-03	1	3	10000	44	FALSE
0.35	0.6	1.00E-05	0	0	1466	1	TRUE
0.35	0.6	5.00E-05	0	0	1304	3	TRUE
0.35	0.65	1.00E-04	0	0	1402	1	TRUE
0.35	0.65	5.00E-04	1	3	10000	32	FALSE
0.35	0.65	5.00E-03	1	3	10000	23	FALSE
0.35	0.65	5.00E-03	2	3	10000	69	FALSE
0.35	0.65	1.00E-05	0	0	894	1	TRUE
0.35	0.65	5.00E-05	0	0	958	1	TRUE
0.4	0.55	1.00E-04	1	3	10000	14	FALSE
0.4	0.55	5.00E-04	1	3	10000	19	FALSE
0.4	0.55	5.00E-03	0	0	9378	2	TRUE
0.4	0.55	5.00E-03	1	3	10000	51	FALSE
0.4	0.55	1.00E-05	0	0	2094	1	TRUE
0.4	0.55	5.00E-05	0	0	1526	1	TRUE
0.4	0.6	1.00E-04	0	0	9854	3	TRUE
0.4	0.6	5.00E-04	1	3	10000	27	FALSE
0.4	0.6	5.00E-03	1	3	10000	42	FALSE
0.4	0.6	5.00E-03	1	3	10000	71	FALSE
0.4	0.6	1.00E-05	0	0	2626	1	TRUE
0.4	0.6	5.00E-05	0	0	3110	3	TRUE
0.4	0.65	1.00E-04	0	0	726	5	TRUE
0.4	0.65	5.00E-04	1	3	10000	53	FALSE

0.4	0.65	5.00E-03	1	3	10000	49	FALSE
0.4	0.65	5.00E-03	1	3	10000	110	FALSE
0.4	0.65	1.00E-05	0	0	2736	2	TRUE
0.4	0.65	5.00E-05	0	0	934	2	TRUE
0.45	0.55	1.00E-04	1	3	10000	31	FALSE
0.45	0.55	5.00E-04	1	3	10000	38	FALSE
0.45	0.55	5.00E-03	1	3	10000	57	FALSE
0.45	0.55	5.00E-03	1	3	10000	56	FALSE
0.45	0.55	1.00E-05	0	0	2326	1	TRUE
0.45	0.55	5.00E-05	1	3	10000	40	FALSE
0.45	0.6	1.00E-04	0	0	1408	1	TRUE
0.45	0.6	5.00E-04	1	3	10000	57	FALSE
0.45	0.6	5.00E-03	1	3	10000	74	FALSE
0.45	0.6	5.00E-03	1	3	10000	90	FALSE
0.45	0.6	1.00E-05	0	0	4000	1	TRUE
0.45	0.6	5.00E-05	1	3	10000	24	FALSE
0.45	0.65	1.00E-04	1	3	10000	42	FALSE
0.45	0.65	5.00E-04	1	3	10000	70	FALSE
0.45	0.65	5.00E-03	1	3	10000	114	FALSE
0.45	0.65	5.00E-03	1	3	10000	74	FALSE
0.45	0.65	1.00E-05	0	0	3600	4	TRUE
0.45	0.65	5.00E-05	1	3	10000	38	FALSE
0.5	0.55	1.00E-04	1	3	10000	60	FALSE
0.5	0.55	5.00E-04	1	3	10000	90	FALSE
0.5	0.55	5.00E-03	1	3	10000	78	FALSE
0.5	0.55	5.00E-03	1	3	10000	67	FALSE
0.5	0.55	1.00E-05	1	3	10000	54	FALSE

0.5	0.55	5.00E-05	1	3	10000	40	FALSE
0.5	0.6	1.00E-04	1	3	10000	66	FALSE
0.5	0.6	5.00E-04	1	3	10000	46	FALSE
0.5	0.6	5.00E-03	1	2	10000	56	FALSE
0.5	0.6	5.00E-03	1	2	10000	81	FALSE
0.5	0.6	1.00E-05	1	3	10000	48	FALSE
0.5	0.6	5.00E-05	0	0	1302	1	TRUE
0.5	0.65	1.00E-04	1	3	10000	57	FALSE
0.5	0.65	5.00E-04	1	3	10000	88	FALSE
0.5	0.65	5.00E-03	1	3	10000	79	FALSE
0.5	0.65	5.00E-03	1	2	10000	86	FALSE
0.5	0.65	1.00E-05	0	0	1264	12	TRUE
0.5	0.65	5.00E-05	1	3	10000	87	FALSE

Table S3: Details on final generation for sexually reproducing predators with low choosiness ($c_\gamma = 6.9078$)

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Final predator morphs*	*Final prey morphs*	*Last generation*	*Final predator population size*	*Extinction*
0.3	0.55	1.00E-04	0	0	1886	2	TRUE
0.3	0.55	5.00E-04	0	0	6580	1	TRUE
0.3	0.55	5.00E-03	0	0	2448	4	TRUE
0.3	0.55	5.00E-03	0	0	1872	1	TRUE
0.3	0.55	1.00E-05	0	0	664	1	TRUE
0.3	0.55	5.00E-05	0	0	926	2	TRUE
0.3	0.6	1.00E-04	0	0	1278	1	TRUE
0.3	0.6	5.00E-04	0	0	9856	2	TRUE
0.3	0.6	5.00E-03	1	3	10000	30	FALSE
0.3	0.6	5.00E-03	0	0	5490	3	TRUE
0.3	0.6	1.00E-05	0	0	440	2	TRUE
0.3	0.6	5.00E-05	1	3	10000	19	FALSE
0.3	0.65	1.00E-04	1	3	10000	32	FALSE
0.3	0.65	5.00E-04	1	3	10000	23	FALSE
0.3	0.65	5.00E-03	1	3	10000	28	FALSE
0.3	0.65	5.00E-03	2	3	10000	55	FALSE
0.3	0.65	1.00E-05	0	0	432	1	TRUE
0.3	0.65	5.00E-05	0	0	1142	1	TRUE
0.35	0.55	1.00E-04	1	3	10000	26	FALSE
0.35	0.55	5.00E-04	0	0	874	2	TRUE
0.35	0.55	5.00E-03	0	0	3018	1	TRUE
0.35	0.55	5.00E-03	0	0	3052	1	TRUE

0.35	0.55	1.00E-05	0	0	2872	1	TRUE
0.35	0.55	5.00E-05	0	0	958	3	TRUE
0.35	0.6	1.00E-04	0	0	8320	3	TRUE
0.35	0.6	5.00E-04	1	3	10000	44	FALSE
0.35	0.6	5.00E-03	0	0	6042	1	TRUE
0.35	0.6	5.00E-03	1	3	10000	53	FALSE
0.35	0.6	1.00E-05	0	0	582	2	TRUE
0.35	0.6	5.00E-05	0	0	2446	4	TRUE
0.35	0.65	1.00E-04	0	0	2532	1	TRUE
0.35	0.65	5.00E-04	1	3	10000	24	FALSE
0.35	0.65	5.00E-03	1	3	10000	30	FALSE
0.35	0.65	5.00E-03	3	3	10000	77	FALSE
0.35	0.65	1.00E-05	0	0	1816	2	TRUE
0.35	0.65	5.00E-05	0	0	1994	1	TRUE
0.4	0.55	1.00E-04	0	0	1122	1	TRUE
0.4	0.55	5.00E-04	0	0	4820	1	TRUE
0.4	0.55	5.00E-03	0	0	8956	2	TRUE
0.4	0.55	5.00E-03	1	3	10000	32	FALSE
0.4	0.55	1.00E-05	0	0	2662	1	TRUE
0.4	0.55	5.00E-05	0	0	2482	3	TRUE
0.4	0.6	1.00E-04	1	3	10000	37	FALSE
0.4	0.6	5.00E-04	1	3	10000	32	FALSE
0.4	0.6	5.00E-03	0	0	6622	4	TRUE
0.4	0.6	5.00E-03	2	3	10000	106	FALSE
0.4	0.6	1.00E-05	0	0	828	2	TRUE
0.4	0.6	5.00E-05	0	0	3012	1	TRUE
0.4	0.65	1.00E-04	0	0	954	4	TRUE

0.4	0.65	5.00E-04	1	3	10000	60	FALSE
0.4	0.65	5.00E-03	1	3	10000	45	FALSE
0.4	0.65	5.00E-03	2	3	10000	152	FALSE
0.4	0.65	1.00E-05	0	0	1258	4	TRUE
0.4	0.65	5.00E-05	1	3	10000	70	FALSE
0.45	0.55	1.00E-04	1	3	10000	24	FALSE
0.45	0.55	5.00E-04	1	3	10000	42	FALSE
0.45	0.55	5.00E-03	1	3	10000	49	FALSE
0.45	0.55	5.00E-03	1	3	10000	58	FALSE
0.45	0.55	1.00E-05	0	0	2308	3	TRUE
0.45	0.55	5.00E-05	0	0	2604	2	TRUE
0.45	0.6	1.00E-04	0	0	3248	2	TRUE
0.45	0.6	5.00E-04	1	3	10000	42	FALSE
0.45	0.6	5.00E-03	1	3	10000	40	FALSE
0.45	0.6	5.00E-03	2	3	10000	117	FALSE
0.45	0.6	1.00E-05	0	0	2190	4	TRUE
0.45	0.6	5.00E-05	1	3	10000	35	FALSE
0.45	0.65	1.00E-04	1	3	10000	40	FALSE
0.45	0.65	5.00E-04	1	3	10000	61	FALSE
0.45	0.65	5.00E-03	1	3	10000	70	FALSE
0.45	0.65	5.00E-03	2	3	10000	107	FALSE
0.45	0.65	1.00E-05	0	0	4174	3	TRUE
0.45	0.65	5.00E-05	1	3	10000	45	FALSE
0.5	0.55	1.00E-04	1	3	10000	64	FALSE
0.5	0.55	5.00E-04	1	3	10000	62	FALSE
0.5	0.55	5.00E-03	1	3	10000	58	FALSE
0.5	0.55	5.00E-03	2	3	10000	86	FALSE

0.5	0.55	1.00E-05	1	3	10000	47	FALSE
0.5	0.55	5.00E-05	1	3	10000	65	FALSE
0.5	0.6	1.00E-04	1	3	10000	65	FALSE
0.5	0.6	5.00E-04	1	3	10000	82	FALSE
0.5	0.6	5.00E-03	1	3	10000	95	FALSE
0.5	0.6	5.00E-03	2	3	10000	121	FALSE
0.5	0.6	1.00E-05	1	3	10000	56	FALSE
0.5	0.6	5.00E-05	1	2	10000	60	FALSE
0.5	0.65	1.00E-04	1	2	10000	51	FALSE
0.5	0.65	5.00E-04	1	3	10000	102	FALSE
0.5	0.65	5.00E-03	1	3	10000	84	FALSE
0.5	0.65	5.00E-03	2	3	10000	154	FALSE
0.5	0.65	1.00E-05	1	3	10000	71	FALSE
0.5	0.65	5.00E-05	0	0	1372	2	TRUE

Table S4: Details on final generation for sexually reproducing predators with high choosiness ($c_\gamma = 44.3614$)

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Final predator morphs*	*Final prey morphs*	*Last generation*	*Final predator population size*	*Extinction*
0.3	0.55	1.00E-04	0	0	2672	3	TRUE
0.3	0.55	5.00E-04	0	0	866	3	TRUE
0.3	0.55	5.00E-03	0	0	946	2	TRUE
0.3	0.55	5.00E-03	0	0	2052	5	TRUE
0.3	0.55	1.00E-05	0	0	2390	2	TRUE
0.3	0.55	5.00E-05	0	0	1926	3	TRUE
0.3	0.6	1.00E-04	0	0	1656	1	TRUE
0.3	0.6	5.00E-04	1	3	10000	13	FALSE
0.3	0.6	5.00E-03	1	3	10000	29	FALSE
0.3	0.6	5.00E-03	0	0	5202	2	TRUE
0.3	0.6	1.00E-05	0	0	546	2	TRUE
0.3	0.6	5.00E-05	0	0	1994	2	TRUE
0.3	0.65	1.00E-04	0	0	1228	5	TRUE
0.3	0.65	5.00E-04	0	0	1766	2	TRUE
0.3	0.65	5.00E-03	1	3	10000	28	FALSE
0.3	0.65	5.00E-03	3	3	10000	77	FALSE
0.3	0.65	1.00E-05	0	0	498	6	TRUE
0.3	0.65	5.00E-05	0	0	1814	4	TRUE
0.35	0.55	1.00E-04	0	0	3208	5	TRUE
0.35	0.55	5.00E-04	0	0	1454	2	TRUE
0.35	0.55	5.00E-03	1	3	10000	36	FALSE
0.35	0.55	5.00E-03	2	3	10000	48	FALSE

0.35	0.55	1.00E-05	0	0	2202	3	TRUE
0.35	0.55	5.00E-05	0	0	2260	1	TRUE
0.35	0.6	1.00E-04	0	0	1864	1	TRUE
0.35	0.6	5.00E-04	0	0	7486	1	TRUE
0.35	0.6	5.00E-03	1	3	10000	20	FALSE
0.35	0.6	5.00E-03	3	3	10000	105	FALSE
0.35	0.6	1.00E-05	0	0	442	1	TRUE
0.35	0.6	5.00E-05	0	0	1030	2	TRUE
0.35	0.65	1.00E-04	0	0	1226	1	TRUE
0.35	0.65	5.00E-04	1	3	10000	60	FALSE
0.35	0.65	5.00E-03	3	3	10000	125	FALSE
0.35	0.65	5.00E-03	3	3	10000	126	FALSE
0.35	0.65	1.00E-05	0	0	990	3	TRUE
0.35	0.65	5.00E-05	0	0	4202	1	TRUE
0.4	0.55	1.00E-04	0	0	2292	2	TRUE
0.4	0.55	5.00E-04	1	3	10000	22	FALSE
0.4	0.55	5.00E-03	0	0	4874	1	TRUE
0.4	0.55	5.00E-03	2	3	10000	91	FALSE
0.4	0.55	1.00E-05	0	0	1202	3	TRUE
0.4	0.55	5.00E-05	0	0	2236	1	TRUE
0.4	0.6	1.00E-04	1	3	10000	40	FALSE
0.4	0.6	5.00E-04	1	3	10000	36	FALSE
0.4	0.6	5.00E-03	1	3	10000	37	FALSE
0.4	0.6	5.00E-03	3	3	10000	139	FALSE
0.4	0.6	1.00E-05	0	0	1942	3	TRUE
0.4	0.6	5.00E-05	0	0	1884	3	TRUE
0.4	0.65	1.00E-04	0	0	3768	1	TRUE

0.4	0.65	5.00E-04	0	0	988	2	TRUE
0.4	0.65	5.00E-03	0	0	1068	1	TRUE
0.4	0.65	5.00E-03	3	3	10000	120	FALSE
0.4	0.65	1.00E-05	0	0	2952	3	TRUE
0.4	0.65	5.00E-05	0	0	1912	1	TRUE
0.45	0.55	1.00E-04	0	0	1210	2	TRUE
0.45	0.55	5.00E-04	1	3	10000	63	FALSE
0.45	0.55	5.00E-03	1	3	10000	70	FALSE
0.45	0.55	5.00E-03	3	3	10000	95	FALSE
0.45	0.55	1.00E-05	0	0	3732	1	TRUE
0.45	0.55	5.00E-05	0	0	3580	3	TRUE
0.45	0.6	1.00E-04	0	0	3268	1	TRUE
0.45	0.6	5.00E-04	1	3	10000	52	FALSE
0.45	0.6	5.00E-03	3	3	10000	114	FALSE
0.45	0.6	5.00E-03	3	3	10000	132	FALSE
0.45	0.6	1.00E-05	0	0	1170	1	TRUE
0.45	0.6	5.00E-05	1	3	10000	43	FALSE
0.45	0.65	1.00E-04	1	3	10000	60	FALSE
0.45	0.65	5.00E-04	0	0	1472	1	TRUE
0.45	0.65	5.00E-03	2	3	10000	135	FALSE
0.45	0.65	5.00E-03	3	3	10000	153	FALSE
0.45	0.65	1.00E-05	1	3	10000	55	FALSE
0.45	0.65	5.00E-05	0	0	4012	2	TRUE
0.5	0.55	1.00E-04	0	0	6672	3	TRUE
0.5	0.55	5.00E-04	1	3	10000	34	FALSE
0.5	0.55	5.00E-03	1	3	10000	60	FALSE
0.5	0.55	5.00E-03	2	3	10000	126	FALSE

0.5	0.55	1.00E-05	1	3	10000	64	FALSE
0.5	0.55	5.00E-05	0	0	3612	1	TRUE
0.5	0.6	1.00E-04	1	3	10000	51	FALSE
0.5	0.6	5.00E-04	1	3	10000	74	FALSE
0.5	0.6	5.00E-03	2	3	10000	123	FALSE
0.5	0.6	5.00E-03	3	3	10000	103	FALSE
0.5	0.6	1.00E-05	0	0	4470	1	TRUE
0.5	0.6	5.00E-05	1	3	10000	66	FALSE
0.5	0.65	1.00E-04	1	3	10000	89	FALSE
0.5	0.65	5.00E-04	0	0	1128	1	TRUE
0.5	0.65	5.00E-03	0	0	1414	1	TRUE
0.5	0.65	5.00E-03	3	3	10000	127	FALSE
0.5	0.65	1.00E-05	1	3	10000	54	FALSE
0.5	0.65	5.00E-05	1	3	10000	64	FALSE

Table S5: First speciation event in asexual predator communities

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Speciation event*
0.3	0.6	1.00E-03	1000
0.35	0.55	5.00E-03	1000
0.35	0.6	5.00E-04	1000
0.35	0.6	1.00E-03	1000
0.35	0.65	5.00E-04	1500
0.35	0.65	1.00E-03	1000
0.35	0.65	5.00E-03	7000
0.4	0.55	1.00E-03	1000
0.4	0.55	5.00E-03	1500
0.4	0.6	1.00E-04	2000
0.4	0.6	5.00E-04	2500
0.4	0.6	1.00E-03	1000
0.4	0.6	5.00E-03	1000
0.4	0.65	1.00E-04	9500
0.4	0.65	5.00E-04	2000
0.4	0.65	1.00E-03	1000
0.4	0.65	5.00E-03	1000
0.45	0.55	5.00E-04	1000
0.45	0.55	1.00E-03	1500
0.45	0.55	5.00E-03	1500
0.45	0.6	5.00E-04	1500
0.45	0.6	1.00E-03	1500
0.45	0.6	5.00E-03	2000
0.45	0.65	1.00E-04	7000

0.45	0.65	5.00E-04	1500
0.45	0.65	1.00E-03	1500
0.45	0.65	5.00E-03	2000
0.5	0.55	5.00E-04	1500
0.5	0.55	1.00E-03	1500
0.5	0.55	5.00E-03	1500
0.5	0.6	5.00E-04	2000
0.5	0.6	1.00E-03	1500
0.5	0.6	5.00E-03	2500
0.5	0.65	1.00E-04	6000
0.5	0.65	5.00E-04	2500
0.5	0.65	1.00E-03	2500
0.5	0.65	5.00E-03	2000

Table S6: Second speciation event in asexual predator communities

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Speciation event*
0.3	0.6	5.00E-04	1500
0.35	0.6	5.00E-04	2000
0.35	0.6	1.00E-03	3500
0.35	0.65	5.00E-04	3000
0.35	0.65	1.00E-03	8500
0.35	0.65	5.00E-03	7500
0.4	0.6	1.00E-03	4000
0.4	0.6	5.00E-03	3000
0.4	0.65	5.00E-04	4000
0.4	0.65	1.00E-03	2000
0.4	0.65	5.00E-03	3500
0.45	0.6	5.00E-03	7000
0.45	0.65	5.00E-04	4500
0.45	0.65	1.00E-03	5000
0.45	0.65	5.00E-03	6000
0.5	0.55	5.00E-03	8000

Table S7: First speciation event in sexual predator communities

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Choosiness*	*Speciation event*
0.3	0.65	5.00E-03	44.3614	4000
0.3	0.65	5.00E-03	6.9078	1000
0.35	0.55	5.00E-03	44.3614	1000
0.35	0.6	5.00E-03	44.3614	1000
0.35	0.65	5.00E-03	0	10000
0.35	0.65	5.00E-03	44.3614	1500
0.35	0.65	5.00E-03	6.9078	1500
0.4	0.55	5.00E-03	44.3614	2500
0.4	0.6	5.00E-03	6.9078	1000
0.4	0.65	5.00E-03	44.3614	1000
0.4	0.65	5.00E-03	6.9078	2000
0.45	0.55	5.00E-03	44.3614	1500
0.45	0.6	5.00E-03	44.3614	6000
0.45	0.6	5.00E-03	44.3614	1500
0.45	0.6	5.00E-03	6.9078	1500
0.45	0.65	5.00E-03	44.3614	7000
0.45	0.65	5.00E-03	44.3614	1500
0.45	0.65	5.00E-03	6.9078	1500
0.5	0.55	5.00E-03	44.3614	1500
0.5	0.55	5.00E-03	6.9078	2000
0.5	0.6	5.00E-03	44.3614	3000
0.5	0.6	5.00E-03	44.3614	2000
0.5	0.6	5.00E-03	6.9078	3500
0.5	0.65	5.00E-03	6.9078	1500

Table S8: Second speciation event in sexual predator communities

Predator niche width	*Predator efficiency*	*Predator mutation rate*	*Choosiness*	*Speciation event*
0.35	0.6	5.00E-03	44.3614	2500
0.35	0.65	5.00E-03	44.3614	2000
0.35	0.65	5.00E-03	44.3614	2500
0.35	0.65	5.00E-03	6.9078	8500
0.4	0.65	5.00E-03	44.3614	2500
0.45	0.55	5.00E-03	44.3614	6500
0.45	0.6	5.00E-03	44.3614	9500
0.45	0.6	5.00E-03	44.3614	4000
0.45	0.65	5.00E-03	44.3614	4000
0.5	0.6	5.00E-03	44.3614	4000