Effect of environmental fluctuations on adaptive radiation in *Anolis* lizards: a theoretical study

by Dennis H. Sliep (s2958252)
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Supervisors: Jana M. Riederer and Franz J. Weissing
Theoretical Biology Group, University of Groningen

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Abstract

Adaptive radiation is a widespread phenomenon where one ancestral species gives rise to many new species that occupy different environments. This study aims to analyse how adaptive radiations are affected by recurring environmental change by using *Anolis* lizards on the islands of the Greater Antilles as its model species. Anoles live in an area affected by El Niño, a recurring phenomenon that will temporary cause changes to the environment. This could then alter environmental circumstances and change the anole's suitability to each habitat. The expectation is that by chance, the desired phenotype in two habitats becomes either more or less similar than before the change, altering ease of radiation. This analysis was done by using an individual based model, where the environment is made up of six structural microhabitats, called niches here. An individual's survival will depend on how well its phenotype is suited to the niche. The phenotype is made up of six traits. Each niche has a different optimum value for each trait and individuals are more suited to the niche when approaching these optima. Thus all niches will be a certain morphological distance away from each other, which affects the ease of radiation between these niches. This ease is also affected by dispersal rate and selection strength. During simulations, empty niches can eventually become occupied (population size at least 20% of carrying capacity). Individuals can then start to adapt to the niche, full niche adaptation being reached when its population has an average fit (or suitability) to the niche of 0.9 or higher. In the control setup, no environmental change happens. In the environmental change simulations, the environment switches between two states. In the alternative state, each niche will have different optimum values for each trait than in the original state. Three scenarios were considered: reducing morphological distance between niches (convergent), increasing this distance (divergent) and increasing morphological distance for some niches while decreasing it for others (alternating). Convergent change was most effective in maximizing niches with high fit when selection strength starts to increase, while at low selection strength the direction of change was of little influence. Dispersal rate was also found to decrease the influence of selection strength on adaptive radiation. In order to outmatch the effects of genetic drift, carrying capacity also has to be sufficiently high to consistently see adaptive radiations. Whether environmental change reaches a higher number of adapted niches is dependent on the scenario, dispersal rate and selection strength. Without environmental change, niches will never lose adaptation once fully adapted, but with change this is only the case if it is convergent. Divergent and alternating change have shown to sometimes result in adaptation loss under high selection strength and dispersal, even in the original niche.

Introduction

Adaptive radiation is the emergence of phenotypic variation between groups of individuals of the same species, resulting in the creation of new species that share a common ancestor species. This process usually happens when there is a difference in environment between groups of individuals, with each environment favouring a different phenotype. According to the ecological theory of adaptive radiation, the process is ultimately set in motion by divergent natural selection (Schluter, 2000). However, diversification in a species is influenced by a multitude of factors that may be acting simultaneously, which has made it difficult to determine which factors are the main drivers of adaptive radiation. According to one study, these factors include both environmental factors, which will affect the entire ecosystem, and lineage-specific factors, which are specific characteristics for one group of individuals of the same species (Wagner et al., 2012). They argued that adaptive radiation can successfully be predicted when taking both types of these factors into account. These two types of factors will next be discussed in more detail.

Environmental factors can affect a species either directly or indirectly. An example of a direct effect could be specialization on different food sources in order to minimize food competition and evolving morphological traits to become optimally adapted to this food source (Losos and Mahler, 2010). A species can also be indirectly affected, for example when a second species is affected that has an interaction (e.g. predator, prey (Arumugam et al., 2020), parasite (Patz et al., 2000), resource competitor (Losos, 1994; Tran et al., 2014) etc.) with the first species. When density of the second species changes, this may very well affect the density of the first species and vice versa. A species can also respond to environmental change in different ways. It may alter its behaviour in response to changes in its habitat, but genetical changes are possible as well (Berger et al., 2021). When groups of individuals start to show behaviour that is sufficiently different from other individuals, it may drive the groups apart from each other (Tuomainen and Candolin, 2011), which can lead to reproductive isolation and potentially speciation as a result. Even when all individuals live in the same area, reproductive isolation can arise due to assortative mating (Dieckmann and Doebeli, 1999), thus geographic isolation of populations does not necessarily have to be present for speciation to happen.

Lineage-specific factors also should not be left out of the picture. Phenotypic plasticity is an important factor in determining whether speciation would happen or not. Species with high phenotypic plasticity can live in a larger range of potential habitats and thus will in general have an easier time adapting to environmental change compared to a species with low phenotypic plasticity. Phenotypic plasticity can also allow species to adapt more easily to separate instances of environmental changes that rapidly follow up on each other (Charmantier et al., 2008). So phenotypic plasticity on its own can already allow a species to adapt quite easily and make adaptive radiation unnecessary. However, if having phenotypic plasticity is costly, it may disappear in the long run and create different reproductively isolated populations that are each optimally adapted to a different environment. According to the flexible stem hypothesis, if individuals of an ancestral group by chance move to a specific environment on multiple occasions, it should produce a comparable phenotype on each occasion within this environment. This will lead to the accumulation of individuals with similar phenotypes in one area, while an area with different environmental circumstances will similarly accumulate individuals that are phenotypically close to each other, but quite different from the first area. In this way, one ancestral group can be the source of many sister lineages that have undergone adaptive radiation (Gibert, 2017).

One group of species that is known to have undergone adaptive radiation are the lizards of the *Anolis* genus. Of particular interest are the anoles living in the Greater Antilles. Anoles have been shown to have undergone adaptive radiation on each of the four major islands (Puerto Rico, Hispaniola, Jamaica and Cuba) independently of each other (Losos et al., 1998). The divergence of anoles gave rise to different ecomorphs, which is a term initially used by Ernest Williams and is defined as a group of species inhabiting the same structural habitat or niche, with these species also being similar in morphology and behaviour (Williams, 1972). On each island, the anoles diverged into at least four and up to six different ecomorphs (Beuttell and Losos, 1999) and the ecomorphs that were formed on each island were the same ecomorphs as well (with additional ecomorphs being

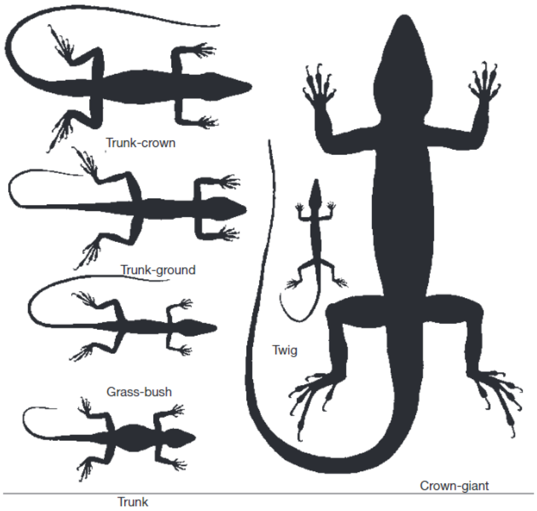

Fig. 1. Characteristics of each of the anole island ecomorphs. Picture was taken from Losos (2009).

present on Hispaniola and Cuba). This rich diversity in anole species, but more importantly differences in behaviour and morphology between the species, makes the *Anolis* genus a very suitable choice to study adaptive radiations. In contrast, anoles that are living on the mainland are believed to not have evolved in parallel like anoles in the Greater Antilles due to selective pressures differing between mainland and islands. The mainland anoles can rarely even be assigned to one of the island ecomorphs (Schaad and Poe, 2010).

A possibility for causing an adaptive radiation is a set of differing optimal values for traits that are relevant for the various structural microhabitats. In the case of anoles, many studies have been done on a variety of traits. SVL (snout-vent length) is known to differ a lot between ecomorphs, with most ecomorphs having small SVL and Crown Giant at the extreme, having very high SVL. Fore- and hindlimb length might be related to each other in some way, since in four of the six ecomorphs there is little difference between them. However, there is a clear difference between them for the Trunk Ground and Grass Bush ecomorphs, both having much longer hindlimbs in proportion to forelimb length. Tail length is a bit more tricky. While functions of it are known (counterbalance during rapid movement (Ballinger, 1973), mid-air manoeuvring (Higham et al., 2001)), its rather large range of lengths across ecomorphs is not fully explained by these. It has been suggested autotomy could hold some advantages (Losos, 2009), however no evidence exists. Number of lamellae also varies significantly between ecomorphs, species up in the trees need them much more than species living at ground level. Especially twig anoles have many lamellae, which is likely because the costs of falling are high and since they venture out on small twigs, they will need to make sure they can hold on to them at all times. Then there is also the movement rate, which is the frequency at which an anole moves around, irrespective of speed. According to Losos (2009), half of the ecomorphs have low movement rates, while the other half has high movement rates. All frequently moving species are living in the trees. The only tree living ecomorph with low movement rate is Crown Giant, which could be due to its massive size compared to other anoles. From this, it becomes clear that the traits all exhibit significant differences between ecomorphs and it is worth investigating if and how they influence adaptive radiations.

Since changes in the environment are a known cause of adaptive radiations, knowing what environmental changes have taken place can shed light on how an adaptive radiation came to be. In the case of anoles in the Greater Antilles, two reoccurring environmental change events are El Niño and La Niña. These are alternating events that happen every 2-7 years and usually have a peak in intensity. El Niño affects the Caribbean area by increasing the average amount of precipitation and the risk of flooding (Reguero et al., 2015), while La Niña is usually accompanied by an increase in tropical cyclones reaching land (Klotzbach, 2011). These could very well influence anole ecomorphs, since the structural microhabitat they inhabit will likely change as a result of at least one of these factors, either directly or indirectly by influencing another species that interacts with the anole. Since this is a reoccurring phenomenon with varying intensity, its effects might not be exactly the same for anole species each time it occurs. If the effects are notable enough, they could potentially give anoles that final push to leave their niche and move into a different one, in which case it could facilitate adaptive radiation. Of course, these changes could also increase the adaptation gap that needs to be bridged to switch niches and effectively survive if the changes drive niches further away from each other. Thus, environmental change may be a phenomenon that could either hinder or aid adaptive radiations depending on the circumstances.

Here I will present a model that takes a closer look at the potential effects of environmental fluctuations on adaptive radiations observed in anoles, but the model should likely be applicable to many other species as well, with some small modifications where needed. Environmental changes are present in most ecosystems, although its impact on the ecosystem or on different species living there may differ in size**.** This may decide whether or not adaptive radiation can occur or not. If the impact size of environmental change is rather small, the difference with the previous environmental conditions might be so small that no to very little adaptation is necessary for a species to survive under the new conditions. If the impact is very large, however, the gap between the old and the new environmental conditions could become so large that species are barely able to or unable to survive. When this happens, it is likely to go extinct due to increased mortality before it has had sufficient time to adapt. Furthermore, the frequency of environmental changes can be different as well. When the frequency is high, individuals may have insufficient time to adapt before the next change occurs depending on the step size of the change and this could lead to increased mortality and in the worst case local extinction. The location of the threshold between extinction and evolutionary rescue is dependent on population size, genetic diversity and the mismatch to the new environmental conditions (Bell and Gonzalez, 2009).

To better analyse characteristics of anole ecomorphs, several studies have used a morphospace (Butler et al., 2007; Pinto et al., 2008), in which each axis represents one or more ecomorph relevant trait(s). Then, an n-dimensional space can be plotted which shows the positions of all individuals. Butler used this system to show the area in morphospace that is occupied by each of the different anole ecomorphs and sexes based on five ecomorph relevant traits and this showed a clear difference between both the ecomorphs and the sexes (Butler et al., 2007). This morphospace can be a useful tool for identifying the range in which adaptive radiations can occur and where the difference in trait values would be too large to allow for adaptive radiations, given that it is known how and to what extent the traits in question are influenced by the genetic code.

Just like a morphospace can be used to show individual positions regarding ecomorph relevant traits, it can also be used to show the “morphological position” of a niche. This position shows the optimal trait values an individual should have to be best suited to that particular niche. When environmental change takes place, these niche optima will change as well. As a result, a niche’s position in morphospace will shift and individuals will have to adapt in order to remain optimally fit to that niche. When they end up too far away from a niche’s optimum, another niche’s optimum may become closer to the individual’s position in morphospace and it could become easier to

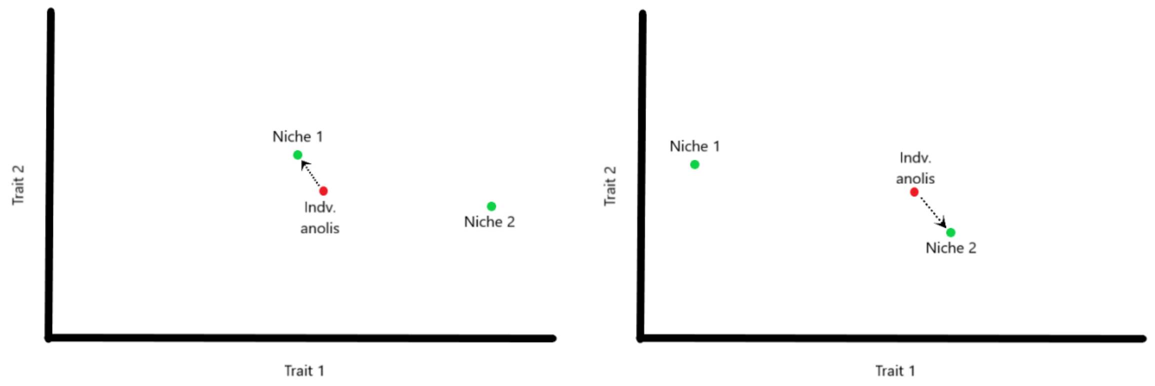

Fig. 2. Possible effects of environmental change on niche adaptation in morphospace. Morphospace shown here is a simple 2-dimensional morphospace with one trait being represented on each axis. A) Original scenario: no environmental change has happened yet and the individual is most likely to adapt to niche 1's trait optima since it is much closer to its own trait values and therefore it will be much more successful in that niche already. B) After environmental change scenario: both niche's optima have shifted to the left, resulting in the individual currently having a higher fit in the second niche, making it more likely to adapt to this niche instead.

instead adapt to the second niche's optimum and potentially have selection push in this direction now. Whether or not this happens is dependent on genetic drift and the strength of selection. This process could then lead to adaptive radiation as long as niches are sufficiently reproductively isolated from each other.

Here I will look at how changes in the environment can influence adaptive radiations, both how its occurrence is influenced as well as the time until it happens. This will be done using an individual based model that is focused mainly on anoles, but can be easily modified and potentially applied to other species as well. The expectation is that environmental change can promote adaptive radiation, but only if the change brings two niche optima closer together. If instead it brings the niche optima further away, it will be harder to switch to the different niche and thus a change in this direction would be expected to obstruct adaptive radiation.

Methods

The model I present here was created using the programming software Microsoft Visual C++. It is an individual based model, which was chosen over others because it allows individual characteristics to be monitored and allows individuals to be different from each other, including differences in trait values. Individual trait value differences in the model arise due to mutations, which play an important role in evolution and adaptive radiation.

Description of niches

The model includes a number of different niches where individuals can live. These niches are all connected to each other and individuals can disperse from any niche to any other niche, although they are only given one opportunity to disperse in their life, which is when they reach adulthood. Individuals can either be male or female, which in the model is only important for the reproduction stage. Then there is a number of traits that will be monitored during the simulation. These traits are relevant to the individual's fit to the niche and different traits are assumed to be unrelated to each other in the model. While in reality certain traits may influence each other to some degree, for simplicity the decision was made to assume completely unrelated traits and keep the model easier to analyse.

For the analysis of anole adaptive radiations, the niches represent the six ecomorphs that are known to exist on (most of) the four larger islands in the Greater Antilles (Williams, 1972) (Crown Giant, Trunk Crown, Trunk, Twig, Trunk Ground and Grass Bush), where adaptive radiations have occurred on each island. Then, six ecomorph relevant traits were chosen, based on both scientific knowledge about trait functions as well as notable differences in trait values between niches observed in empirical studies (Butler et al., 2007; Butler and Losos, 2002). The traits looked at here are snout-vent length (SVL), fore- and hindlimb length, tail length, number of lamellae on toepads and the movement rate, since all have been shown to show considerable differences between ecomorphs on average.

The model starts by creating the niches and assigns the niches optimal trait values for the six aforementioned traits. These niche optima values are those trait values for which an individual would achieve the maximum fit to that niche and maximizes its survival. Fit to the niche is an indicator of adaptation level to the niche and will be explained in more detail later. In my anole focused model, niche optima values are based on a table from Losos containing information about approximate trait values per ecomorph (Losos, 2009). These are by no means values derived from empirical studies and are just estimated values, which is important to keep in mind before drawing conclusions. After niches are created, a starting population of individuals of the same species is created. The model currently assumes sexual reproduction and individuals can be either male or female. The model has been simplified by keeping the population haploid. Even though anoles are diploid species, creating diploid individuals will complicate phenotype determination since dominance of alleles comes into the equation. The general pattern observed should still be the same

Table 1. List of all estimated niche optima for each trait. Values are relative, with -10 representing the lower limit and 10 representing the upper limit. Note that boundaries only apply to niche optima; individual trait values are not bound to this and can go beyond these values. Niche optima for environmental change scenarios are also given below. Original: original set of niche optima present at start and the set a niche will return to after environmental change scenario has passed. Converging: all niche optima become closer together compared to other niches. Diverging: all niche optima become further apart from other niches. Alternating: some niche optima come closer to optimum trait values of other niches, while some become further apart from trait values of other niches.

(Original)	**SVL**	**Forelimb**	**Hindlimb**	**Tail**	**Lamellae**	**Move rate**
Crown Giant	8	-4	-4	4	0	-5
Trunk Crown	-3	-4	-4	4	6	5
Trunk	-6	1	0	-4	0	5
Twig	-3	-8	-8	4	-6	5
Trunk Ground	0	0	6	4	0	-5
Grass Bush	-6	0	4	8	0	-5
(Converging)	**SVL**	**Forelimb**	**Hindlimb**	**Tail**	**Lamellae**	**Move rate**
Crown Giant	4	0	0	2	-2	0
Trunk Crown	-3	-2	-2	1	3	0
Trunk	-3	-1	0	-2	1	0
Twig	-1	-4	-4	2	-3	0
Trunk Ground	1	-1	3	2	1	0
Grass Bush	-4	-1	2	4	-1	0
(Diverging)	**SVL**	**Forelimb**	**Hindlimb**	**Tail**	**Lamellae**	**Move rate**
Crown Giant	10	-8	-8	8	3	-10
Trunk Crown	-6	-8	-8	8	10	10
Trunk	-10	4	4	-8	-2	10
Twig	-6	-10	-10	8	-10	10
Trunk Ground	-2	2	10	8	-2	-10
Grass Bush	-10	2	8	10	2	-10
(Alternating)	**SVL**	**Forelimb**	**Hindlimb**	**Tail**	**Lamellae**	**Move rate**
Crown Giant	6	-3	-3	5	2	0
Trunk Crown	-3	-3	-3	5	9	5
Trunk	-6	2	1	-4	1	5
Twig	-3	-8	-8	5	-4	5
Trunk Ground	0	1	8	5	2	0
Grass Bush	-4	1	8	8	3	0

and therefore I will use haploid individuals in the model for simplicity, although the model can be easily expanded to a diploid model if so desired. Individuals at the start are initialized with the same trait values and fit to the niche and they will all inhabit one and the same niche for now. The mismatch to niche *i*, $\Delta_{i,}$ depends on the distance between individual trait values and the niche optima:

$$\Delta_i = \sqrt{(\sum_{j=1}^{n} (x_j - \theta_{ij})^2)}$$

with *n* being the number of traits, x_j the individual's value of trait *j* and θ_{ij} being the optimum value of trait *j* in niche *i*.

Throughout the model, age of individuals is tracked. When they reach adulthood, they will have the option to disperse to a different niche (one time only) and gain the ability to start reproducing. A maximum age is also included in the model; upon reaching this age, the individual in question will perish regardless of its survival probability.

After initial setup is completed, the time loop will start. For this model, one timestep is assumed to be equal to one year, so that each timestep will include one breeding season and therefore one reproduction event.

Dispersal

Every timestep starts with a dispersal opportunity, where any eligible individuals (individuals reaching adulthood) can disperse to a different niche with a given probability. Regardless of dispersing or not, individuals will be bound to that niche afterwards and will not gain any further opportunities to disperse to a different niche. The model can be varied for its mode of dispersal. The first and most explored option is to set the dispersal rate with a fixed probability *d* and set the new niche to be completely random, while excluding the current niche. The second option is to keep *d* fixed while making niche choice depend on fit to the new niche, so that niches where the individual would have higher fit are more likely to be chosen. After dispersal has taken place, the individual will have its fit to the niche recalculated based on the niche optima of the new niche.

Survival

After dispersal, the model checks if individuals survive. As mentioned before, the survival probability will partially depend on fit to the current niche. The model will calculate the mortality of individual *i*, m_i. To calculate mortality, first the fit to the niche, ϕ_i, needs to be known:

$$\varphi_i = \frac{1}{1 + \lambda \Delta_i}$$

where λ is the strength of selection and Δ_i is the mismatch to niche *i*. Strength of selection is a measure of how disadvantageous it is to have a suboptimal phenotype in a niche. With a high selection strength, the penalties suffered for having a suboptimal phenotype are increased. It is also important to note that the selection strength for males and females is always the same in the model. Mortality is then given by:

$$m_i = \frac{D_{max}}{1 + e^{k(\varphi_i - x_0)}}$$

where D_{max} is a regulator of maximum mortality, x_0 is the point (or fit value) where selection is strongest and *k* is a regulator of the steepness of the mortality curve (how fast mortality will go from

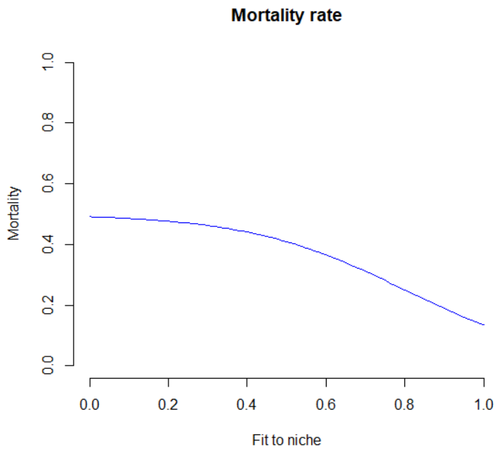

Fig. 3. Mortality curve used in model calculations. Curve shown uses the parameter values $D_{max} = 0.5$, $k = 5$ and $x_0 = 0.8$. While not fully visible for these values, the full curve shows an S-shape, with mortality decreasing fastest around fit values around x_0, which is the S-curve's inflection point.

maximum to minimum around x_0. ϕ_i is the individual's fit to the niche. Any individuals that perish will be removed from the population, while survivors will now gain the opportunity to reproduce.

Reproduction

Reproduction will only happen between individuals living in the same niche. Within each niche, random mating will occur between males and females. The model simulates this by first checking if a female will find a mate and produce offspring using the following formula to calculate the probability of giving birth for individual i, b_i:

$$b_i = b_0(1 - \frac{N}{K})$$

where b_0 is the basal birth rate, N is the current population size within the niche and K is the niche's carrying capacity. The model will then check if a female reproduces by using this formula. If successful, a male within the niche will be chosen at random to reproduce with the female. To keep things easy and ignore factors like sperm competition, females will only mate with a single male, after which they will not mate again for the rest of the timestep. Males can mate with any number of females within a timestep and can therefore be chosen again after mating with a female to mate with a second female, and so on.

When birth happens, a female will produce a number of offspring that can be varied in the model. The number of offspring per female per timestep can be set as always the same or have a standard deviation from the average. If a standard deviation is used, a decimal number is generated that will be rounded to the closest whole number and cannot be smaller than zero. The created offspring will have its sex randomly assigned and inherit trait values from their parents, after which recombination takes place. To simulate recombination, after an individual inherits its trait value from either parent, a recombination event may take place and have it instead inherit the trait value from the other parent. The model will then check if a mutation happens for each trait. If a mutation occurs, a value will be drawn from a Cauchy distribution ($a = 0$, $b = 0.1$) which will represent the step size of the mutation. This value can be either positive or negative and will be added to the current trait value to determine the new value. After that, the individual will have its fit to the niche determined based on the new trait values and is then added to the population.

All this together will create a base model that already functions well enough on its own to allow for adaptive radiations to occur and have the individuals conquer different niches if the optima of niches are not too far away and selection strength is in the right range; it cannot be too high or individuals will die before reaching the alternate optimum but neither can it be too low or individuals will not adapt since adaptations yield so little advantage. Now that the base model is ready, environmental change can be added into the equation.

Environmental changes

Environmental change is added into the model as an option that can be turned on or off. When it is on, the model will check for an environmental change event every timestep. Different model variants were tried that differed in how often these changes happen and in standard deviation of this average time between environmental change events. When such a change occurs, the niche optima for each trait and each niche will be shifted to match the new environmental conditions. The size of this niche optima shift has been varied between model simulations to check what changes for different frequencies and impacts of environmental change. While events will change the niche optima, all draws of new niche optima are still centered around the average for the current environmental state; for example when switching to the El Niño state, a value will be drawn that can either be positive or negative and is then added to the average optimum value for the corresponding trait in the corresponding niche to finally arrive at the actual optimum trait value for this particular El Niño event. This is to prevent niches from drifting too far apart and hit boundaries or attain unrealistic values.

For anoles, one reoccurring environmental change event is El Niño. El Niño events are known to happen every 2-7 years on average and vary in intensity. To mimic El Niño, three scenarios are considered. The distance between optimum trait values of different niches can either increase or decrease and this effect can be different per niche and per trait. Therefore three sets of niche optima averages are used to create three different environmental change scenarios (which are again just experimental averages and not actually based on empirical data): one with all niche optima coming closer together (convergent), one with all niche optima going further away from each other (divergent) and one with a mix of both (alternating), with the trait optimum either always increasing or decreasing for the same trait within one niche (direction for a shift in trait optimum can be opposite for different niches). When the El Niño event passes (El Niño is currently set to last equally long as the original environmental state), niche optima will return to their original values.

Table 2. List of parameters used in the model and their (range of) values.

Parameter	Description	Value	Notes
b	Average number of offspring per female per timestep	5	
μ	Mutation rate	0.001	
r	Recombination rate	0.5	
A_{adult}	Age of adulthood	1	
A_{max}	Maximum age an individual can reach	10	
K	Carrying capacity per niche	variable	Mainly 100 or 500
d	Dispersal rate	variable	Mainly 0.01 or 0.0001
λ	Selection strength	variable	Mainly 0.1, 0.5, 1.0
iSR	Initial sex ratio	0.5	
D_{max}	Maximum mortality regulator	0.5	
k	Steepness of mortality vs fit curve	5	
x_0	Fit value where selection is strongest	0.8	
B_b	Basal birth rate	1	
t_c	Average timesteps between environmental change events	7	
σ_t	Standard deviation of time between env. change events	variable	Mostly kept at 0
σ_s	Standard deviation of size of niche optima shift during env. change event	variable	Mostly kept at 0

Visualization

Finished simulation data was visualized and analysed using R Studio to create graphs. Multiple simulations were run for various parameter settings to explore how simulation outcomes are influenced by those parameters. The number of replicates per parameter setting varies depending on the stability of the outcome; if the outcome is always the same, it is unnecessary to take as high a number of replicates as when outcomes differ a lot between replicates.

Results

As stated before, the model was run for a multitude of combinations of parameter settings. Before going into individual parameter settings, it is first important to know what an adaptive radiation will typically look like. Since there were many replicates and parameter settings used, a large quantity of graphs were generated in total and it would be impossible to show everything here. Therefore, a selection was made to show the most relevant information and findings, with more data available as Supplementary Material. All the results shown below have all standard deviations set to 0.

Characteristics of an adaptive radiation

Firstly, all replicates showing radiation from one niche to another usually generate similar graph shapes. Still leaving environmental change out of the equation, a typical radiation looks as described below (Fig. 4). The population starts in a single niche and for some time, this will remain the only niche that is occupied. This amount of time is dependent on both carrying capacity and dispersal rate, which have decreasing effects on time until an additional niche becomes occupied as they become higher. Eventually, another niche can become occupied when at least one male and one female disperse to that niche and survive, gaining the opportunity to reproduce. If offspring then survive long enough as well, they can reproduce as well to eventually reach a stable population size. This does not mean that a population is adapted to its niche (or has a high fit to the niche). A niche is considered occupied when its population size is at least at 20% of the carrying capacity.

Adaptation is the process where individuals slowly alter their trait values to become as close as possible to the niche's optimum. This process is slow due to its dependence on mutation rate, but was sped up during simulations by using a Cauchy distribution for its step size, in order to find larger step sizes more frequently. With more individuals in a niche, the probability of a beneficial mutation

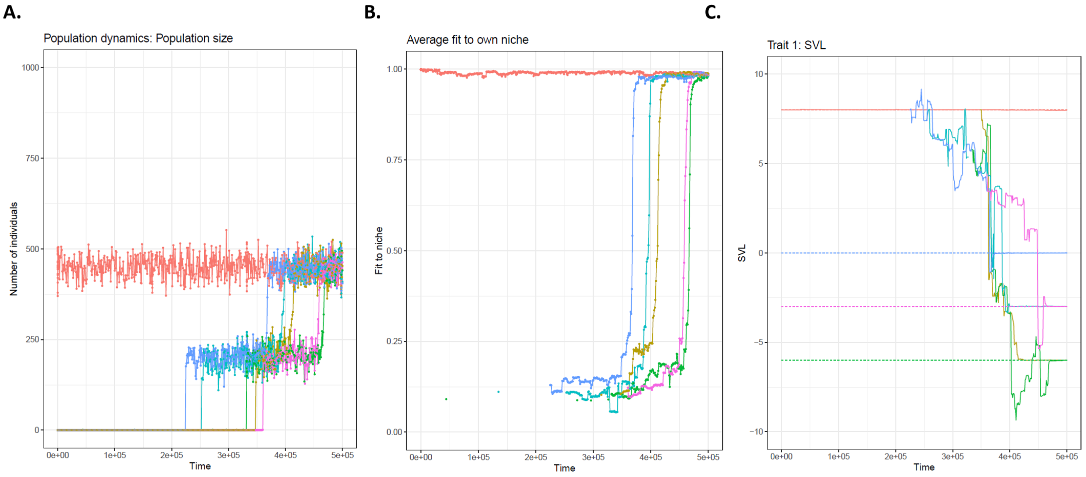

Fig. 4. Typical time course of a full adaptive radiation in absence of environmental change. Parameter values used: K = 500, d = 0.0001, λ = 0.5, environmental change absent. A) Population size. B) Average fit to niche. C) Average trait values. Note: averages (B and solid lines in C) are given per niche and not for the combined population size of all niches.

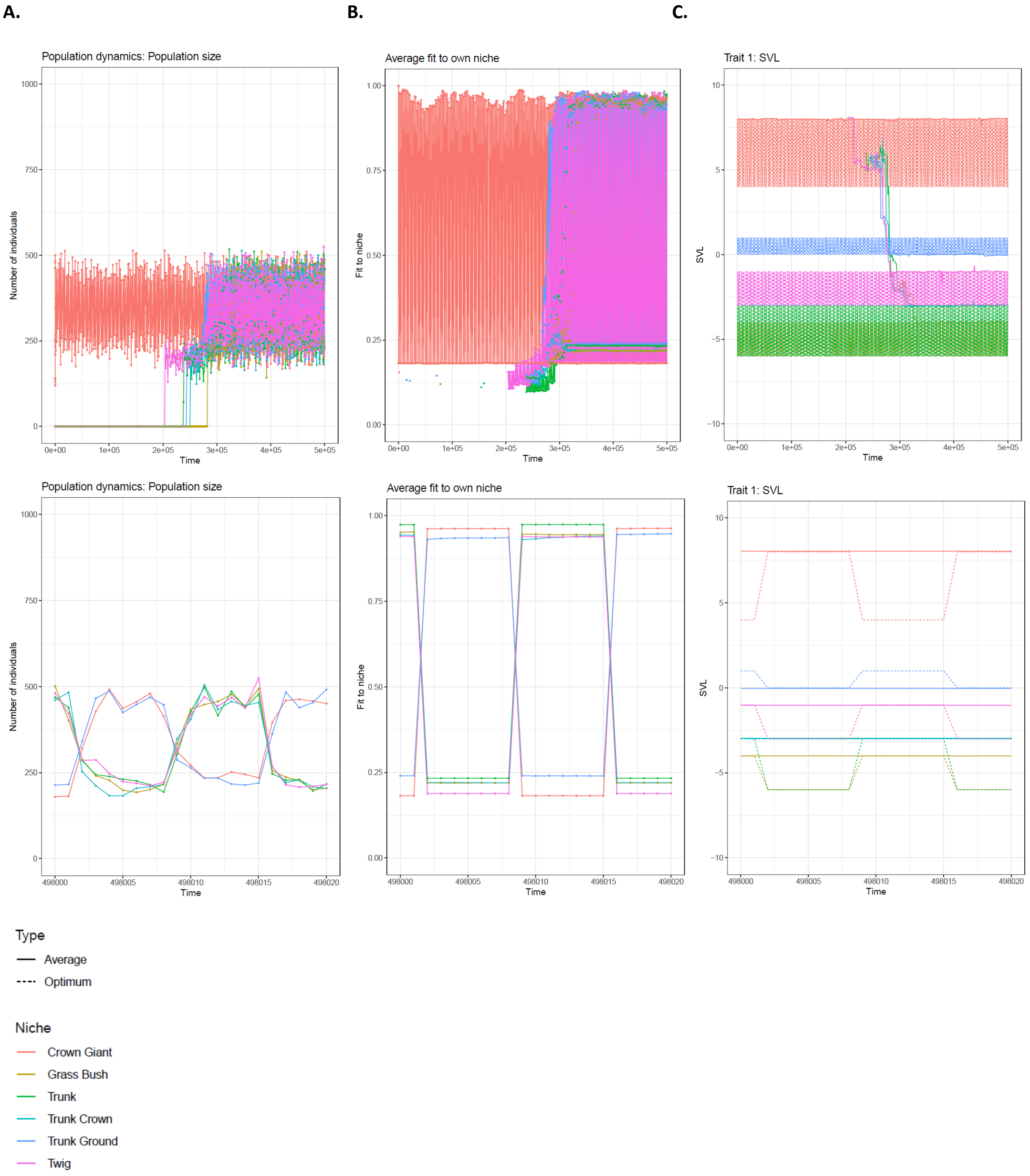

Fig. 5. Typical time course of a full adaptive radiation in presence of environmental change. Top graphs show data over the course of the entire simulation, while bottom graphs are zoomed in at the end of the simulation to show a close-up of equilibrium dynamics. Parameter values used: K = 500, d = 0.0001, λ = 0.5, converging environmental change. A) Population size. B) Average fit to niche. C) Average trait values.

(one that is closer to the niche's optimum trait value) happening increases and adaptation will go faster. Once such a mutation arises, chances are that it will spread through the niche's population due to its increase in fit to the niche and therefore lower mortality. When this process is repeated enough times, eventually the niche's population will reach average trait values approaching the niche's optimum trait values, meaning a population now has a high fit to the niche. Here, a population occupying a niche is considered fully adapted when the niche's population has an average fit to the niche of at least 0.9 (with 1.0 being the maximum fit to the niche).

different trait value, resulting in more genetic variation overall. This will increase the likelihood of an individual by chance being closer to an unadapted niche's optimum. If it then happens to migrate to this niche, it will have an advantage over other less fit individuals in that niche and have a higher probability of spreading its genes within that niche. This is also visible in Fig. 6, where adaptation happens in three niches after it happened in another within the same amount of time. The remaining sixth niche can also be seen to increase in average fit to the niche, so it is likely that if a longer simulation time was used, a full radiation to all six niches would have been achieved eventually.

Comparison for different intensities of dispersal and selection strength

Three main parameter settings were looked at more in depth, namely dispersal rate, selection strength and carrying capacity, both in absence and presence of environmental change. Carrying

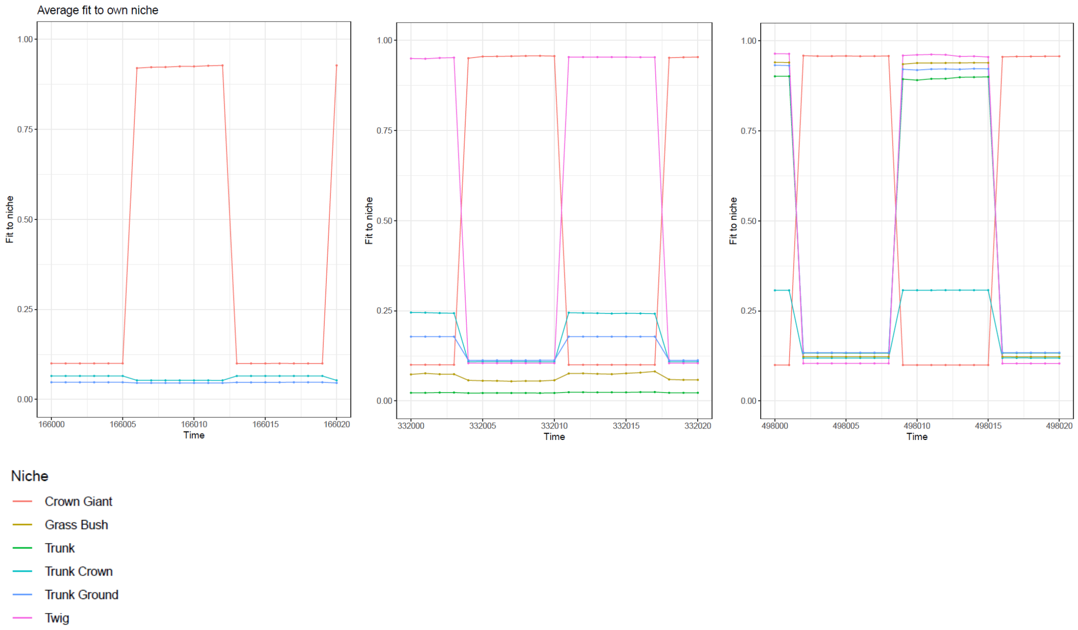

Fig. 6. Example of a partial radiation to five of the six niches. Graphs show average fit to niche at three different times in the simulation, the last being near simulation end. Parameter values used: K = 500, d = 0.0001, λ = 1.0, converging environmental change.

capacity was tested for values of 50, 100 and 500, but only at the value of 500 were adaptive radiations observed when any notable level of selection strength was present. Adaptive radiations were never observed at all under environmental change scenarios for a carrying capacity of 50, while a carrying capacity of 100 did have radiations but more so increased the probability of losing adaptation in all niches, including the original one. This is why only results for a carrying capacity of 500 will be shown here (Fig. 7). Full details for K = 50 and K = 100 can be found in Supplementary Material 3.

For dispersal rate, two main scenarios were analysed in more detail, namely a dispersal rate of 0.0001 and one of 0.01. For each of these cases, selection strength was varied between 0.1, 0.5 and 1.0 to see how this impacts simulation outcomes. To start off, let's look at a low dispersal rate of 0.0001. Regardless of selection strength (in the range used, at least) and environmental change being present, adaptive radiation to at least one additional niche is observed in at least one replicate per setting. So at this level of dispersal, neither the presence nor the direction of environmental change prevents adaptive radiation. There are, however, differences in the number of adapted niches at the end of the simulation between settings. This becomes especially clear when looking at the average number of adapted niches per setting (Table 3). With λ = 0.1, there is little difference in adaptive radiations between environmental change scenarios due to the lower penalty enforced (smaller decrease in fit to niche) on individuals regarding mortality when their trait values are somewhat away from the niche's optimum. All environmental change scenarios do achieve a higher number of adapted niches on average than when environmental change is absent, however. This pattern is also observed with λ = 0.5, although diverging change now achieves only slightly more radiations than no change, while converging and alternating change remain almost unaffected. All scenarios are affected when λ is set to 1.0, with converging change still achieving around double the amount of adapted niches on average as the other scenarios.

The pattern is different when looking at a dispersal rate of 0.01. Again using λ = 0.1, now a full radiation to all niches is observed in every replicate with environmental change absent and happens in the majority of cases with environmental change present as well. With alternating change, the final niche remains unadapted significantly more often than in other environmental change scenarios. Upon analysing these replicates (Fig. 8), this was caused by the niches representing Twig, Trunk and to a lesser extent Trunk Crown ecomorphs only having a slight change in niche optima compared to other niches, resulting in these niches sometimes not adapting to one set of niche optima, but going in between to keep their fit constant, but slightly lower than would be possible

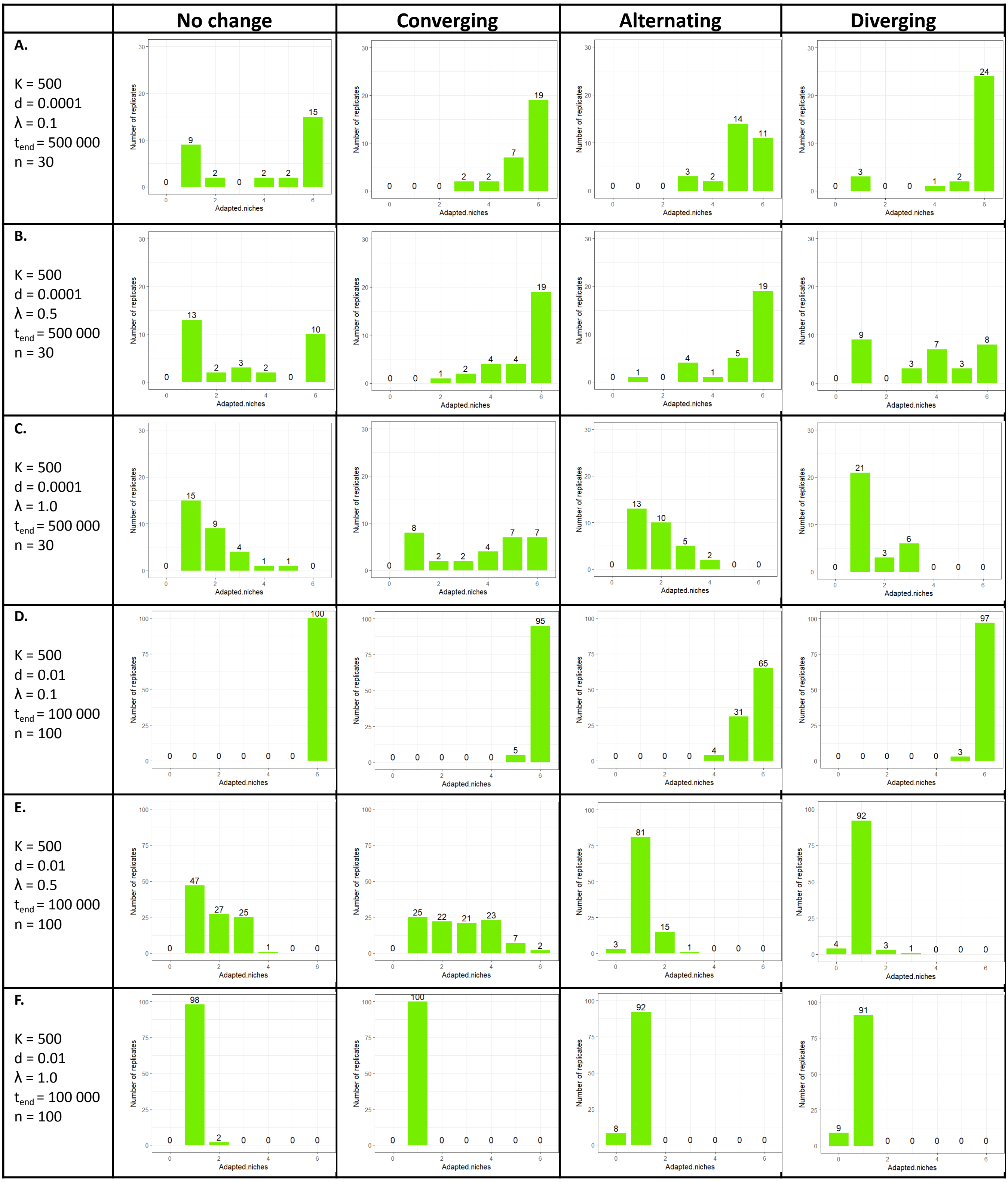

Fig. 7. Adaptation in niches at time of simulation end for various parameter settings. A niche is considered adapted when

the average fit to the niche of individuals in that niche is higher or equal to 0.9. Each column shows the outcomes for no environmental change present, convergent change, alternating change and diverging change, respectively. Standard deviations are kept at zero in all simulations shown here. Corresponding niche occupation graphs can be found in Supplementary Material 2.

when adapting to one set of niche optima. This did cause the fit to the niche to fall slightly below 0.9 in some cases, but since this avoids a much lower fit during the other environmental state, it can be considered a viable strategy.

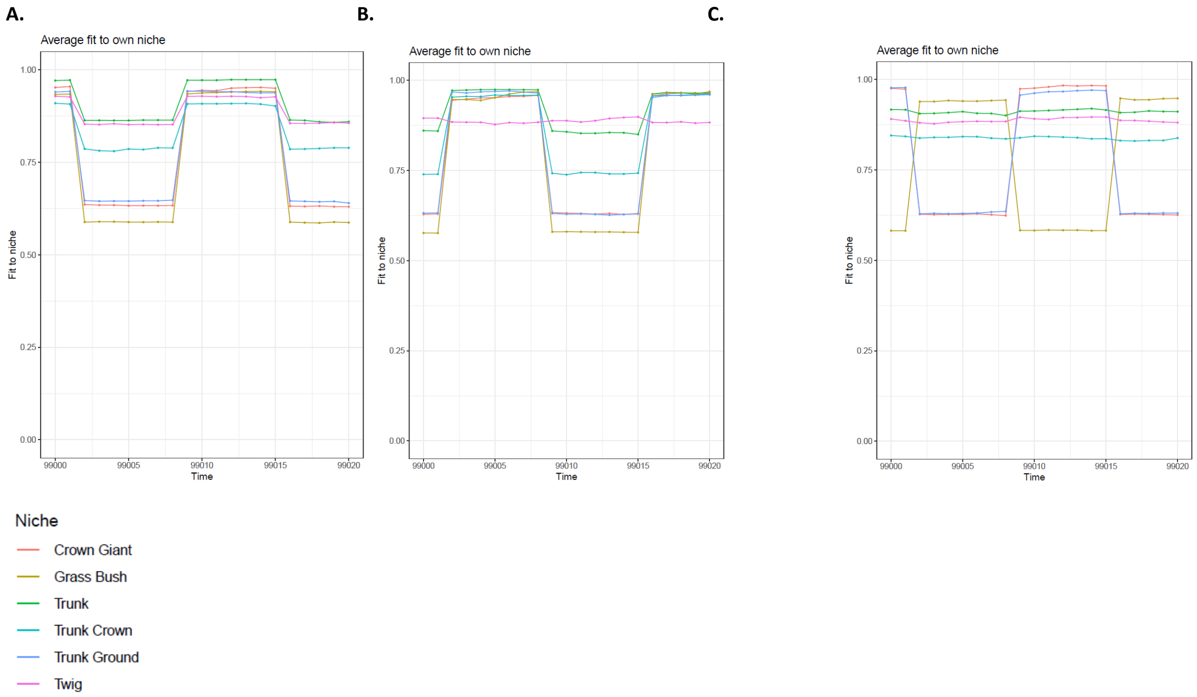

Fig. 8. Average fit to the niche shortly before simulation end when using the following parameter settings: K = 500, d = 0.01, λ = 0.1, alternating environmental change. Each graph shows a different replicate. A) All niches adapt to one set of niche optima. B) One niche reaches an all-time stable fit to the niche. C) Three niches achieve an all-time stable fit to the niche. This stable fit to the niche is achieved by not adapting to either set of niche optima and instead aiming for trait values in between to retain the same fit to the niche when the environmental state switches.

Although this "intermediate" strategy can also be observed with d = 0.0001 and λ = 0.1 and thus still being viable at low dispersal rates, it only seems to work at low selection strength. Still having d = 0.01, setting λ to 0.5 significantly decreases the number of adapted niches for all scenarios. Convergent change is still the best performing scenario regarding adaptive radiation, while both divergent and alternating change now achieve a smaller number of adapted niches on average than with environmental change absent. With λ = 1.0, selection strength seems to be too high to achieve adaptive radiation at all when environmental change is present in any form. If it is possible, it has not been observed within 100 replicates. Without change, a radiation to one niche is rarely observed. For both λ-values of 0.5 and 1.0, in some replicates for diverging and alternating change adaptation is also lost in the original niche (Crown Giant), while this was never observed for converging change or without environmental change.

Some simulations were also done for a standard deviation of 3 for the number of timesteps between two environmental change switch events (Supplementary Material 5). These yielded slightly lower numbers of adapted niches at simulation end on average, but results were so similar to those without a standard deviation that it is hard to say if there is truly a difference between these parameter settings regarding the simulation outcome. This could be different for larger values of standard deviation, but this will make the model much more unpredictable and hard to analyse, as well as create situations that will be very unlikely to happen in reality.

Discussion

From the simulations run it becomes clear that adaptive radiation possibility, probability and speed all are dependent on a variety of factors. Naturally, a higher selection strength will decrease the likelihood of radiations and, if sufficiently high, even prevent them. Convergent environmental change seems to be the most reliable scenario to maximize the number of adapted niches as selection strength increases, while the direction of change has little influence with low selection strength. Whether or not environmental change is preferable over no environmental change depends on the dispersal rate and selection strength both.

Table 3. Niche occupation and adaptation as observed across various parameter settings. Niche occupation is defined as having a population size that is equal to or higher than 20% of the carrying capacity. Niche adaptation is defined as having an average fit to the niche of at least 0.9. NO = no change, CON = converging change, ALT = alternating change, DIV = diverging change. For K = 100, no adaptation was seen with convergent change and therefore further simulations for alternating and diverging change were deemed unnecessary, resulting in the blank spaces in the table. Supplementary Material 1 includes a table showing replicate averages for parameter settings left out here as well.

d		0.0001	0.0001	0.0001	0.0001	0.0001	0.01	0.01	0.01	0.01	0.01
K		100	100	500	500	500	100	100	500	500	500
t_{end}		$1.0\cdot10^5$	$1.0\cdot10^5$	$5.0\cdot10^5$	$5.0\cdot10^5$	$5.0\cdot10^5$	$2.5\cdot10^5$	$2.5\cdot10^5$	$1.0\cdot10^5$	$1.0\cdot10^5$	$1.0\cdot10^5$
λ		0.1	0.5	0.1	0.5	1.0	0.1	0.5	0.1	0.5	1.0
n		100	100	30	30	30	100	100	100	100	100
NO	occupied	1.030	1.000	4.133	3.833	4.000	6.000	5.320	6.000	6.000	6.000
	adapted	**1.020**	**0.980**	**4.033**	**3.133**	**1.800**	**5.870**	**0.910**	**6.000**	**1.800**	**1.020**
CON	occupied	1.540	0.000	5.967	5.967	5.567	6.000	5.250	6.000	6.000	6.000
	adapted	**0.680**	**0.000**	**5.433**	**5.267**	**3.700**	**0.470**	**0.090**	**5.950**	**2.710**	**1.000**
ALT	occupied			5.500	5.333	5.367			6.000	6.000	6.000
	adapted			**5.100**	**5.200**	**1.867**			**5.610**	**1.140**	**0.920**
DIV	occupied			5.667	5.600	5.633			6.000	6.000	6.000
	adapted			**5.367**	**3.633**	**1.500**			**5.970**	**1.010**	**0.910**

Dispersal rate seems to exert quite some influence on adaptive radiation occurrence and speed. A low dispersal rate allows for a higher tolerance to selection strength, but this comes at the cost of some radiation speed. Meanwhile, higher dispersal rates increase the speed of radiation at low levels of selection strength, but when selection strength becomes higher adaptive radiations quickly occur less and less. Thus, the maximum selection strength at which radiations are likely to happen has been reduced when dispersal rates are high. This is likely due to migrants that aren't fit to their new niche invading. If these migrants by chance happen to survive, they can reproduce and spread their genes through the niche, hindering adaptation. With lower dispersal rates, this effect is minimized and mostly prevented. If selection strength is low, populations will achieve more radiations with a high dispersal probability, while a low dispersal probability is preferred to maximize radiations at higher selection strength.

Just like adaptive radiations do not happen or at least are very unlikely to happen above a high selection strength threshold, selection strength is also likely to have a lower boundary below which no adaptive radiations happen. Setting the selection strength to zero would give every individual the same fit to the niche regardless of phenotype and the niche they are in. Thus all advantages will be lost, preventing adaptation from happening. It is likely that when selection strength is sufficiently close to zero, the influence of fit to the niche is still too low to allow adaptation to happen.

Carrying capacity also has to be sufficiently high to provide enough individuals in the entire ecosystem (all niches combined) to keep things stable. Low levels of carrying capacity increase the effects of genetic drift, which will hinder adaptive radiation. Especially at higher selection strength and/or dispersal rate, this can drastically reduce the probability of an adaptive radiation and usually result in adaptation loss even in the original niche.

One very interesting finding regarding environmental change was to see that some niches' populations would not adapt to one of the two environmental state's optima, but instead keep their morphological position in between these two so that their fit to the niche would be constant, regardless of the environmental state. This only occurred when selection strength was low ($\lambda = 0.1$) and the gap between the niche's normal and altered environmental state was small (only small enough with the alternating change scenario from all scenarios tested here). For higher values of selection strength used, the fit gap between the two niche optima became too large and using aforementioned strategy would result in a constant fit to the niche that was too low to give any major benefits, hence this strategy was never observed at higher selection strength levels. It is important to keep in mind here that this strategy would likely not be very viable when niche optima will not always alter between the same exact values, but instead have a standard deviation added to it. Still, it remains interesting to see if this strategy might be viable at higher levels of selection strength under different circumstances.

It is important to note that all simulations here were run with the number of offspring per female per timestep set to 5. Changing this value around can cause mortality to outweigh the number of births for the same values used in the mortality function. When applying the model to species with a lower number of offspring, adaptive radiation may not happen without manipulation of the x_0 parameter from the mortality function. This could be done, but it must be kept in mind that only a lower fit needs to be achieved than currently in order to start gaining benefits in the form of increased survival rates when having a high fit to the niche. Lowering x_0 too much may lead to improbable scenarios where fit to the niche will barely affect survival unless it is very close to zero.

Next, there are some factors that were excluded from the model or were ignored to keep the model simple. Firstly, the model presented here assumes unrelated traits, while in reality many traits will to some extent usually be related to each other. For anoles, which provided the traits and trait value estimates in my model, it is known that body size affects the limb lengths as well. However, even when removing body size effects, forelimb, hindlimb and tail length were all found to still be correlated with each other (Losos, 1990). The reason why these traits were still used in the model is because currently there are no traits known, or at least not to my knowledge, which are proven to be unrelated to any other traits. It could then be argued to correct for these correlations in the model, however the level of correlation between traits may very well be different for each ecomorph and even for different species of anoles. Since relatedness is likely different per ecomorph, it can be assumed that relatedness is not a fixed variable and should be made dynamic, adding an additional layer of complexity to the model. An ideal scenario is therefore to use unrelated traits that are all known to change according to the environment, however in reality such traits have not been identified yet.

Another consideration to keep in mind is that the model assumes haploid individuals. While anoles are diploid organisms, creating a diploid model will add heterozygosity and dominance of alleles as additional complexity layers. While such a model would be closer to reality, when a new mutation arises, the dominance of its allele would be unknown. Assigning a random value here could be an option, however for simplicity the decision was made to keep this model haploid. It could be interesting to see for a future study how the outcome changes when using a diploid model, though.

Lastly, the model assumes random mating. Anoles are known to have sexual selection going on in many species, which could lead to female preference and/or sexual dimorphism. When a female preference exists, sexual selection acts in a direction that may by chance be opposing the direction of natural selection. Even if it does not and instead moves in the same direction, it could speed up the time until evolution since there are now two types of selection both pushing towards there. Sexual dimorphism could cause one sex to perform better than the other in a given niche due to their differences in average intersexual trait values. In any case, model outcomes could be quite different than when assuming random mating, which is an important consideration to keep in mind.

As mentioned before, low dispersal rates were shown to decrease the influence of selection strength on adaptive radiations. Another study found similar results and also found that phenotypic plasticity is similarly affected by dispersal (Thibert-Plante and Hendry, 2011). While phenotypic plasticity was not included in my model for simplicity, it is an important factor to consider when looking at adaptive radiations in reality. This could indicate that adaptive radiation can still happen if there is sufficient reproductive isolation between two niches if phenotypic plasticity is high, but only when dispersal rate is low enough. Thibert-Plante and Hendry did not look at environmental changes in their simulations, however. Phenotypic plasticity could very well become more impactful when the environment's optimum trait values switch around every few timesteps, which could allow individuals to become more resistant to environmental change, as was found in other animals as well (Charmantier et al., 2008). Of course, this will also remove the need for a population to adapt according to the change, so whether or not this enhances adaptive radiations with ongoing environmental change remains to be seen. The flexible stem hypothesis mentioned earlier (Gibert, 2017) also remains an option, but this will require phenotypic plasticity to be costly as well.

A remaining question is how aware individuals are of the environment around them. If they live in one niche and are optimally suited for a different niche, would they be more likely to move to that niche? Simulations were already run where a migrating individual would be more likely to migrate to a niche it is more adapted to (Supplementary Material 4), however the model outcomes did not differ too much from random niche selection. However, dispersal rate could also be made dependent on an individual's fit to its niche. While this may not always change general patterns observed, it may have the potential to increase the speed of adaptive radiation. As a result, this could also allow adaptive radiations under slightly higher selection strength than was possible before, making the populations in all niches more tolerant to environmental change overall. This is of course just speculation, but would be a promising direction for a future project.

There are also some more environmental change scenarios that would be interesting to explore in future studies. While this model switched between two environmental states in regular intervals, El Niño is known to last shorter than the "normal" environmental state. Implementing this into the model could cause fewer niche populations to adapt to the "El Niño" niche optima due to its fit benefits only applying so shortly, making it much more viable to adapt to the "original" niche optima due to its lengthier benefits. Similarly, adding a standard deviation different from zero to both optima every time a switch between states happens will create more varied niche optima and prevents populations from adapting to one set of trait values, instead making it a range of values relatively close to each other. Adaptive radiation might become harder to achieve as the standard deviation increases, especially under higher strength of selection. However, it remains debatable if this standard deviation should be made very large in the case of anoles, since only El Niño is known to vary in intensity and the original state should not be all that different from the last after El Niño ends. A scenario where only the “El Niño” optima vary could be closer to reality, but may promote adapting to the never changing “original” optima, in which case results would likely not be too different from those found with the model presented here for no environmental change scenarios.

Even though this model has been simplified here and there, it does show that adaptive radiation could be achieved by island anoles if the circumstances are right. Whether circumstances allow for adaptive radiation depends on carrying capacity, selection strength, dispersal rate and the environmental change scenario. More factors may have impact in reality that were not included here, but this model could serve as a base that can be expanded on where necessary. With potentially some changes here and there, it could also be applied to different species of animals and may give some insights in their potential to undergo adaptive radiation.

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