Supplementary material part 3

ODD Template

[1]The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models.

1. Purpose

This study aims to understand how thermal breadth and dispersal distance evolve simultaneously during range shifting (part 1). Also, the effects of an evolvable thermal optimum on evolutionary dynamics in dispersal and thermal breadth are examined (part 2).

2. Entities, state variables, and scales

The individual

-x and y coordinate
-TP: Thermal performance of an individual
-P_{mort}: Chance of mortality during competition phase
-σ_{disp}: Standard deviation of a Gaussian distribution determining dispersal (evolvable)
-x_{adap}: Distance of local optimum to global optimum along x-axis (fixed at 0 or evolvable)
-$T_{breadth}$: Width of the thermal breadth (evolvable)

The landscape

-x_{opt}: x-coordinate of global optimum
-climate window(only herein, survival of individuals is allowed)
-range shifting: climate window is static or shifting to the right of the landscape along the x-axis.

Scales

The landscape is rectangular with one short y-axis (100 cells) and a long x-axis (2048 cells). One time step corresponds to one generation of a semelparous species. In total, one simulation runs for 2000 time steps.

3. Process overview and scheduling
At the start of a simulation, individuals are initialized in the landscape. During the first 1000 time steps of a simulation, the climate window is fixed along the x-axis. However, afterwards, the climate window starts moving along the x-axis to simulate range shifting. Per time step, several events occur in a discrete order (Figure 1). All individuals execute these events simultaneously. During dispersal, the x and y coordinate of an individual are updated.

[1] References are given in the manuscript.

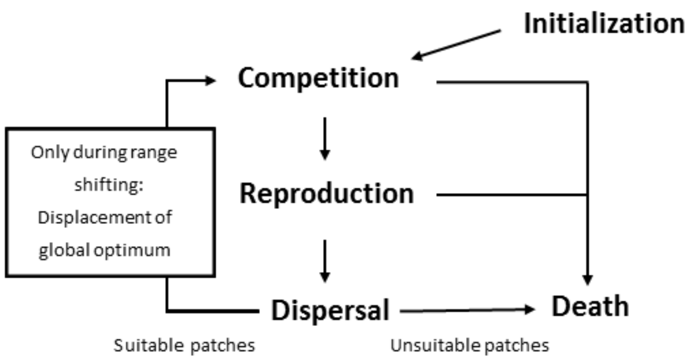

Figure 1: Overview of the life cycle of an individual

4. Design concepts

Questions: There are eleven design concepts. Most of these were discussed extensively by Railsback (2001) and Grimm and Railsback (2005; Chapter. 5), and are summarized here via the following questions:

Basic principles.
This study combines the theory on thermal performance with spatial selection during range shifting.
<u>The thermal performance curve:</u>
Thermal performance is considered a phenotypically plastic trait and is therefore visualized by a reaction norm, named the thermal performance curve (Angilletta, 2009). The independent variable of this reaction norm represents temperature and the phenotype represents a measure of performance (e.g. movement, growth, assimilation, development, or fecundity) (Angilletta, 2009). It is characterized by a critical minimum temperature (Tmin), an optimal temperature (Topt), a thermal breadth (Tbreadth) and a critical maximal temperature (Tmax) (Huey and Stevenson, 1979). In part 1 of this study, the thermal breadth of the reaction norm is evolvable, whereas in part 2, both the thermal breadth and thermal optimum are evolvable.

<u>Range shifting:</u>
With increasing global temperature, species are observed to shift upward in elevation [1] or polewards in latitude [2], in order to keep track of their suitable niche. Due to spatial sorting, selection occurs for those individuals reaching the leading edge of a range first [3,4]. Those individuals have the highest dispersal ability and if dispersal is heritable, breeding results in more dispersive offspring (the Olympic Village effect) [4]. As such, spatial selection results in individuals with a ‘fat-tailed’ dispersal kernel at the leading edge of a range [5,6]. Spatial selection is expected to be stronger with increasing speed of climate change [7].

Emergence and adaptation.
Finally, the distribution of thermal breadth, optimum temperatures and level of dispersal are compared before and during range shifting. During range shifting, individuals adapt their thermal performance curve and dispersal behavior, depending on their position within the shifting range (front, middle or back).

Objectives.
The objective of an individual is to have offspring. Those genotypes which have the highest reproductive success will be selected at the end of a simulation.

Interaction. Within the competition phase, individuals compete for resources according to their thermal performance curve.

Observation.
In all simulations, 10000 individuals were randomly sampled per replicate just before the global optimum starts to move, and again 1000 generations later. The timing at which equilibrium is reached in the evolving traits at the leading edge was visually identified. Of the sampled individuals, the values of the genes encoding the traits under selection were determined. For all figures represented in the next section five replicas are used, which is justified considering the low degree of variation between replicates. Moreover, in order to efficiently use computing power and given our pilot analyses demonstrating low levels of variability among replicates, we performed extensive sensitivity analyses to gain insights on the generality of our results. Generality was confirmed (see appendices) since all sensitivity analyses yielded the same qualitative results.
To be complete, the course of evolution was investigated from the moment range shifting starts for the back, middle and front of the population. To achieve this, the mean values for $T_{breadth}$ and σ_{disp} were determined within 5 columns at the back, middle and front of the climate window for each time step using 5 replicates. The thermal optimum was either fixed or static and a always equaled 1.

5. Initialization

Each simulation starts with the initialization of 2000 individuals within the first 100 columns of the landscape. Until equilibrium is reached in the evolving traits, the population is only allowed to survive in this restricted range. During initialization, the values of the parameters under selection are randomly drawn from a uniform distribution with values between 0 and 5 for σ_{disp} and between -50 and 50 for x_{adap}. The interval from which the values of $T_{breadth}$ are drawn depends on whether the thermal optimum is evolvable or not. In the former case the interval is [0-0.5] whereas in the latter case it is [0-6] when a (increasing with strength of the thermal breadth- thermal performance trade-off) equals 1 or 5 or [0-2] when a equals 10.

6. Submodels

Competition

Individuals that are best adapted to local conditions gain access to limited resources first, excluding the competitively weaker individuals from the population. As such, individuals interact by their competitive strength. This strength is dependent on an individual's performance capacity as determined by its TPC described by the following formula following Chaianunporn and Hovestadt (2012):

$$TP = e^{-\frac{\left(x-(x_{opt}+x_{adap})\right)^2}{100*T_{breadth}}} \cdot TP_{max} \cdot e^{-a*T_{breadth}} \quad \text{(eq. 1)}$$

Here, TP refers to the thermal performance of an individual and TP_{max} to the maximum value of TP. a represents a flexible parameter describing the strength of the performance (TP_{max}) – thermal breadth ($T_{breadth}$) trade-off (see Fig 1 for an illustration of the effect of a). Within the competition phase, competitive strength is directly related to performance capacity. As such, the TPC function is used as a measure for the competitive strength of an individual. We assumed that when TP is zero or negative, local conditions are too unsuitable for an individual to reproduce. x refers to an individual's x-coordinate and x_{adap} to the deviation of an individual's local optimum in space to x_{opt} (the location of the global optimum along the x-axis). E.g. when x_{opt} equals 50 and x_{adap} 20, the local optimum of the individual is positioned within the column with x-coordinate 70. When the thermal optimum is not evolvable (part 1) x_{adap} will equal 0 for all individuals. As such, the local optimum of an individual

always coincides with x_{opt} (the global optimum of the population positioned within the central column along the x-axis of the climate window).
After determining the competitive strength of all individuals within a cell, the chance of mortality (P_{mort}) was defined for each individual as:

$$Pmort = 1 - \frac{N^*}{\sum TP_{x,y}/TP} \quad \text{(eq. 2)}$$

Here, N^* stands for the carrying capacity within a cell which was fixed at 50. Within a cell the chance of mortality P_{mort} for each individual was weighted for the total competitive strength of all individuals within that cell $(\sum TP_{x,y})$. By doing this, an individual will have a higher survival chance when the sum of the competitive strength of all individuals within a cell $(\sum TP_{x,y})$ is low.

Reproduction

Each individual has on average three (λ) offspring. The exact number is drawn from a Poisson distribution with mean λ, including demographic stochasticity. During reproduction the mutation rate for each gene under selection is 0.001, allowing evolution. In case a mutation occurs, the value for the offspring of that gene is sampled out of the following interval: [parental value – mutation size, parental value + mutation size] with the mutation size being 0.5 for σ_{disp} and 5 for x_{adap}. For $T_{breadth}$, the mutation size equals 0.5 when the thermal optimum is not evolvable, but 0.05 when it is evolvable. The different mutation sizes are chosen in such a way that the speed of reaching equilibrium is optimized, reducing computational effort. These chosen mutation sizes do not affect the outcome of our model (see supplementary material part 2). As the implemented species is considered to be semelparous, an individual dies after reproducing.

Dispersal

The dispersal distance is drawn from a Gaussian probability distribution with standard deviation (σ_{disp}). The larger the value of σ_{disp}, the wider the tail of the Gaussian distribution resulting in an individual dispersing further and more frequently. The direction of dispersal is random [7,9]. Individuals who arrived outside the climate window will not be able to reproduce and expire.

7. References

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