

## Model overview

This agent-based model (ABM) simulates trait-based population-level responses to climatic and environmental change. The premise of ABMs lies in the principle that micro-level agent-agent and agent-environment interactions produce emergent macro-level outcomes for systems too complex or too specific to model with standard structural equations (Tisue & Wilensky, 2004). Our rule-based ABM simulates the fates of metapopulations whose fitness is controlled by an evolving functional trait that responds to selection based on environmental conditions. Functional traits are phenotypic characteristics that interface with the environment (McGill et al., 2006; Polly et al., 2016). Environmental change potentially affects trait performance and population fitness, consequently driving trait evolution or population extinction., which in turn affects functional trait distribution in local community assemblages (Jönsson et al., 2015; Morales-Castilla et al., 2015; Polly & Head, 2015).

The functional trait modeled is tooth crown height of mammalian herbivores, such as horses. The evolution of high-crowned teeth in these herbivores is climatically driven; in fact, the relationship between crown height, environment, and climate is well-understood both functionally and evolutionarily (Damuth & Janis, 2011; Eronen et al., 2010; Fortelius et al., 2002; King et al., 2005; Semprebon et al., 2019). In environments with abrasive or dusty/gritty vegetation, higher-crowned (hypsodont) teeth provide greater fitness despite the metabolic and mineral costs of producing them. The silica content of grass and gritty arid environments select for hypsodonty; non-gritty forests select for brachydonty (low-crowned teeth). Although the specifics of our model are teeth, diet, and environment, the implementation is abstract enough that results can be generalized to other climate-environment-trait systems.

Our virtual world consists of a continent that is gridded in spatially distinct habitat “patches.” Each patch denotes a local environment, which determines the local fitness optimum for inhabitant populations. Each “agent” in this model represents one local population of a species. Each species can consist of many populations, each of which occupies a single patch, thus making them the equivalent of metapopulations (*sensu* Hanski, 1999). A patch can be occupied by a maximum of one agent of any given species—the same patch can be occupied by multiple agents, given that the agents are of different species. Each individual run is divided into temporally distinct “time steps.”

Our model incorporates five key processes: climate change, dispersal (including gene flow), selection, speciation, and extirpation. Model parameters can be adjusted for each of these mechanisms except for speciation, which we treat as a constant process so that our model runs end with a predictable number of species with identical patterns of common ancestry and divergence times so that variance between model runs is due only to change in climate and the aforementioned controllable demographic parameters. Populations do not compete with one another; similarly, this helps the model largely focus on population-environment interactions in a changing climate. During each time step, each local population undergoes selection, dispersal, and the possibility of extirpation. (Populations also undergo genetic drift.) Speciation events act at predetermined time steps. Additionally, climate change periodically produces shifts in precipitation and biome type that influence the selective optimum for patches. The crux of the model lies in the interaction of these mechanisms. Adjusting parameters either independently or simultaneously allows us to test which combinations confer resilience under gradual, moderate, or rapid climatic change scenarios. For the purposes of this model, we measure resilience via three metrics: number of species existing at the end of each model run (species number), number

of populations of each species (species abundance), and successful colonization of new biomes that arise during the run.

Our ABM extends Polly et al. (2016)'s trait-climate-environment model in two important ways. This model integrates climate change and dynamic environments; the previous model was limited to static environments. Additionally, we have ported the model to NetLogo 6.1.1. Underlying mechanics remain consistent with the earlier model. Readers are referred to it for full justification of implementation and parameter choices.

### *NetLogo*

NetLogo is an ABM programming environment suitable for simulating spatially and temporally explicit phenomena (Tisue & Wilensky, 2004; Wilensky, 1999). Spatial settings and rules for agent behavior are highly customizable (Tisue & Wilensky, 2004). We used NetLogo's BehaviorSpace tool to record the numerical output of each model run; spatial results were identified through model interface images.

### *Model algorithm*

Each individual run lasts for 400 time-steps. Several parameters—selection intensity (adaptive peak width), phenotypic variance, trait heritability, dispersal probability, and extirpation probability—can be adjusted in the setup. Populations undergo extirpation, dispersal, selection, gene flow, and genetic drift every time step; speciation occurs every 100 steps.

### *Model world and characteristics of patches*

The model world consists of the virtual continent, Hesperia, with varied topography. Hesperia is divided into 822 spatially distinct square patches, each of which is assigned values for grit, temperature, and mean annual precipitation. Patches are categorized into vegetative biomes (tundra, forest, desert, or grassland) based on temperature and precipitation (Whittaker, 1967). In this way, Hesperia is environmentally heterogeneous. Local selective optimums for hypsodonty values are calculated based on grit, precipitation, and biome type. Climate becomes more arid as the model progresses, transforming forest into grassland and desert and shifting selective optimums.

We determined biome type (grassland, tundra, forest, or desert) from a function of temperature and precipitation following Whitaker (1967). If temperature  $\leq -5$  °C, the patch is categorized as tundra biome. If temperature  $> -5$  °C and precipitation  $\leq 20$  cm/year, the patch biome is categorized as desert. If temperature  $\geq 5$  °C and precipitation  $> 20$  cm but  $\leq 90$  cm, the biome is categorized as grassland. All other patches are classified as forest biomes.

### *Characteristics of populations*

Each local population is represented in NetLogo using an agent called a “turtle.” Each population is assigned numerical characteristics: ID number, species assignment, trait value, and population size (number of individuals, which determines rate of genetic drift). Population trait value represents the population mean. For consistency with the 2016 model, population size is set to 100 individuals. Names assigned to species in the model output indicate species ancestry and the model step at which it originated.

### *Functional trait and its local optimum*

Tooth crown height is our functional trait. In mammals, crown height varies with environmental parameters affecting diet abrasiveness. The selective optimum (ideal trait value) in any local environment (patch) is a function of grit  $g$ , precipitation  $p$ , and biome  $b$ . The optimum ranged from 0 (low-crowned or brachydont) to 3 (high-crowned or hypsodont). High-crowned teeth are more suited to dry and gritty environments and tough vegetation; in contrast, low-crowned teeth are more suited to wet environments with little grit and tender vegetation (Janis and Fortelius, 1988; Damuth and Janus, 2011). Following Polly et al. (2016), the local selective optimum,  $\theta_i$ , for each patch was set as a function of precipitation, biome, and grit, where  $g$  is grit,  $p$  is precipitation, and  $b$  is biome.

$$\theta_i = g + \delta[p] + \delta[b]$$

where  $\delta[p]$  is the piecewise function:

$$\text{For } p \leq 100, \delta[p] = 100 - p$$

$$\text{For } p > 100, \delta[p] = 0$$

and  $\delta[b]$  is the piecewise function:

$$\text{For } b = \text{"forest"} \text{ or } \text{"tundra"}, \delta[b] = 0$$

$$\text{For } b = \text{"desert"}, \delta[b] = 0.5$$

$$\text{For } b = \text{"grassland"}, \delta[b] = 1$$

Population fitness is determined by proximity of mean functional trait value and local selective optimum of the occupied patch. Smaller differences between the actual and optimal trait value indicate higher fitness.

### *Extirpation*

Extirpation is the local extinction of a population from a patch. Species extinction occurs if all local populations of the species are extirpated. Extirpation occurs stochastically, with a greater probability  $p(e)$  in populations with trait value far from local optimum:

$$p(e) = \text{ESF} * |z - \theta_i| / \text{APW}$$

where  $z$  is population trait value,  $\theta_i$  is local selective optimum, ESF is extirpation scaling factor (a user-controllable parameter ranging from 0 to infinity), and APW is adaptive peak width (selection intensity; see below). Essentially, if trait value is far from the selective optimum relative to selection intensity, extirpation probability increases toward 1.0. Setting  $\text{ESF} < 1$  decreases the probability, whereas setting  $\text{ESF} > 1$  increases it. This method is comparable to the Lynch and Lande (1993) function and identical to that of Polly et al. (2016).

### *Dispersal*

During a dispersal event, a turtle creates a copy of itself on an adjacent terrestrial patch. The user-controllable dispersal probability parameter (ranges from 0 to 1) determines probability of dispersal into an individual adjacent terrestrial patch.

### *Selection and genetic drift*

Each step, the trait value of each population is modified by selection:

$$z_{\text{new}} = h^2 z_{\text{old}} + (1 - h^2) \theta_i$$

where  $z_{\text{old}}$  is trait value before selection,  $\theta_i$  is local selective optimum,  $w^2$  is adaptive peak width (equal to standard deviation of the normal curve used to model the adaptive peak),  $h^2$  is

heritability, and  $v$  is phenotypic variance. This equation, used in Polly et al. (2016), comes from theoretical evolutionary genetics models of adaptive peaks (Arnold et al., 2001; Lande, 1976; Simpson, 1944).

Each trait value is further modified by a neutral genetic drift event. The genetic drift term is randomly chosen from a normal distribution with mean 0 and standard deviation  $\sqrt{h^2 v / N}$ , where  $h^2$  is heritability,  $v$  is phenotypic variance, and  $N$  is population size. This standard deviation derives from Lande (1976). The genetic drift value is added to  $z_{new}$ .

### *Genetic flow*

Each patch can only support one turtle of each species. After dispersal, if two or more populations of the same species occupy the same patch, gene flow between populations occurs. The amalgamated population takes on the mean of the populations occupying the patch and the local population size is reset to 100.

### *Speciation*

Speciation via a simplified peripheral isolation model occurs at time-steps 0, 100, 200, and 300 (Polly et al., 2016). Every species undergoes the same speciation process. First, the most peripheral turtle of each species is determined. The mean x-coordinate ( $x_{mean}$ ) and mean y-coordinate ( $y_{mean}$ ) of all turtles of species  $k$  represent the geographic center of the species range. The population located farthest from the center (determined by Euclidean distance) becomes the founder of a new species on the same patch. The “child” population is identical to the “parent.” The four speciation events will result in a maximum of 16 species at the end of the run.

Species are named systematically. The progenitor population is designated species 1. The first speciation event creates species 2. For future speciation events, the “child” population is named species  $(2x + 1)$ , where  $x$  is the current species name. The “parent” population is designated species  $(2x + 2)$ . For example, at 100 time-steps, species 1 produces species 3. All populations of species 1 are relabeled as species 4.

### *Tracking variables*

Utilizing NetLogo’s BehaviorSpace tool, relevant population-related variables were recorded during each time-step. For the aggregate of all populations on the continent, the mean trait value and standard deviation of trait value were recorded. On the species level, the number of populations, mean trait value and standard deviation of trait value were recorded. The number of existing species was also tracked.

For each patch, the average trait value of all species, trait value of individual species, and species richness (number of occupant species) were also reported during each time step. A species was considered to have colonized a region if 5 patches of the region were occupied by run’s end.

### *Barriers to dispersal*

Barriers to dispersal in our model are emergent properties from the interaction of environmental parameters, selection intensity, extirpation risk, and dispersal rate. A population can disperse into any adjacent grid cell regardless of the parameters, but if the trait optimum is substantially different in the new location there is a high probability of immediate extirpation because of low fitness. While the mountains are not modeled as physical barriers, they produce environmental barriers because of their rain shadow, grit cloud, and temperature gradient (which

along with precipitation determines vegetation biome). If extirpation scaling factor is low or if adaptive peak width is high (i.e., weak selection) an environmental gradient will pose less of a barrier because a poorly adapted population can still survive. Because extirpation is modeled as a probability rather than a certainty, even a step environmental gradient can be breached by chance if the dispersal rate is high enough. Rate of dispersal affects the likelihood of eventual success because it determines the number of times a population ventures into a cell where it has low fitness. The only impassible physical barriers are the oceans at the continental margins.

## **Climate change modeling**

### *Climate change mechanics*

We modeled three scenarios of climate change (gradual, moderate, and rapid) by altering annual precipitation, which influences biome type as well as the local selective optimum. At predetermined time steps, all patches decrease precipitation levels by a preset amount. All model runs, regardless of the rate of climate change, begin and end with all patches on Hesperia having the same environment. Each model starts with high precipitation such that most Hesperian patches possess forest biomes, with few tundra patches at high elevations. By the end of the model, precipitation across all patches decreases by 200 cm and most patches have changed to desert. In the gradual climate change scenario, precipitation decreases 5.13 cm every ten steps, in the moderate scenario it decreases 28.57 cm of the total change every 50 steps, and in the rapid scenario the precipitation decreases 100 cm twice during the run. Minimum precipitation is floored at 0 cm per year. During climate change events, each patch's biome type is reclassified using the previously described method. Then, the ideal trait value of each patch is also recalculated.

## **Experiments**

We conducted four experiments varying demographic parameters, each repeated across three different climate change scenarios. Experiment A varied dispersal with consistently high extirpation (DISP varies between 0 and 1.0, APW = 1.0, ESF = 2.0). Experiment B varied dispersal under consistently low extirpation (DISP varies between 0 and 1.0, APW = 1.0, ESF = 1.0). Experiment C varied ESF under high dispersal (ESF varies between 0 and 2.0, APW = 1.0, and DISP = 1.0). Experiment D varied APW under high ESF and high dispersal (APW varies between 0 and 3.0, ESF = 2.0, DISP = 1.0). An alteration of Experiment D varied APW under low ESF and high dispersal (APW varies between 0 and 3.0, ESF = 1.0, DISP = 1.0). See **Extended Results & Figure 3** for selected model output and **Files S3** for detailed results on each model run.