

Supplementary material part 1

Information use during movement regulates how fragmentation and loss of habitat affect body size

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This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models [1,2].

1. Purpose

Our goal is to study the effect of habitat configuration on the body size distribution of a population or community of arthropods. As the level of information perceived during movement is crucial for movement and therefore body size evolution, we also investigate a possible interaction with this trait.

By applying an individual-based approach, we were able to include intra-specific size variation and stochasticity within our model. This approach in conjunction with the assumption of asexual reproduction and equivalent ontogenetic and interspecific scaling exponents [3,4], implies that our results can be interpreted both at the metapopulation and metacommunity level.

2. Entities, state variables, and scales

The consumer

The consumer species is individually modeled and has the following state variables:

- W (kg): referring to the current mass of an individual.

- W_0 (kg): the egg mass of an individual

- W_{max} (kg): referring to an individual's maximum adult mass.

- t_d (days): referring to the developmental age of an individual.

- E_r (Joule): each individual has an energy reservoir in which assimilated energy is stored which can be invested in growth, reproduction, movement or the cost of basal metabolic rate.

-Developmental stage: A distinction is made between juvenile and adult consumers. Juveniles invest their assimilated energy in growth, whereas, adults invest their assimilated energy in reproduction.

-Type of movement: As the interaction with movement type is investigated we define three different movement types (informed, partially informed or uninformed). The level of informed movement regulates the settlement behavior of an individual and not departure.

-x and y coordinate

The landscape

The configuration of the landscape is defined by two state variables:

- P : The amount of suitable cells within the landscape

- H : The level of spatial autocorrelation

The landscape is cellular consisting out of several grid cells.

A grid cell

The resource species is not individually modeled, instead, resource amounts are defined per cell.

Per cell, the following state variables are defined:

-Suitability: Whether or not a cell is suitable for the resource to grow.

- $R_{x,y}$ (Joule): Per cell a resource amount is defined in Joule.

- K (Joule): Carrying capacity of the resource (Joule).

- r : Growth speed of the resource (Joule).

- Enc (Joule): amount of resource present per cell which is non consumable by the consumer.

-A list of consumers present in a particular cell

- p : probability of moving of the consumer is calculated per time step per cell

- x and y coordinate

Scales

The landscape is a cellular grid of 100 by 100 cells and is generated using the Python package NLMpy [5]. Each cell has a dimension of 0.25×0.25m. One time step corresponds to one day. Total runtime differs between simulations and varies from 2400 to 20000 time steps (days). (See supplementary material part 3 for an overview of the exact runtime per simulation.)

3. Process overview and scheduling

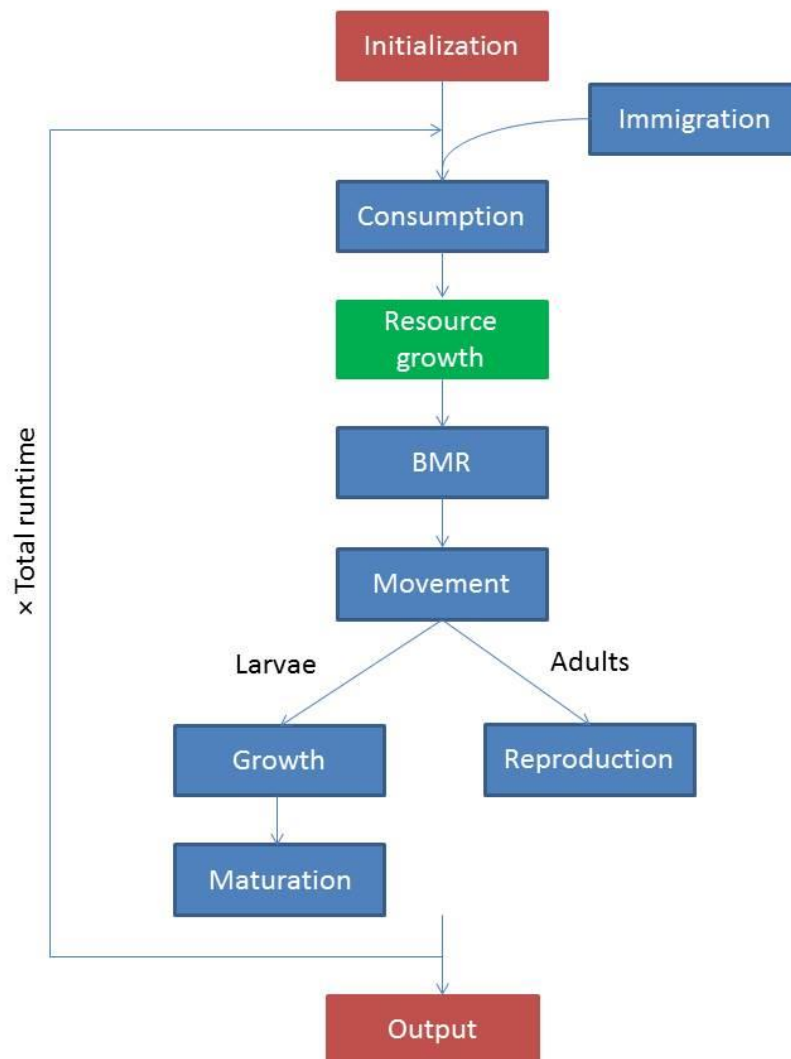


Figure 1: This figure depicts an overview of all events within the model. BMR stands for the basal metabolic rate costs. Initialization and output generation are regulated at the level of the model. Blue boxes do represent events of the consumer and the green box represents the event regulating resource growth.

The applied model is a spatially explicit, discrete-time model with overlapping generations. One time step corresponds to one day within the lifetime of the consumer. We here took an arthropod-centered approach and parameterized allometric rules for a haploid, parthenogenetic arthropod species feeding on plants (the resource), with a semelparous lifecycle.

In case immigration is allowed (according to immigration rate q), an immigrant is initialized within the landscape at the start of a day.

Next, an individual nourishes its energy reserve by consumption. Second, the energy reserve is depleted by the cost of daily maintenance (i.e. basal metabolic rate) and the cost of movement. To assess the effect of informed settlement on our results, three different types of movement (see below) were implemented within the model. Third, juveniles may further deplete the energy reserve by growth, eventually resulting in maturation if they approximate their adult mass (W_{max}). Consumed energy that was not expended during a day remains in the energy reserve. Adults can only reproduce if their internally stored energy (E_r) exceeds a predefined amount. As the consumer species is semelparous, adults die after reproduction.

During growth, an individual's mass is updated. When moving, an individual's x and y coordinate change. If maturation is allowed, a larva becomes an adult (updating an individual's developmental stage). Resource quantities per cell decrease during consumption but replenish during resource growth.

All events are executed simultaneously by all consumers. As competition for resources is scramble, the order at which individuals consume does not affect the outcome.

During a simulation, summarizing output variables are collected, which are written out at the end of a simulation.

4. Design concepts

Basic principles:

An organism's body size is one of its most comprehensive characteristics. As described by the metabolic theory of ecology, body size is strongly correlated with an array of functional traits [6,7]. Based on this theory, we linked many individual traits to body size (e.g. basal metabolic rate, movement speed, ingestion rate, clutch size, developmental time). It is crucial to include these allometric rules within the model as body size represents the outcome of several selective pressures acting on different life history traits, setting boundaries to the ecology, physiology and functioning of an individual [6].

As habitat fragmentation and destruction progress, the spatial distribution of resources is altered. The importance of resource distribution for body size distributions is advocated by the 'textural discontinuity hypothesis' of Holling. We test this hypothesis by investigating the effect of habitat configuration and destruction on body size distributions. Moreover, not only resource availability, but also the type of movement regulate how populations and communities are spatially structured [8]. Therefore, we try to detect the effect of movement ecology in our study by implementing three levels of informed movement [9]. Type of movement (three types) and landscape type (seven types) are fixed per simulation. Therefore, 21 different simulation types exist in total.

Finally, the results of our model show the importance of including allometric rules when investigating

community responses to habitat fragmentation and destruction. Moreover, a possible interaction with level of informed movement is investigated.

Emergence:

As habitat fragmentation and destruction progress, the spatial distribution of resources is altered, yet the consequences for (future) body size distributions are unclear. On the one hand, large-bodied individuals may be selected as they have high starvation resistance and are able to cover large distances [6,10,11]. On the other hand, small-sized individuals may have the benefit of short developmental times and low energy requirements [6]. Therefore, the most important output of the model are the observed differences in body mass distributions between simulation types (defined by habitat configuration and level of informed movement).

Body size distributions will consequently feedback on the overall food web dynamics (overall instability and resource distributions). These feedbacks are also investigated by collecting data of resource distribution and fluctuations in resource amount and consumer numbers.

Adaptation:

Body size is linked to many features of an individual. In this model, larger individuals move faster, develop longer, have larger clutch sizes, have larger basal metabolic rates, and have higher ingestion rates. These traits also change during the developmental phase of an individual, corresponding to its body mass.

Further, the energy invested in growth and movement depends on the energy available within an individual's energy reserve. As such, an individual will never die due to exhaustion by moving too far. Also, the available energy is invested in the events in the following order: (1) basal metabolic rate, (2) movement and (3) growth or reproduction. As such, an individual's priority is investing energy in basal metabolic rate cost. Secondly, it will try to guarantee access to resources the following day by moving. Thirdly, it will invest remaining energy in growth or reproduction if some energy is left. Energy for reproduction is collected during several days as only one clutch is produced during the lifetime of an individual.

Probability of moving (p) decreases with resource availability in a cell but also increases with the sum of the ingestion rates of all individuals within that cell. As such, individuals have higher chances of moving when a lot or large conspecifics are present and resources are scarce. The settlement rule differs between simulations (informed, partially informed or uninformed).

Objectives:

The short term objective of an individual, is to consume resources. The long term objective, however, is to produce a clutch of individuals. Those individuals which have the most optimal body size, are selected and as such most abundant within the community or population.

Sensing:

When present within a cell, an individual may sense the amount of resources present and also estimate the total consumption pressure within that cell. Based on this information it decides whether it will start moving or not. When moving, however, the level of information perceived during settlement differs between simulations.

Informed movement: an individual can sense the exact amount of resources within a cell.

Partially informed movement: an individual can differentiate a suitable from an unsuitable habitat cell.

Uninformed movement: an individual can not differentiate between cells.

Interaction:

Interactions between individuals are always indirect. During consumption, competition for resources is scramble. Also, the number and size of consumers present within a cell are taken in account when calculating the probability of moving for individuals within that cell.

Stochasticity:

Stochasticity is included when defining which individuals will move from a particular cell. Also, stochasticity regulates the mutation events of the allele describing the maximum mass of an individual.

In the case of uninformed movement, an individual's cell of destination is randomly sampled out of its' searching area. In case of partially informed movement, the cell of destination is randomly selected out of all suitable cells within an individual's searching area. When movement is informed and multiple cells exist with the maximum amount of resources within an individual's searching area, stochasticity is also implemented.

Collectives:

Between consumer individuals, a distinction is made between juveniles and adults. Juveniles invest their energy in growth, whereas, adults invest their energy in reproduction.

Observation:

During each simulation, we traced changes in the mean amount of resources per cell, total number of adults and juveniles, average adult mass (W_{max}) and the coefficient of variation, skewness, and kurtosis of the consumer's adult mass (W_{max}) distribution. Every 500 time steps, the value of W_{max} of maximum 50 000 randomly sampled individuals was collected.

Variability

In order to infer the temporal stability of the community at different scales we calculated the α , β_2 and γ variability for each simulation run. This calculation is based on samples of total consumer biomass every 10 time steps during the final 100 time steps of a simulation within 100 pre-selected, suitable cells. α variability is a measure of the local temporal variability and is calculated by

$$\alpha_{CV} = \left(\frac{\sum_m \sqrt{w_m}}{\sum_m \mu_m} \right)^2 \text{ (eq. 1)}$$

with w_m referring to the temporal variance and μ_m to the temporal mean of population or community consumer biomass in cell m [12]. The temporal variability at the metapopulation or metacommunity scale or γ variability was calculated by:

$$\gamma_{CV} = \frac{\sum_{m,n} w_{mn}}{(\sum_m \mu_m)^2} \text{ (eq. 2).}$$

with w_{mn} referring to the temporal covariance of population or community biomass between cells m and n [12]. Finally, β_2 variability or asynchrony-related spatial variability was determined by:

$$\beta_2 = \alpha_{CV} - \gamma_{CV} \text{ (eq. 3).}$$

Reproductive success and movement

Throughout the final 600 days of a simulation, 1000 eggs were randomly selected to be followed during their lifetime. The movements and reproductive success of the resulting consumer individuals were recorded.

5. Initialization

Per parameter combination, 10 simulations were run. At the start of a simulation, adult individuals were introduced with an average density of two individuals per suitable cell. The adult mass of each individual (W_{max}) was defined as ten raised to the power of a value drawn from the uniform interval $[-5, -2.522878745]$. In other words, we sample a value between 0.00001 kg (minimum adult mass) and 0.003 kg (maximum adult mass). As such, individuals with masses of different orders of magnitude have an equal chance of being initialized in the landscape. Moreover, initialized distributions are skewed to small individuals. Also, each initialized individual carried enough energy within its energy reserve to survive the first day. This amount of energy is calculated based on an individual's mass and accounts for the cost of basal metabolic rate and movement during one day. Initial resource availability per cell corresponded to the maximum carrying capacity. Because of computational limitations, total runtime differed between simulations. For an overview, see supplementary material part 2.

6. Submodels

The resource

Resources are not individually modeled but by a logistic growth model for each habitat cell. Local resource biomass is represented as the total energetic content of resource tissue within that cell ($R_{x,y}$ in Joules). This resource availability grows logistically in time depending on the resource's carrying capacity (K) and intrinsic growth rate (r). In any cell, a fixed amount of resource tissue (E_{nc} , in Joules, fixed at 1 J) is non-consumable by the consumer species, representing below-ground plant parts. As such, E_{nc} is the minimum amount of resource tissue present within a suitable cell, even following local depletion by the consumer species.

The consumer

Individual body mass at maturity (W_{max} , in kg) is coded by a single gene. Adult mass is heritable and may mutate with a probability of 0.001 during reproduction. This mutation rate is commonly applied within theoretical models [13,14]. A new mutation is drawn from the uniform distribution $[W_{max} - (W_{max}/2), W_{max} + (W_{max}/2)]$ with W_{max} referring to the adult mass of the parent. New mutations may not exceed the predefined boundaries [0.01g, 3g] that represent absolute physiological limits. As such, our minimum adult mass corresponds to the mass of a small grasshopper such as *Tetrix undulata* (0.01 g) and the maximum mass (3 g) to that of some longhorn beetles (Cerambycidae), darkling beetles (Tenebrionidae), scarab beetles (Scarabaeidae) or grasshoppers (Acrididae). New variants of

this trait may also originate by immigration (see below). Mutation enables fine-tuning of the optimal body size, whereas immigration facilitates fitness peak shifts.

Immigration

The frequency with which immigrants arrive in the landscape is described by q . This variable is fixed at one per 100 days. The process of determining an immigrant's adult mass is similar as during initialization (see above). An immigrant is always introduced within a suitable cell and its energy reserve contains just enough energy to cover the cost of basal metabolic rate and movement during the first day.

Consumption

Individual ingestion rate (IR , in Watts) of an individual increases with its mass (W , in kg) by the following equation:

$$IR = 2 * W^{0.80} \text{ (eq. 4)}$$

Following log transformation, the slope (0.80) was found by Peters (1983) to be the mean of several studies focusing on ingestion rates of poikilotherms [6]. The intercept of this equation lays within the observed range of elevations [0.12 to 2] of these studies [6].

Based on eq. 4, the amount of energy ingested per day for an individual (i_{max} in Joules) is determined as

$$i_{max} = 2 * W^{0.80} * t_f \text{ (eq. 5)}$$

with t_f referring to the time devoted per day to consumption (in seconds), which is fixed at 15 hours. Individuals compete for resources by means of scramble competition according to the following equation:

$$E_c = i_{max} \quad \text{if } \sum i_{max_{x,y}} \leq R_{x,y} \text{ (eq. 6)}$$

$$E_c = R_{x,y} * \frac{i_{max}}{\sum i_{max_{x,y}}} \text{ if } \sum i_{max_{x,y}} > R_{x,y}$$

with E_c being the energy consumed by an individual, $R_{x,y}$ the total amount of energy available within cell _{x,y} and $\sum i_{max_{x,y}}$ the sum of the ingestion rates of all individuals present within cell _{x,y} . However, when we consider that the consumer feeds on young terrestrial foliage, it may only assimilate 65 percent of its daily ingested energy [6,15]. Moreover, we assume that the consumer loses 10 percent of its ingested energy to processing costs (i.e. specific dynamic action) [15]. As such, only 55 percent

of the ingested energy remains available to the organism. Therefore, the energy that is being assimilated by an individual (E_a in Joules) is described by

$$E_a = 0.55 \cdot E_c \text{ (eq. 7)}$$

Basal metabolic rate

The standard metabolic rate of poikilotherms (M , in watts) is described by

$$M = 0.14W^{0.751} \text{ (eq. 8)}$$

with W being body mass (in kg) [6:16]. As such, the total standard metabolic rate costs per day (M_{day}) are calculated according to

$$M_{day} = 0.14W^{0.751} * (3600 * 24 - t_m) \text{ (eq. 9)}$$

If an individual has stored less energy within its reserve (E_r) than M_{day} , it dies at the beginning of the day. The standard metabolic rate exhibited during movement is already included within the cost of movement [6]. Therefore, the cost of daily existence is only calculated based on the time that an individual is not moving per day. The time an individual moves per day (t_m , in seconds) varies between individuals and over time (see below).

The movement phase

Probability of moving (p)

Whether an individual moves depends on the ratio of the amount of energy present within a cell ($R_{x,y}$) relative to the maximum amount of energy that can be consumed by all consumers present within that cell. This latter factor is determined by calculating the sum of all individuals' daily ingestion rates within that cell ($\sum i_{max_{x,y}}$).

By assuming a symmetric competition, the probability of moving (p) is equal for all individuals present within the same cell and is calculated by (based on [17]) :

$$p = 1 - \frac{R_{x,y}}{\sum i_{max_{x,y}}} \text{ if } \frac{R_{x,y}}{\sum i_{max_{x,y}}} < 1 \text{ (eq. 10)}$$

$$p = 0 \quad \text{if } \frac{R_{x,y}}{\sum i_{max_{x,y}}} \geq 1$$

Defining searching area

As one time step in our model corresponds to one day, we do not model the movement behavior of an individual explicitly but instead, estimate the total area an individual can search for resources

during a day. This area is called an individual's searching area is calculated once per time step, for each moving individual. As all cells within a particular distance from the origin are equally intensively searched, the searching area is circular with a radius (rad) and a center corresponding to the current location of an individual [18]. An individual's searching area increases with an individual's optimal speed (v_{opt}), movement time (t_m) and perceptual range (d_{per}). Both optimal speed and perceptual range depend on body mass, resulting in larger searching areas for larger individuals. The cost of movement includes the energy invested by an individual in prospecting its total searching area. Therefore, it is dependent on the size of the total searching area instead of the shortest distance between the cell of origin and cell of destination.

An individual's average speed of movement (v_{opt} , in meters per second) is calculated by means of the following allometric equation, derived for walking insects [6:19]:

$$v_{opt} = 0.3 \cdot W^{0.29} \text{ (eq. 11).}$$

With W referring to the mass of an individual in kg, while ignoring the mass of stored resources. The time an individual invests in movement per day (t_m , in seconds) is maximally 1 hour. In case too little internally stored energy (E_r) is present to support movement for one hour, t_m is calculated by:

$$t_m = \frac{E_r}{c_m} \text{ (eq. 12).}$$

c_m refers to the energetic cost of movement (in joules per second) and is calculated by the following formula, which is based on running poikilotherms [6:19]:

$$c_m = (0.17W^{0.75} + 3.4W) \text{ (eq. 13).}$$

The cost of moving during the time t_m ($t_m \cdot c_m$) is subtracted from an individual's energy reserve. Based on t_m and v_{opt} , the total distance an individual covers at day t (d_{max}) is determined:

$$d_{max} = v_{opt} \cdot t_m \text{ (eq. 14)}$$

Next, the perceptual range of an individual is determined by means of the following relationship:

$$d_{per} = 301W + 0.097 \text{ (eq. 15)}$$

For simplicity, this relationship is linear and based on the assumption that the smallest individual (0.01g) has a perceptual range of 0.10 m and the largest individual (3g) a perceptual range of 1m. The effect of this relationship has been tested (see supplementary material part 3). Moreover, the positive relationship between body size and perceptual range or reaction distance has been illustrated over a wide range of taxa, including arthropods (supplementary information of [20]).

The searching area of an individual is circular and its radius (rad , in m) is calculated by taking into account the total distance the individual has covered during the day and the individual's perceptual range (see supplementary material part 4 for an explanation of the formula calculating rad):

$$rad = \sqrt{\frac{2 \cdot d_{max} \cdot d_{per} + \pi \cdot d_{per}^2}{\pi}} \text{ (eq. 16).}$$

In order to avoid side-effects of applying the variable rad for a continuous landscape within a cellular landscape, a value drawn from the following distribution, $[-0.5 \cdot SL, 0.5 \cdot SL]$, is added to rad .

Habitat Choice

The selection process for finding a new location within this searching area depends on the selective ability of the individual. Here, we make a distinction between three types of selection procedures during movement.

Case 1- Uninformed movement

Within this scenario, movement is completely uninformed. As such, no distinction can be made between matrix and habitat. Within the searching area, the new location is randomly sampled.

Case 2- Partially informed movement

Here, an individual is able to distinguish matrix from habitat and will always prefer the latter above the former. An individual will sample its location randomly from the suitable cells within its searching area.

Case 3- Informed movement

Here, an individual moves to the cell with the highest amount of resources within its searching area.

Growth

The applied growth model is the one described by West et al. (2001) [4] for deterministic growth

$$W = W_{max} \times \left\{ 1 - \left[1 - \left(\frac{W_0}{W_{max}} \right)^{1/4} \right] e^{-at_d/4W_{max}^{1/4}} \right\}^4 \text{ (eq. 17).}$$

Within this formula, W refers to an individual's actual mass (in kg) at developmental age t_d (in days), W_{max} to an individual's genetically inherited adult mass (in kg), W_0 to an individual's egg mass (in kg) and a to a species specific constant. Here, a was fixed at 0.2 which is a realistic value for species with deterministic growth [4]. When applying the formula, W_{t_d} , W_{max} and W_0 are converted to gram. According to West et al. (2001) [4] the proportion of available energy that is devoted to growth (A) is described by

$$A = 1 - \left(\frac{W}{W_{max}} \right)^{0.25} \text{ (eq. 18).}$$

In ideal conditions, an individual's total amount of assimilated energy during one day (E_a) should correspond to $0.55 \cdot i_{max}$. Here, we assume that an individual will only increase its developmental age by one day if $A \cdot 0.55 \cdot i_{max}$ Joules is still available within its energy reserve. Otherwise, its developmental age is not increased by one but by $E_r / (A \cdot 0.55 \cdot i_{max})$ with E_r being the energetic content of an individual's energy reserve. This value is larger than or equal to 0 and smaller than 1.

This implies that individuals experiencing a shortage in energy will grow at a slower rate than individuals developing under ideal conditions.

Maturation

Juveniles reaching 99 percent of their adult mass (W_{max}) mature.

Reproduction

During reproduction, the relationship between total clutch size (CS , in kg) and mass (W , in kg) is determined by the following equation which is based on aquatic poikilotherms [21]

$$CS = 0.158W^{0.92} \text{ (eq. 19).}$$

However, an adult is only allowed to produce a clutch of this size if it has collected enough energy within its energy reserve and when it is located within a suitable patch. The entire clutch is deposited within that single patch, simultaneously. The required energy to produce such a clutch is calculated by

$$E_{CS} = CS \cdot 7 \cdot 10^6 \frac{J}{kg} + N \cdot E_i \text{ (eq. 20).}$$

Here, 1 kg of wet tissue is considered to have an energetic content of $7 \cdot 10^6$ Joules [6]. For simplicity, the number of eggs per clutch (N) is assumed to be fixed at 15. Further, each newly laid egg is provisioned with the necessary energy to survive its first day (E_i , in Joules). The mass of a newly laid egg (W_0 , in kg) is calculated as follows:

$$W_0 = \frac{CS}{N} \text{ (eq. 21).}$$

Also, we guarantee that the adult size of an individual is never smaller than the size it obtained during the egg stage (i.e. $W_0 \leq W$). Such contradictions might occur as the egg size of an individual depends on the adult size of its parent, not on its own adult size.

Table S1.1: Overview and definition of all parameters. In case a parameter is fixed, this value is given. In case a parameter depends on an individual's size, the corresponding allometric rule is given.

Parameter	Unit	Definition	Fixed value or equation
P	-	Amount of suitable habitat within the landscape	0.90, 0.50, 0.20, 0.05
H	-	Spatial autocorrelation	1, 0.5, 0

t	day	Time since the start of the simulation	
$R_{x,y}$	Joule	Total energetic content of resource tissue present within cell _{x,y}	
K	Joule	Carrying capacity of resource per cell	2000 Joules
r		Growth speed of the resource	0.5
E_{nc}	Joule	Fixed amount of non-consumable resource energy per cell	1 Joule
W_{max}	Kg	Adult size of an individual	
W	Kg	Current mass of an individual, depending on its developmental age t_d	eq. 17
W_0	Kg	Egg mass of an individual	eq. 21
IR	J/s	Ingestion rate of an individual with mass W	eq. 4
i_{max}	Joule	An individual's maximum ingestible amount of energy at time t	eq. 5
t_f	seconds	Time devoted per day to consumption	15 hours
E_c	Joule	Energy being consumed by an individual at time t	eq. 6
E_a	Joule	Energy being assimilated by an individual at time t	eq. 7
M	J/s	The standard metabolic rate of an individual with size W	eq. 8
M_{day}	J	Total standard metabolic rate costs for an individual at time t	eq. 9
t_m	seconds	Time devoted to movement at time t	eq. 12
p	-	Probability of moving at time t	eq. 10
v_{opt}	m/s	Average speed of movement for individual with size W	eq. 11
d_{max}	meter	Maximum distance an individual can cover at time t	eq. 14
d_{per}	meter	Perceptual range of an individual	eq. 15
rad	meter	Radius of searching area at time t	eq. 16
c_m	Joule	Cost of movement at time t	eq. 13
q	1/day	Immigration rate	1 per 100 days
a	-	Species specific constant within formula of West et al. (2001)[4]	0.2
t_d	day	An individual's developmental age	
A	-	Proportion of available energy being devoted to growth at time t	eq. 18
E_r	Joule	Energy available within energy reservoir at time t	

CS	Kg	Total clutch size of an individual with size W	eq. 19
E_{CS}	Joule	Required energy to produce a clutch of size CS	eq. 20
N	-	Number of eggs within one clutch	15
SL	m	Side length of a cell within the landscape	0.25

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