EcoSim, an enhanced artificial ecosystem: addressing deeper behavioral, ecological, and evolutionary questions

ODD Description of EcoSim

EcoSim is an individual-based ecosystem simulation (Gras *et al.* 2009; Mashayekhi *et al.* 2014.b) to simulate animals’ behaviors in a dynamic, evolving ecosystem. The individuals of EcoSim are prey and predators acting in a simulated environment. A description of the older version of EcoSim can be found in (Mashayekhi *et al.* 2014.a, 2014.b). In addition to the main features outlined above, EcoSim has been expanded by adding several smaller features such as: new individuals' perceptions of their environment, new actions, new physical traits (governed by what we call the physical genome), sex-linked genes, various modes of reproduction, modified acting priority for individuals, new ways to control the dynamics of the environment, and new crossover and mutation operations that consider an individual’s sex. Below, we describe the new version of EcoSim following the updated 7-points Overview, Design concepts, and Details (ODD) standard protocol (Grimm *et al.* 2006; Grimm *et al.* 2010). EcoSim source code (in C++) can be obtained from the repositories at https://github.com/EcoSimIBM, and more information on EcoSim can be found at https://sites.google.com/site/ecosimgroup/home.

Purpose

EcoSim was designed to simulate animal behavior in a dynamic and evolving ecosystem. The main purpose of EcoSim is to study biological, ecological, and evolutionary theories by constructing a complex adaptive system that leads to a generic virtual ecosystem with behaviors like those found in nature. Due to the complexity, scale, and resource requirement of studying these theories in real biological systems, simulations of this nature are necessary. EcoSim uses a fuzzy cognitive map (FCM; Kosko 1986) to model an individual's behavior. Since the FCM is coded in the genome and heritable, behavior can evolve during the simulation. Importantly, the fitness of a given set of behaviours and physical traits is not pre-defined. Instead, fitness emerges from interactions between the model organisms and their biotic and abiotic environment.

Entities, state variables, and scales

Individuals

EcoSim has two types of individuals: prey and predators. Each individual possesses two types of traits: acquired and inherited traits (Table 1). The former varies depending on the environmental conditions and the latter is encoded in an individual’s genome and is fixed during its lifetime. The age and speed are initialized to zero for new born individuals while energy, a crucial property of the individual, is initialized based on the amount of energy invested into a newborn by its parents at reproduction time (*State of Birth* or *SOB* – see *Reproducing* under *Submodels*). Afterward, energy is provided to the individuals by resources (food) they find in their environment. Prey consume grass, which is dynamic in quantity and location (see *Submodels* for grass diffusion model), whereas predators hunt for prey individuals or scavenge their remains when they die. *Strength* of an individual is calculated based on its current energy (*Energy*), maximum energy (*MaxEnergy*), age (*Age*), maximum age (*MaxAge*) and reproductive age (*RepAge*) of the individual. Young (*Age* is less than *RepAge*) and old individuals (*Age* is greater than or equal to *MaxAge* minus *RepAge*) have less *Strength*. *Strength* can range from 25% of an individual’s *MaxEnergy* (if the individual is too young or old and has energy approaching zero) to 100% of the individual’s *MaxEnergy* (if the individual has energy greater than or equal to 1/3 of its *MaxEnergy* and the individual is not too young or old).

**Table 1.** Several physical and life history characteristics of individuals from five independent runs. The values for the inherited features are the values at initialization, and for the acquired features they are the average values over 20000 time steps.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Type | Characteristic | Male Predator | Female Predator | Male Prey | Female Prey |
| Inherited | Maximum Energy | 3000 | 3000 | 2500 | 2500 |
| Maximum Age | 50 | 50 | 46 | 46 |
| Vision | 20 | 20 | 8 | 8 |
| Maximum Speed | 20 | 20 | 6 | 6 |
| Minimum Age  of Reproduction | 5 | 5 | 6 | 6 |
| State of Birth | 14 | 18 | 12 | 16 |
| Defense | N/A | N/A | 0.05 | 0.05 |
| Cooperative Defense | N/A | N/A | 0.05 | 0.05 |
| Acquired | Average Energy | 2312.2 | 2211.4 | 1664.9 | 1678.3 |
| Average Age | 16.5 | 13.7 | 14.3 | 12.3 |
| Average Speed | 3.4 | 2.9 | 6.5 | 6.0 |
| Average Strength | 3306.3 | 3107.9 | 2478.9 | 2439.7 |

Each individual performs one unique action during a time step, based on its perception of the environment and state (see *Emergence* under *Design Concepts*). At each time step, each individual spends energy depending on its selected action (*e.g.* reproduction, eating, moving), the complexity of its behavioral model (number of existing edges in its FCM – see *Adaptation* under *Design Concepts* for details), and its physical characteristics (encoded in its physical genome – see *Adaptation* under *Design Concepts* for details). To achieve a realistic rate of energy expenditure we involved as many of its contributory factors as possible and used empirically-determined physiological scaling rates (see Eq. 1, per time step energy penalty for prey, and Eq. 2, per time step energy penalty for predators). In general, any action performed by a living organism is involved in spending some amount of energy (Butler *et al.* 2004) dependent on what the action is (Blaxter 1989). Thus, the action performed was included as a contributing factor in energy expenditure (Eqs. 1 and 2). Moreover, the size of a living organism plays a fundamental role in its metabolic rate (Chapman and Reiss 1999). In EcoSim, the size of each individual is modeled through its *MaxEnergy* and *Strength*. *MaxEnergy* is a heritable limit on an individual’s capacity to store energy whereas *Strength* is a slightly more complex proxy of size, being derived from an individual’s *MaxEnergy*, *Energy*, and *Age*. Experimental and empirical investigations have demonstrated that there is a nonlinear relationship between adult animal body mass and their metabolic rate, which is best described by a ¾ scaling exponent (Kleiber 1932; Hemmingsen 1960; Kleiber 1961; Stahl 1965; Stahl 1967; Pedley 1977; Prothero 1979; Schmidt-Nielsen 1984; Peters 1986; Niklas and Enquist 2001). Consequently, the metabolic rate of an individual in EcoSim is quantified through a power function of coefficient ¾ on its *MaxEnergy* (Eqs. 1 and 2). Energy expenditure associated with movement is also modeled in EcoSim using the kinetic energy equation (KE) and here we use *Strength* as a proxy of mass (KE = mass speed2, Eqs. 1 and 2). The complexity of an organism's behavioral model increases an individual’s energy expenditure because it has been accepted that species belonging to a higher-level taxonomic affiliation require more energy to survive (Mueller and Diamond 2001; Nagy 2005). Individuals with a larger brain also require more energy as the brain is an expensive organ in terms of specific chemical and thermoregulatory needs (Wheeler 1984; Falk 1990). Consequently, possessing a large brain leads to a heavier metabolic requirement (Safi *et al.* 2005). The complexity and the size of the brain vary in different species; while some species possess a very simple and small brain, many higher vertebrates have a brain so large and complex that it is considered as the most complex organ in these species (Shepherd 1994). Therefore, we also include this parameter in calculating individual’s energy spent. Taking these points into consideration, energy spent by prey (1) and predators (2) at any time step is given by the following equations:

(1)

(2)

Where *NbArcs* is a measure of the complexity of the individual’s brain based on the number of edges in its FCM (see *Adaptation* under *Design Concepts* for details), *Vision* refers to the distance up to which the individuals can see (which is initially 8 cells for prey and 25 cells for predator), *Defense* quantifies the ability of the prey individuals to protect themselves when they are attacked by predators, *CoopDefense* quantifies the ability of a prey individual to protect other prey in its cell, and *RepAge* is the age at which the individuals can start reproducing.

All individuals first perceive their environment (all the surrounding cells in their vision range) before using their behavioral model to choose a single action (see *Emergence* under *Design Concepts* for details of how individuals choose actions). After perceiving its environment (including grass resources, prey, predators, *etc.*), the possible actions for a prey individual are: evade (escape from predator), search for food (if there is not enough grass available in its cell, prey can move to another cell to find grass), socialize (moving to the closest prey in the vicinity, moving to the cell with strongest prey, moving to the cell with the greatest total prey strength, and moving to a cell with the least total prey strength), explore, rest (to save energy), eat, and reproduce. Predators also perceive their environment to gather information used to choose an action among: hunt (to catch and eat a prey), move to the cell with strongest prey, move to the cell with the least total prey strength, move to the cell with the weakest prey, searching for food, socialize (moving to the closest predator in the vicinity, moving to the cell with strongest predator), explore, rest, eat, and reproduce. See the *Submodels* section for a full description of actions. Every individual takes one action per time step then its energy level and its strength are adjusted. The age of all individuals is also increased by one unit at each time step. In addition to the acquired physical traits mentioned above, each individual has many state variables that, together, represent its state of mind. These variables are the values held in the nodes of each individual’s FCM. Each FCM node has a single value which is its activation level (degree of stimulation) of its represented concept. Concepts are either be sensory, such as the individual’s perception of local food, internal, such as the individual’s hunger, or action, such as the individual’s willingness to perform the eat action (see *Emergence*, *Adaptation*, and *Submodels* for more information).

Time step

Each time step involves each individual perceiving its environment, making a decision, and performing one action. In addition, species memberships are updated and all relevant variables (*e.g.*, quantity of available grass) are recorded (see *Process Overview and Scheduling* for algorithm).

Cells and virtual world

The smallest units of the environment are cells. Each cell represents a large space which may contain an unlimited number of individuals, some limited amount of food, and some limited amount of fertilizer. The number of individuals a cell can host, therefore, is indirectly limited by the amount of food a cell contains. There are two types of food: grass, which only prey can eat, and meat, which only predators can eat. Grass amounts are controlled by a grass diffusion and growth model, and meat is generated when predators kill prey (see *Submodels* for grass diffusion model and meat generation). Fertilizer is produced by individuals residing in a cell (see *Submodels* for fertilizer dynamics). The virtual world consists of a matrix of 1000×1000 cells. The world is large enough such that an individual moving in the same direction during its whole life cannot even cross half of the world and thus high-level movement patterns can be observed. The virtual world wraps around to remove any spatial bias. In addition, the dimensions of the world are adjustable, but expanding the dimensions increases the computational complexity of the simulation.

Species

By default, numerous prey and predators coexist in the simulation at any time step. Alternatively, the simulation can be run without predators. For each type, there is some number of species determined by the genetic makeup of the sets of individuals. There is at least one prey species and one predator species unless an extinction occurs, and at most there can be one species per individual. A species is a set of individuals with sufficiently similar genomes (see *Collectives* under *Design Concepts* for more details about speciation).

Process Overview and Scheduling

At each time step, the value of the state variables of individuals and cells are updated. The overview and scheduling of every time step is as follows:

1. For prey individuals:
   1. Perceive environment
   2. Compute next action
   3. Increase *Age*
   4. Females that chose to *Reproduce* act in order of decreasing *Strength* (to simulate female choice in mate selection)
   5. Remaining prey act in order of decreasing *Strength*
   6. Update list of prey (as some may have died due to depletion of *Energy* or maximum *Age*)
2. For predator individuals:
   1. Perceive environment
   2. Compute next action
   3. Increase *Age*
   4. Females that chose to *Reproduce* act in order of decreasing *Strength* (to simulate female choice in mate selection)
   5. Remaining predators act in order of decreasing *Strength*
   6. Update list of predators and prey (for predators, some may have died due to depletion of *Energy*, maximum *Age*, or combat with prey; for prey, some may have died due to predation)
3. Sort prey in order of decreasing *Strength*
4. Sort predators in order of decreasing *Strength*
5. Update prey species
6. Update predator species
7. For every cell in the world
   1. Update *Fertilizer* level
   2. Update *Grass* level
   3. Update *Meat* level

The complexity of the simulation algorithm is mostly linear with respect to the number of individuals. If we consider that there are *N1* prey and *N2* predators and we exclude the sorting parts which have a complexity of *O(N1logN1)* and *O(N2logN2)* but are negligible in computational time, then the complexity of part 1 and part 2 of the above algorithm, including the clustering algorithm used for speciation, will be *O(N1)* and *O(N2)* respectively (Aspinall and Gras 2010). This virtual world of the simulation has 1000×1000 cells, therefore the complexity of part 3 will be *O*(*k* = 1000×1000). The complexity of part 4 will be *O(N1+N2)*. As a result, the overall complexity of the algorithm is *O(2N1+ 2N2+ k)*, which is *O(N = 2N1 +2N2)*. In terms of computational time, the speed of simulation per time step is related to the number of individuals. Recent executions of the simulation produced approximately 20000 time steps in 60 days.

Design concepts

Basic principles

The genome of each individual consists of two parts: a physical genome and a behavioral genome. An individual’s genome is fixed at birth. When a new offspring is created, it receives a genome that combines the genomes of its parents with some possible mutations. An individual’s physical genome determines its physical characteristics and its behavioral genome determines its behavioral characteristics. An individual’s physical genome comprises of values that represent its physical attributes (see Table 1, inherited traits).

The behavioral model of each individual is encoded as a FCM (Gras *et al.* 2009) (Figure 1). Formally, a FCM is a directed graph which contains a set of nodes *C* and a set of edges *I* (Figure 1; Kosko 1986). Each node *Ci* represents a concept and each edge *Iij*representing the influence of the concept *Ci* on the concept *Cj*. A positive weight associated with the edge *Iij* corresponds to an excitation of the concept *Cj*from the concept *Ci*, whereas a negative weight represents inhibition. A zero value indicates that there is no influence of *Ci* on *Cj*. The edges of an FCM can be represented by an *n*×*n* matrix, *L*, in which *n* is the number of concepts and *Lij* is the influence of the concept *Ci*on the concept *Cj*. If *Lij = 0*, there is no edge between *Ci* and *Cj*. An individual’s behavioral genome is its set of FCM edges – its matrix *L*. Since the edges of the FCM are encoded in the genome, the behavioral model is heritable, mutable, and subject to evolution. Individuals act at each time step by using their FCM to compute their action (see *Emergence*). The activation level (degree of stimulation) of each concept, represented as the value held in its corresponding node, is dynamic in each individual. Collectively, the activation levels of all of an individual’s nodes represent the individual’s behavioral state. In each FCM, three kinds of concepts are defined: sensory (such as distance to foe or food, amount of energy, *etc.*), internal (fear, hunger, curiosity, satisfaction, *etc.*), and action (evade, socialize, explore, reproduce, *etc.*). At each time step, the activation level of a sensory concept is computed by performing a fuzzification of the information the individual perceives in the environment (changing its real scalar value into a fuzzy value, *i.e.*, transforming the input value by a potentially nonlinear function). Subsequently, for an internal or action concept *C*, the activation level is computed from the weighted sum of the current activation level of all input nodes by applying a defuzzification function (another nonlinear function transforming the fuzzy input value into the final 'real' value).



**Fig. 1.** An example FCM of a predator (a) and prey (b). Red edges between nodes indicate negative association (inhibition) of a concept (where the edge begins) on another (when the edge points to), and blue edges indicate positive association (excitation). Thickness of the edges represents magnitude of the gene. The leftmost column of nodes are sensory concepts, the middle are internal concepts, and the rightmost are action concepts. There are many unconnected nodes because we aim to observe evolution in action; over time new edges may form and others may disappear.

We will illustrate the operation of the FCM with a simplified example prey FCM (Figure 2) consisting of only four nodes (*EnemyClose*, *EnemyFar*, *Fear*, and *Evade*). *EnemyClose* and *EnemyFar* are sensory concepts, whereas *Fear* is internal and *Evade* is an action. All sensory nodes appear in pairs like *EnemyClose* and *EnemyFar*, the activation level of one of these nodes is always equal to 1 - *a* where *a* is the activation level of the other. The individual perceives its environment to get a raw value for the distance to the nearest predator; this raw value is fuzzified to compute values between 0 and 1 for the activation levels of *EnemyClose* and *EnemyFar* by nonlinearly transforming it. To compute the activation level of *Fear*, a weighted sum of the activation levels of all nodes with incident edges to *Fear* is computed and the weights are the edge values from the behavioral genome. From our example, *Fear* has incident edges from *EnemyClose* and *EnemyFar*, thus we use edge weights from the behavioral genome for *EnemyClose*🡪*Fear* and *EnemyFar*🡪Fear to compute the weighted sum. The same computation is performed for the activation level of *Evade*. Finally, if *Evade* is the action selected by the individual (if, of all action concepts, it has the highest activation level), the speed of evasion is computed by defuzzifying the activation level of *Evade*. In the behavioral genome where no edge exists between two nodes (for instance *EnemyClose*🡪*Evade*), the corresponding genes have values of zero. However, as individuals evolve, new edges can be added and pre-existing edges could be removed.

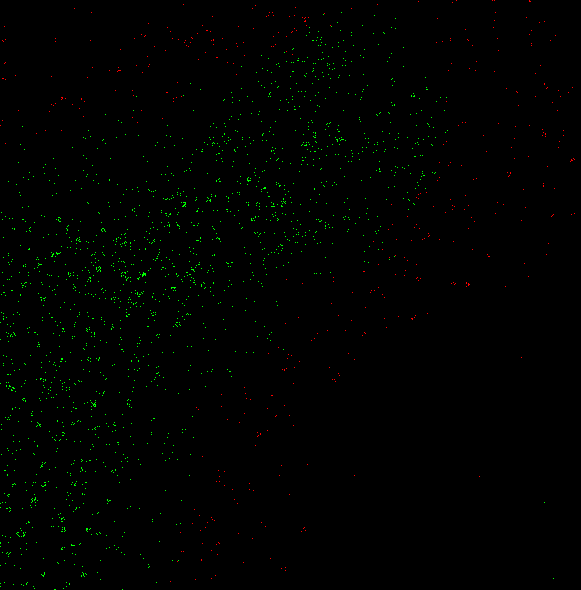
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**Fig. 2.** A simplified example prey FCM for detection of predators (bottom left), with fuzzification (top left) and defuzzification (top right) functions, and its matrix (bottom right) which is the behavioral genome of the individual. *EnemyClose* and *EnemyFar* are sensory concepts, *Fear* is an internal concept, and *Evade* is an action concept. Edges of the FCM show influence of the activation level of a node on another. In the matrix, rows represent influencing concepts and columns represent those that are influenced. Row and column indices of 0 represent *EnemyClose*, 1 represent *EnemyFar*, 2 represent *Fear*, and 3 represent *Evade*.

Emergence

This representation of the behavioral model allows the apparition of positive and negative feedback loops. For instance, an individual may evolve a positive edge between the internal concept *Fear* and itself – this positive feedback loop can allow complex phenomena such as paranoia to emerge. Similarly, negative feedback loops can evolve which stabilize individual behavior. For instance, a negative association between *EnergyHigh* and *Hunger* with a positive association between *Hunger* and *Eat* means that after an individual replenishes its energy by performing the *Eat* action, it is less willing to eat again until its energy levels are lower. The fuzzification and defuzzification mechanisms allow for nonlinear transformations of the perception signal, which permits, for example, the representation of saturation of information. An individual’s action is selected based on the action node with the highest activation level. Because of how the behavioral genome determines the behavior of individuals and how the physical genome determines their physical capabilities, the evolution of behavioral and physical properties of individuals is emergent and it also influences other emergent properties of the system such as number of individuals, spatial compactness of individuals (a proxy of competition for resources), and number of species.

At the initiation of the simulation, prey and predators are scattered randomly all around the virtual world (see *Stochasticity* for a description of this process). Through the course of the simulation, the distribution of the individuals in the world changes based on many different factors such as behavior selection (prey escaping from predators, individuals socializing to form groups, and individuals moving to find food resources). In addition, emergent high-level migration phenomena and grouping patterns with spiral waves can be observed because of these complex interactions between the individuals and their environment. The distribution of individuals forming spiral waves is one property of prey-predator models (Golestani and Gras 2012; Figure 3).



**Fig. 3.** A cropped image of an EcoSim run at time step 20000. Hungry predator individuals (red) chase fleeing prey individuals (green) – one of the many contributory factors to the emergent high-level movement patterns we observe.

Adaptation

The behavioral genome maximal length is fixed (663 genes for prey and 756 for predator), where each site corresponds to an edge between two concepts of the FCM. However, many edges have an initial value of zero; only 117 edges for prey and 131 edges for predators have non-zero values at initialization. Each gene of the behavioural genome follows the continuum-of-alleles model (Bürger 2000) and can take values between -12 and 12. These alleles represent the strength of the positive or negative influence of one concept on another, such as the strength of the association between level of hunger and willingness to eat. In addition to the behavioral genome, every individual has a physical genome that describes its physical characteristics with each trait coded by one gene. Maximum energy (*MaxEnergy*), maximum age (*MaxAge*), vision (*Vision*), maximum speed (*MaxSpeed*), minimum reproductive age (*RepAge*), and state of birth (*StateOfBirth*) are physical traits that both prey and predators possess. Prey have two more traits: defense (*Defense*), and cooperative defense (*CoopDefense*), so they can protect themselves from predators. The mechanisms involving the various physical traits are described further below and under *Submodels*.

Both genomes have two representations – a lightweight byte vector representation used for efficient storage in save files and for computing of evolutionary distances and evolutionary operations, and a floating-point vector representation used for all other computing (activation levels, action selection, physical distances, energy dynamics, *etc.*). The mapping between these representations differ between the genomes. Both representations are fixed at birth for the individual’s lifespan. For the behavioral genome, the byte value of zero maps to the floating-point value of zero. Any byte value less than 128 is reduced by 128 and then divided by 10 to get its associated floating-point value. Any byte value greater than or equal to 128 is reduced by 127 and then divided by 10 to get its associated floating-point value. Thus, byte values from zero to 127 take the range of [-12.7, 0] and byte values from 128 to 255 take the range of [0.1, 12.8]. For example, under this representation, a byte value of 76 yields a floating-point value of -5.2 ((76-128)/10) and a byte value of 200 yields 7.3 ((200-127)/10). For the physical genome, the floating-point representation of each gene has a *minimum* and *step*. For byte value *k*, its floating-point equivalent is *minimum* + (*k* × *step*). For instance, *MaxEnergy* has a minimum of 100 and a step of 25. Thus, a byte value of 17 for *MaxEnergy* yields a floating-point value of 525.0.

The genomes of two parent individuals are transmitted to an offspring individual after recombination and potentially some mutations. EcoSim incorporates genetic recombination through crossover and in the behavioral genome this includes epistasis (*e.g.*, multiple stimuli can influence a given drive) but no pleiotropy (each gene influences only one link between nodes). To model this form of linkage, alleles of the behavioral genome are transmitted by blocks. All incident edges for a given FCM node are transmitted together from a randomly selected parent with equal probability (there is no recombination among genes representing edges to a given node). Sex-linkage occurs for perception nodes as the selected parent is of the same sex as the offspring. Sex-linkage of *MaxEnergy* occurs as it is a weight sum of that of its parents. The parent with the same sex as the offspring has five times the influence on the offspring’s *MaxEnergy* as the other parent (Eq. 3, *MaxEnergy* is abbreviated to *ME*; subscripts *o*, *m*, and *f* represent offspring, mother, and father respectively). Sex-linkage occurs for *StateOfBirth* as well, as an offspring’s *StateOfBirth* is equal to that of its parent of the same sex. All genes in the physical genome are potentially mutated after crossover with some probability (t-test *p* = 0.001). A mutation on a gene in the physical genome is a modification of its byte value (randomly drawn from a truncated normal distribution between -6 and +6). Mutations in the behavioral genome occur due to the formation of new edges (with probability of 0.001), removal of existing edges (with probability of 0.0005), and changes in the weights associated to existing edges (with probability of 0.005). The effect of a given mutation is modification of the value randomly drawn from a truncated normal distribution between -0.6 and +0.6 on the floating-point value of a gene. The probability of mutation in the behavioral genome is doubled for old individuals (*Age* > *MaxAge* – *RepAge*). New genes may emerge from the initial pool of edges with a zero value. This emergence and disappearance of the genes in FCM is due to natural selection and genetic drift which lead to adaptability of individuals (Gras *et al.* 2015).

(3)

Fitness

To measure the capacity of an individual to survive and produce offspring that can also survive, the fitness of a species is calculated as the average fitness of its individuals. The fitness of an individual is defined as the age of death of the individual plus the sum of the age of death of its direct offspring. Accordingly, the fitness value represents the individual's ability to survive and produce well-adapted offspring. There is no pre-defined explicit fitness-seeking process in the simulation; rather, fitness is a consequence of natural selection. Individuals which are better adapted to the environment sustain a higher level of energy, live longer, are able to have more offspring, and transfer their efficient genomes to them (Gras *et al.* 2009; Gras *et al.* 2015). The fitness value is only computed for analysis the results of the simulation and is not used in process during the simulation.

Prediction

So far, there is no learning mechanism for individuals and they cannot predict the consequences of their decisions. The only information available to an individual for decision making comes from its perception at a given time step and the value of the activation level of the internal and action concepts at the previous time steps. The activation levels of the concepts of an individual are never reset during its life. As the previous time step activation level of a concept is involved in the computation of its next activation level, this means that the previous states of an individual participate in the computation of its current state. Therefore, an individual has a basic memory of its own past that will influence its future behaviour. As the action undertaken by an individual at a given time step depends on the current activation level of the action concepts, the behavior of the individual depends on a complex combination of the individual's perception, the current internal states, the past states it went through during its life, and its genome.

Sensing

Every individual in EcoSim can perceive its local environment inside of its range of vision. Some of these senses are common between prey and predator; both can perceive nearby friends and foes, how close food is, their energy level, the amount of food in their cell, how many potential reproductive partners are in their cell, and their age. Additionally, new to EcoSim, all individuals can perceive their *Strength* and the maximum *Strength* of potential mates in their cell. Also new to EcoSim, prey individuals can sense the sum of *Strength* of prey in their cell and the sum of *Strength* of the cell within vision range that has the highest sum of prey *Strength*. Similarly, predator individuals can sense the sum of *Strength* × (1 + *Defense*) of prey in their cell, the distance to the cell in vision range with the highest sum of prey *Strength* × (1 + *Defense*), and the maximum strength × (1 + *Defense*) in their cell. These new sensory concepts serve several purposes related to the notion of prey defending against predators, new to EcoSim. With these new sensory concepts, prey can use strength-related sensory information to join a cell with other strong prey to bolster cooperative defenses. Similarly, predators can use strength-related information to avoid conflict with stronger prey individuals or groups of strong prey. Alternatively, if the predator is very strong, it may use this information to gain a larger energy reward for killing stronger prey. Individuals can only reproduce with individuals of the same type in their current cell. Having the ability to sense strong individuals and move to them means that (with the right combination of edges) there is potential to improve the chance of reproducing with strong individuals. Thus, these concepts can also lead to some potentially interesting evolutionary phenomena, such as a strength-based evolutionary arms race between prey and predator populations.

Interaction

In EcoSim, there are direct and indirect interactions amongst individuals and between individuals and their environment. These interactions stem from actions that prey and predator individuals can perform. The only direct interaction that requires a coordinated decision by two individuals is *Reproduction*. *Reproduction* occurs between two prey or two predators. For *Reproduction* to be successful, the two parents need to be in the same cell, have sufficient *Energy*, choose the *Reproduction* action, and be genetically similar. The individuals cannot determine their genetic similarity with their potential partner – they try to mate and if the partner is too dissimilar (the dissimilarity between the two genomes is greater than some percentage of the speciation threshold, by default 62.5%), the reproduction fails. See *Reproducing* under *Submodels* for more details of the *Reproduction* action.

The *Hunting* action of predators is a direct interaction that occurs between a predator and some number of prey existing in a cell. For *Hunting* to succeed, the predator must be able to move to the cell containing its target prey individual and it must have greater *Strength* than its target’s *Energy*. Should the *Hunt* succeed, the prey target is killed and the predator receives some amount of *Energy*. The predator also receives an *Energy* penalty if the target prey tries to defend itself, or if other prey in the cell were defending the target. See *Hunting* under *Submodels* for more details of the *Hunting* action.

Lastly, there are several ways individuals can indirectly interact with each other and their environment. An individual’s perception of its local environment causes its actions and movement to be influenced by the distribution of other individuals and food resources. Moreover, individuals that share a cell compete for the limited resources that the cell contains (food and mates), and this yields density dependence. Competition generally comes in two main forms, which represent opposites along a gradient. Contest competition arises when a single individual claims all of its local resources, leaving other individuals with nothing (Brännström and Sumpter 2005). This allows individuals to potentially monopolize resources because strong individuals continue to claim resources while the weak starve and ultimately perish. Scramble competition, in contrast, occurs when individuals share resources equally and are thus equally penalized by local density increases (Brännström and Sumpter 2005). Competition in EcoSim, like in most ecosystems, is neither purely contest or scramble competition; elements of both forms of competition can be observed.

Stochasticity

To produce variability in the ecosystem simulation, several processes involve stochasticity. At initialization, the number of grass units is determined for each cell following a uniform random distribution (a value between 1 and *MaxGrass*). Similarly, at initialization, individuals are randomly distributed across the world in clusters. The simulation takes as input a clustering radius and a number of prey and predator individuals per cluster (see *Initialization and Input Data*). Let *x* and *y* be random coordinates for the center of a cluster, *ClusteringRadius* be the clustering radius, and *k* be the number of prey individuals in a cluster. Then, for each of the *k* prey individuals, *xn* and *yn* (the x and y coordinates for the position of *n*th individual in the cluster) are produced by taking *x* and *y* and subtracting from or adding to them a random value between zero and *ClusteringRadius*. This process occurs until the entire initial set of prey individuals is placed in the world. The same process then occurs for the predators. The age of an individual is also determined randomly at birth from a uniform distribution in [1, 24] for prey and [1, 35] for predators. Similarly, the initial energy of an individual is randomly generated in a uniform distribution, ranging from 40% to 100% of the initial maximum energy of the individual. *Age* and *Energy* are randomly generated in this manner to avoid apparition of synchronicity in action selection and death cycles early in runs that would cause instability leading to extinction of prey or predators. The sex of an individual at initialization or at birth is randomly generated with equal probability to be male or female. Stochasticity is also included in several kinds of actions of the individuals (see *Submodels* for full descriptions of each action). For instance, if a hunting predator cannot find a prey within its vision range, the direction of its movement will be random. Furthermore, the direction of the exploration action is always random.

Mutation and crossover both involve stochasticity, as described under *Adaptation*. Further, when individuals perceive their environment, they perform a radial sweep about their position along the four cardinal directions. The sweep begins at a distance of one and increments to the individual’s vision range. The starting cardinal direction and the direction of the radial sweep are randomly generated to remove any biases in perception and movement. Lastly, stochasticity is incorporated in the grass diffusion model (see *Submodels* for elaboration). To understand the extent of stochasticity in EcoSim, Golestani and Gras (2010) examined whether chaotic behavior (one signal of non-randomness) exists in time series generated by the simulation. The authors concluded that the overall behavior of the simulation generates emergent patterns that are non-random and instead like those observed in complex biological systems (Kantz and Schreiber 1997).

Collectives

An EcoSim run persists while there is at least one prey individual. If all prey die, the run is complete due to extinction as the predators can only eat prey. EcoSim can be run with or without predators, though typically there are predators as it is designed to observe predator-prey interaction. A typical EcoSim run has 60000-1000000 prey and 2000-30000 predators at any time step, depending on the parameterization of the run.

In EcoSim, the genetic distance between any two genomes of the same type (prey or predator) is necessary to compute to establish the notion of species. This distance calculation does not include sex-linked genes (see *Reproducing* under *Submodels*). To compute this distance, it is first initialized to zero. For every element of the behavioral genome in its byte vector form, the absolute difference between the pair of corresponding values from each genome is added to the distance. Subsequently, for every gene of the physical genome, a weight is computed by taking the absolute difference of corresponding floating-point values and then dividing by the range of values for that gene. This weight is then multiplied by the difference between genes, multiplied by five, and added to the distance.

Species emerge from the evolving sets of prey and predators. Species membership is strictly used in data analysis – it is not used to govern any mechanics related to reproduction. There is a separate genetic similarity threshold used for reproduction which is much lower than the speciation threshold, and this allows hybridization (reproduction between members of different species) to occur (see *Reproducing* under *Submodels*). At initialization of EcoSim, there is one species per type. Species can become extinct if all their members die. EcoSim implements a species based on the genotypic cluster definition (Mallet 1995) in which a species is a set of individuals sharing a high level of genomic similarity. In addition, in EcoSim, each species is associated with the average of the genetic characteristics of its members, called the ‘species center’. The speciation mechanism implemented in EcoSim is based on the gradual divergence of individual genomes. The speciation method begins by finding the individual *A* in a species *S* with the greatest genetic distance from the species center. Next, the individual *B* in *S* with the greatest distance to *A* is found. If this distance is greater than a pre-defined threshold for speciation, a 2-means clustering is performed (Aspinall and Gras 2010), otherwise *S* stays unchanged.

To initialize the 2-means clustering process, one center is assigned to a random individual, denoted *Ir*, and the other center is assigned to the individual which is the most genetically different from *Ir*. After, eight cycles of the 2-means clustering algorithm, two new sister species are created to replace *S*. Each species for each type in EcoSim has a unique species identifier, starting at one and incrementing automatically when a new species is formed. Of the two sister species replacing *S*, one retains the species identifier of *S* and the other obtains the next available identifier.

Observation

EcoSim produces a large amount of data at each time step, recording many statistics like the number of individuals, the characteristics of each individual, and the status of each cell of the virtual world. Information regarding individual characteristic include spatial position, level of energy, choice of action, species identity, parents, FCM, *etc.* Information about the individuals, species, and virtual world for every 20 time steps are stored in a file, optionally using HDF5 format (The HDF Group 2000) with an average size of 6 gigabytes. Also there is a possibility to store all of the values of every variable in the current state of the simulation in a separate file, giving the possibility to restore the simulation from that state afterwards. The overall size of this file, which is only stored every 20 time steps (by default – this frequency can be modified in the parameters file) of the simulation, is a few gigabytes depending on the numbers of individuals and species. All the data is stored in a compact special format, to facilitate the storage and future analysis. There are also several program utilities which can be used, for example, to analyze the simulation outputs, to calculate the species and individual fitness, to generate images of the world for each time step of the simulation, generate the video of the world throughout a run or some portion of it, and to draw the FCM of the individuals.

Initialization and input data

A parameter file (with filename “*Parameters1.txt*”) is defined for EcoSim, which is used to assign the values for each state variable at initialization of the simulation. Example parameters include width and height of the world, initial numbers of individuals, thresholds of genetic distance for prey/predator speciation, speed of grass growth, probability of grass diffusion, initial maximum age, initial maximum energy, initial maximum speed, initial maximum vision range, initial values of FCM edges for prey/predators, and the characteristics of the fuzzification functions for sensory input. Any of these parameters can be changed for specific experiments and scenarios. Initialization involving stochasticity (such as the initial distribution of individuals in the world) is described under *Stochasticity*, above. Many of these initial parameters are only important in stabilization the simulation in its early stages, before the emergent properties of the system are observable. These parameters have been tested extensively to ensure that EcoSim is stable in a wide variety of scenarios (if grass levels are low, if grass levels fluctuate regularly over time, if grass diffusion probability is reduced, if prey reproduce asexually rather than sexually, *etc.*). EcoSim is designed to be highly generalized. Typically, the emergent properties of at least two sets of runs initialized identically (or very similarly) with few mechanical differences are studied and compared, to observe the effect of these few mechanical differences on the evolution of the populations. Thus, the physiological scaling rates are informed from empirical biological studies (as noted above under *Individuals*) but the aim of the initial parameters of EcoSim is to produce a stable system and thus they are largely arbitrary. An example of a list of common user specified parameters for initially running the EcoSim are presented in Table 2.

**Table 2.** Values for user specified parameters.

|  |  |
| --- | --- |
| User Specified Parameter | Used Value |
| Number of Prey | 80000 |
| Number of Predators | 4000 |
| Max Grass Quantity in each cell | 4000 |
| Prey Maximum Energy | 2500 |
| Predator Maximum Energy | 3000 |
| Prey Vision Range | 8 |
| Predator Vision Range | 20 |

Submodels

Food Sources: Grass and Meat

There are dynamic processes for the resources in each cell such as grass growth, grass diffusion, and variation in the amount of meat at each time step. At initialization, there is no meat in the world and the amount of grass energy units is randomly determined for each cell as described under *Stochasticity*.

The grass growth rate in each cell is regulated by several factors: *SpeedGrowGrass* (200 by default), *ProbaGrowGrass* (0.035 by default), *MaxGrass* (4000 by default), and *Fertilizer*. The first, *SpeedGrowGrass*, is a parameter in the EcoSim parameter file which determines the speed of grass growth. For a cell not already containing grass, grass can diffuse from an adjacent cell with a probability of *ProbaGrowGrass* at a rate of *SpeedGrowGrass*, provided that one of the eight cells around the cell contains a non-zero amount of grass. *Fertilizer*, a feature new to EcoSim, is derived from excretions of individuals. *AmountOfFertilizer*, the amount of fertilizer in a cell, is proportional to the sum of maximum energy (*MaxEnergy*) of prey and predators residing in that cell, limited to a total of 20000. If *AmountOfFertilizer* is less than *SpeedGrowGrass*, then the fertilizer does not have any effect. Otherwise, the rate of grass growth is equal to *AmountOfFertilizer* and limited to triple *SpeedGrowGrass*. For a cell already containing grass, the rate of grass growth is simply added to the grass amount currently in the cell at a given time step. *AmountOfFertilizer* decreases at a rate of 10% per time step. The amount of grass in a cell is limited to *MaxGrass*.

Another new EcoSim feature is that *MaxGrass* can be set to fluctuate cyclically following a cos wave by setting the *FluctuatingResources* parameter in the parameter file. The period, minimum (as a ratio of *MaxGrass*), and amplitude (as a ratio of *MaxGrass*) of the wave can be set using the parameters *FluctuationCycle, FluctuationMinimumRatio*,and *FluctuationAmplitudeRatio* respectively. Another new feature is that *MaxGrass* can be set such that it creates regularly positioned circular patterns throughout the world using the *CircularFoodGrowth* parameter. The diameter of the circles, the maximum grass level at the center of the circle (as a ratio of *MaxGrass*, though limited still by *MaxGrass*), and the minimum amount of grass in any cell (as a ratio of *MaxGrass*) are set using the *FoodCircleDiameter*, *FoodCircleMaxRatio*, and *FoodCircleMinimumRatio* parameters. *FoodCircleMaxRatio* is used to increase the rate at which *MaxGrass* increases closer toward the center of a circle, and *MaxGrass* increases following a cos wave from *FoodCircleMinimumRatio* to *FoodCircleMaxRatio* from the edge of a circle to the center.

The amount of meat in each cell is limited to *MaxMeat* (4000 by default) and increases every time step by the *Strength* of the prey killed in that cell during that time step. It also decreases at each time step by 1000, even if no meat has been eaten in this cell.

Actions

For each movement action *M* the movement speed is equal to *MaxSpeed* × *ActivationLevel*(*M*), thus the speed at which an individual moves during the action depends on its willingness to perform it. Movement speed is the straight-line distance that an individual can move in a single time step. Each action has its own corresponding submodel:

1. *Evading* (for prey only). An evading prey moves in the direction opposite to the barycenter of the five closest predators within its vision range, with respect to its position. If no predator is within the vision range of the prey, the direction is chosen randomly.
2. *Hunting* (for predators only). The predator selects the closest cell (including its current cell) that contains at least one prey and moves toward that cell. If it reaches the corresponding cell based on its speed, the predator selects a prey target and tries to kill it. When there are several prey in the destination cell, one of them is chosen randomly as the target. If the speed of the predator is not enough to reach the cell, it moves at its speed toward the cell and the hunt has failed. Similarly, the hunt has failed if there is no prey in the vicinity. When a predatorʼs hunt succeeds, the *Strength* of the killed prey is added to the cell in meat energy units. Afterward, the predator consumes the meat to gain its required energy, *min*(*MaxEnergy* – *Energy*, *MeatUnits*), where *MeatUnits* is the number of meat energy units produced by the killed prey. The remaining units of meat energy are allocated to the cell and can be consumed by other predators using their *Eat* action. Prey have a defence capability as well as cooperative defence and use them in a battle against the predator (Arnold 2000).

Every prey has its own defense and cooperative defense capabilities, allowing it to defend against predators on its own or with other prey. Prey defense and cooperative defense is passive; prey defend automatically if they have a non-zero *Defense* value and are targeted by a predator, or if they have a non-zero *CoopDefense* value and share a cell with a target. Prey spend energy when trying to defend, and predators receive an energy penalty (*P* in Eq. 4, *AP.D* and *AP.S* are *Defence* and the *Strength* of the attacked prey. *CPi.D*, *CPi.CD,* and *CPi.S* are the *Defence*, *CoopDefence*, and *Strength* of the prey *i* in the same cell) when they attempt to attack a prey individual with defense or a cell containing prey defending cooperatively. It is even possible for a predator to be killed by defending prey, particularly if the predator already has low *Energy*. Additionally, the prey which are involved in a cooperative defence also lose some amount of *Energy* based on the strength of the predator (0.2 × *PredatorStrength* / *NumberOfDefenders*). The target prey loses *Energy* equal to 100% of the attacking predator’s *Strength* if it is not cooperatively defended, otherwise it loses 80% of the attacking predator’s *Strength*. If, after the attack, the prey’s *Energy* is greater than zero, the prey survives and the hunt has failed.

(4)

1. *Searching for food*. The direction toward the closest food (grass for prey, meat for predators) within the vision range is computed. If the individual’s speed is high enough to reach the food, the individual is placed in the cell containing this food. Otherwise, it moves at its speed toward this food. If no food is within vision range, the individual moves in a random direction.
2. *Socializing*. The direction toward the closest possible mate within the vision range is computed. If the individual’s speed is high enough to reach this mate, the individual is placed in the cell containing this mate. Otherwise, the individual moves at its speed toward this mate. If no mate is within vision range, the individual moves in a random direction.
3. *Exploring*. A direction is computed randomly. The individual moves at its speed in this direction.
4. *Resting*. Nothing happens.
5. *Eating*. If the current amount of grass (meat) in the prey’s (predator’s) cell is greater than 0, the prey (predator) consumes the grass (meat) to gain its required energy, *min*(*MaxEnergy* – *CurrentEnergy*, *EnergyUnits*), where *EnergyUnits* is the number of grass (meat) energy units in the cell. *EnergyUnits* is decreased by the amount consumed by the individual.
6. *Reproducing*. Chromosomes in eukaryotic cells are usually present in pairs (diploid organisms). The chromosomes of each pair separate in meiosis, one going to each gamete. In many animal species, sex is determined by a special pair of chromosomes called sex chromosomes (allosomes), the X and Y. All other chromosomes are called autosomes. The sex chromosomes are an exception to the rule that all chromosomes of diploid organisms are presented in pairs of morphologically similar homologs. While females have two X chromosomes, the males have one X chromosome along with a morphologically unmatched chromosome, called the Y chromosome. All somatic cells in male and female organisms have a complete set of autosome and sex chromosomes. Every egg cell contains an X chromosome, while only half of sperm cells contain an X chromosome and the other half contain a Y chromosome. This difference is a chromosomal mechanism for determining sex at the time of fertilization. In other words, while autosome chromosomes are randomly obtained from both parents; Y chromosome in male offspring is exclusively acquired from the father (Hartl and Jones 2004). Individuals in EcoSim, in contrast to the common case, are haploid. That is, their chromosomes are present as singletons that are generated from specialized evolutionary operations described below. To model more realistic individuals, we made it so that all perception genes, *MaxEnergy* genes, and *StateOfBirth* genes exist on allosomes (that is, they are sex-linked), while all other genes exist on autosomes. Thus, there is an evolving differentiation between male and female behavior.

As per the section *Process Overview and Scheduling*, females intending to reproduce act first. This is because females initiate reproduction in EcoSim, to simulate female choice. Females can attempt to reproduce with any male in their cell, however success is not guaranteed and individuals always act in order of decreasing strength. There are several ways a reproduction attempt can fail in EcoSim. Reproduction fails if there are no males in the current cell. Otherwise, the female randomly selects a potential male partner. A reproduction attempt with a single male can fail if: the male has already reproduced (with a different, stronger female), the male has selected a different action (e.g. *Eat* or *Evade*), the male is below reproduction age, the male has insufficient energy to reproduce, or the genetic distance between the female and male is too great. The genetic distance threshold for reproduction failure is greater than the speciation threshold, therefore individuals from different species can reproduce to generate hybrid offspring. In this case, the hybrid offspring is assigned to the species which has a smaller genetic difference between its average genome and the genome of the offspring. The female can attempt to reproduce with each male in the current cell, but loses two *Energy* for each failed attempt. If reproduction succeeds, the process of generating a new offspring consists of the following steps. When a new offspring is created, it is given a genome which is a combination of the genomes of its parents using a specialized crossover operation along with some possible mutations (as explained under *Adaptation*). The sex of the offspring is randomly determined with equal probability to be male or female. Then, the initial *Energy* (*Energy0*) of the offspring is computed (Eq. 5) based on the parents’ *MaxEnergy* (abbreviated to *ME* in the equation) and *StateOfBirth* (abbreviated to *SOB* in the equation).

(5)

Finally, the *Energy* of the two parents is decreased. The energy penalty for the mother, *penaltym* is calculated based on Eq. 6, where the subscript *m* and *f* mean mother and father respectively. The parameter *Energy* is the newborn individual's *Energy*. *FPP* is the first-time pregnancy penalty for the mother, which is five percent of its energy and zero for the next pregnancies. The energy penalty for the father is based on Eq. 7.

(6)

(7)

1. *Move2StrongestPrey/Predator* (for prey/predator, respectively). The direction toward the strongest possible mate within the vision range is computed. If the speed of the individual is high enough to reach the mate, the individual is placed in the cell containing this mate.Otherwise, the individual moves at its speed toward this mate. If no mate is within the vision range of the individual, the direction is chosen randomly.
2. *Move2StrongestPreyCell* (for prey only). This action is similar to *Move2StrongestPrey/Predator,* except that the direction of movement is toward the cell with the highest cumulative *Strength* of prey individuals. This allows prey to benefit from cooperative defence against predators.
3. *Move2WeakestPreyCell* (for prey only). This action is similar to *Move2StrongestPreyCell,* but the direction of movement is toward the cell with the lowest cumulative *Strength* of prey individuals. This allows prey to have higher chance of success in competition with other prey individuals for accessing food or mates.
4. *Move2StrongestPreyDistance* (for predator only). The predator moves toward the strongest prey individual to acquire more energy after possible hunting. If the speed of the individual is high enough to reach the prey, the individual is placed in the cell containing this prey. If the speed of the predator is not enough to reach the prey, it moves at its speed toward this prey.
5. *Move2WeakestPrey* (for predator only). This action is similar to *Move2StrongestPreyDistance*, with the exception that the direction of movement is toward the weakest prey individual for easier hunting in the future.
6. *Move2WeakestPreyCell* (for predator only). This action is similar to *Move2WeakestPrey*, but the direction of movement is toward the cell with the lowest cumulative *Strength* of prey individuals to minimize the possible effect of cooperative defence by prey individuals.

**Description of Parameter File**

What follows is a description of the parameters provided to EcoSim in the parameters file (“Parameters1.txt”).  
  
**HDF5** – should save files use HDF5 encoding (more efficient,1 = yes, 0 = no)  
**Width** – width of the virtual world in number of cells  
**Height** – height of the virtual world in number of cells  
**ValueGrass** – no longer used  
**MaxGrass** – maximum grass energy units per cell   
**SpeedGrowGrass** – rate at which grass replenishes per time-step  
**ProbaInitialGrass** – probability that a cell has grass upon initialization   
**ProbaGrowGrass** – probability of diffusion of grass to new cells   
**MaxMeat** – maximum meat energy units per cell  
**ProbaMut** – probability of standard mutation  
**ProbaMutLow** – probability of deletion/insertion mutation  
**PercentMut** – no longer used  
**PercentMutHigh** – no longer used  
**RadiusCluster** – Radius of each cluster for initial population   
**DistanceMin**: 1  
**MaxSave** – number of time-steps between creation of restore points  
**MinSave** – number of time-steps between saving of data for each individual  
**MinSave\_Compressed** – number of time-steps between saving compressed data for each individual (does not save FCM values)  
**WorldSave** – number of time-steps between saving of world state data  
**Tar\_MinSaveWorld** – tar (aggregate into an archive file) minsaves and worldsaves every 1000 time-steps? 1 = yes, 0 = no  
**PerSpeciesPrey** – produce per-species data for prey (1 = yes, 0 = no)  
**PerSpeciesPred** – produce per-species data for predators (1 = yes, 0 = no)  
**Restore** – restore from MaxSave (1 = yes, 0 = no)  
**MatingMode** – mode of mate selection during mating: 0-Random mate selection method, 1-Good gene mate selection method, 2-Intermediate  
**IsWithoutPredator** – does this run not have predators? 1 = yes, 0 = no  
**FertilizerDivideTo** – divide sum of fertilizer to decrease its effect  
**Visualizations** – 0 means no images of the world state are produced, otherwise visualizations every this number of steps  
**FluctuatingResources** – 0 means maxGrass is constant, 1 means it fluctuates regularly  
**FluctuationAmplitudeRatio** – the amplitude of fluctuation as a ratio of maxGrass  
**FluctuationMinimumRatio** – the minimum of maxGrass as it fluctuates, as a ratio of maxGrass  
**FluctuationCycle** – how long a fluctuation cycle takes, in time-steps  
**CircularFoodGrowth** – 0 means grass grows normally, 1 means it grows in circular patches  
**FoodCircleDiameter** – diameter of the circular grass patches  
**FoodCircleMaxRatio** – the peak of maxGrass, as a ratio of maxGrass... determines essentially the area of the world that has maxGrass set to the real maximum  
**FoodCircleMinimumRatio** – between patches, what is the minimum value the grass can take, as a ratio of maxGrass  
**Persuasion** – 1 means males can be persuaded by females to choose reproduction, 0 means EcoSim behaves normally  
  
**Prey Parameters**:  
**InitNbPrey** – initial number of prey  
**ValuePrey** – no longer used  
**AgeMaxPrey** – initial maximum age of prey  
**EnergyMaxPrey** – initial maximum energy of prey  
**SpeedMaxPrey** – initial maximum speed of prey  
**AgeReprodPrey** – initial age of reproduction of prey  
**StateBirthPreyMale** – initial state of birth for male prey   
**StateBirthPreyFemale** – initial state of birth for prey female  
**VisionPrey** – initial vision range of prey  
**PerClusterPrey** – the number of prey per cluster upon initialization  
**DistanceSpeciesPrey** – the genetic distance threshold between most distantly related prey individuals within a species  
  
**Predator Parameters:**  
**InitNbPredator** – initial number of predators  
**AgeMaxPred** – initial maximum age of predators  
**EnergyMaxPredator** – initial maximum energy of predators  
**SpeedMaxPredator** – initial maximum speed of predators  
**AgeReprodPred** – initial age of reproduction of predators  
**StateBirthPredMale** – initial state of birth for male predators  
**StateBirthPredFemale** – initial state of birth for female predators  
**VisionPredator** – initial vision range of predators  
**PerClusterPredator** – the number of predators per cluster upon initialization  
**DistanceSpeciesPred** – the genetic distance threshold between most distantly related predator individuals within a species  
  
**FCM Parameters for Prey:**  
**nbSensPrey** – number of prey sensory FCM nodes  
**nbConceptsPrey** – number of prey internal FCM nodes  
**nbMotorDepPrey** – number of prey movement actions  
**nbMotorFixPrey** – number of prey actions without movement  
  
Subsequently, the initial prey FCM is displayed, followed by parameters that govern the fuzzification of prey perceptions, followed by parameters that govern the fuzzification of internal and action states of prey.  
  
**FCM Parameters for Predators:**   
**nbSensPredator** – number of predator sensory FCM nodes  
**nbConceptsPredator** – number of predator internal FCM nodes  
**nbMotorDepPredator** – number of predator movement actions  
**nbMotorFixPredator** – number of predator actions without movement  
  
Subsequently, the initial predator FCM is displayed, followed by parameters that govern the fuzzification of predator perceptions, followed by parameters that govern the fuzzification of internal and action states of predators.

Description of Outputs

EcoSim produces a number of output files. A description of each of them follows.  
  
MinSave – per-individual save files, including FCM of newborn individuals, data for final states of dead individuals, and state information for all other individuals  
MinSave\_C – same as MinSave, but does not contain FCM information  
MaxSave – file used for restoring the state of a successfully terminated run (i.e., not failed due to extinction)  
Results\_Pre\*.csv files – average data across all living individuals per time-step for predators, prey, females, and males (examples: speed, energy, strength, physical genome data, activation level of all FCM states)  
Results\_SpeciesPre\* directories:  
 Result\_Pre\*.csv – same as Results\_Pre\*.csv files, but results are displayed per species (that is, if there are k species in a given time-step, there will be k lines pertaining to that time-step)  
 Result\_Pre\*FCM\*.csv – mean and variance of all genomic elements for prey and predators, males and females, per species

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