

# EcoSim, an Enhanced Artificial Ecosystem: Addressing Deeper Behavioral, Ecological, and Evolutionary Questions



Ryan Scott, Brian MacPherson and Robin Gras

**Abstract** This chapter discusses individual-based models (IBMs) and uses the Overview, Design concepts, and Details (ODD) protocol to describe a predator-prey evolutionary ecosystem IBM called EcoSim. EcoSim is one of the most complex and large-scale IBMs of its kind, allowing hundreds of thousands of intricate individuals to interact and evolve over thousands of time steps. Individuals in EcoSim have a behavioral model represented by a fuzzy cognitive map (FCM). The FCM, described in this chapter, is a cognitive architecture well-suited for individuals in EcoSim due to its efficiency and the complexity of decision-making it allows. Furthermore, it can be encoded as a vector of real numbers, lending itself to being part of the genetic material passed on by individuals during reproduction. This allows for meaningful evolution of their behaviors and natural selection without predefined fitness. EcoSim has been enhanced to increase the breadth and depth of the questions it can answer. New features include: fertilization of primary producers by consumers, predator-prey combat, sexual reproduction, sex-linkage of genes, multiple modes of reproduction, size-based dominance hierarchy, and more. In addition to describing EcoSim in detail, we present data from default EcoSim runs to show potential users the types of data EcoSim generates. Furthermore, we present a brief sensitivity analysis of some variables in EcoSim, and a case study that demonstrates research that can be performed using EcoSim. In the case study, we elucidate some evolutionary and behavioral impacts on animals under two conditions: when primary production is limited, and when energy expenditure is reduced.

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## 1 Introduction

Among biological disciplines, behavioral ecology has a strong tradition of accounting for the role of organism–environment interactions in behavior [69]. Behavioral ecology and the related field of optimal foraging theory [118] model animal behavior in terms of optimal adaptation to environmental niches. The goal is not to test whether organisms actually behave optimally, but to use normative expectations to interpret behavioral data and/or generate testable hypotheses. One approach for understanding the behavior of complex ecosystems is through individual-based models (IBMs), which provide a bottom-up approach allowing for the consideration of the traits and behavior of individual organisms. Ecological modelling is still a growing field, at the crossroads between theoretical ecology, mathematics, and computer science [109]. Since natural ecosystems are very complex (in terms of number of species and of ecological interactions), ecosystem models aim to characterize the major dynamics of ecosystems in order to synthesize the understanding of such systems and to allow for predictions of their behavior. Ecosystem simulations can also help scientists to understand theoretical questions regarding the evolutionary process, the emergence of species, and the emergence of learning capacities. One of the most interesting aspects of such ecosystem simulations is that they offer a global view of the evolution of the system, which is difficult to observe in nature. However, the scope of ecosystem simulations has always been limited by the computational possibilities of their time. Today, it is possible to run simulations that are more complex than ever, due to the availability of high performance computing resources.

Several ecosystem simulation platforms with various features exist. For example, Echo, one of the first such models, is a basic ecosystem simulation in which resources are limited and agents evolve [58]. In Echo, each agent, upon obtaining the required resources to copy its genome, replicates itself with some mutations. The agents, through interaction with other agents (combat, trade, or mating) or the environment, can acquire resources. Polyworld is another such IBM software [129] to evolve artificial intelligence through natural selection and evolutionary algorithms. It displays a graphical environment in which trapezoidal agents search for food, mate, and create offspring. The number of agents is typically only in the hundreds, as each agent is rather complex and the environment consumes considerable computational resources. In this model, each individual makes decisions based on a neural network which is derived from each individual's genome. Recently, Polyworld has been used to study the effects of different neuromodulation models on the adaptability of its individuals [131], finding that neuronal plasticity modulation (decreasing or increasing the rate at which neuron weights change) tends to produce individuals that adapt more effectively. It has also been used to study the way in which network topologies influence the evolved complexity of the networks [130] and, most recently, the level of chaos as the individuals in the system evolve [128]. Avida is another artificial life software platform for studying the evolutionary biology of self-replicating and evolving computer programs [97], inspired by the Tierra system [122]. Unlike Tierra, Avida assigns every digital organism its own protected region of memory and

executes its program with a separate virtual CPU. A second major difference is that the virtual CPUs of different organisms can run at different speeds. The speed at which a virtual CPU runs is determined by several factors, but most importantly by the tasks that the organism performs: logical computations that the organisms can carry out to reap extra CPU speed as a bonus. With increasing computational power, individual-based simulation platforms such as Tierra, Avida, Polyworld, and EcoSim [45, 74, 108, 129] can be used to address increasingly difficult questions in biology [22, 23, 43, 75]. EcoSim [45], in particular, has been designed to model large-scale virtual ecosystems.

Recently, much has been done in the field of ecological IBMs on three main fronts: formalization and development practices of IBMs, pragmatic modelling, and paradigmatic modelling. In regard to formalization and development practices, some insist that there is an increasing need for developers of IBMs to be transparent about the process used to develop a model [5, 49, 113]. They argue that potential clients need to have a thorough understanding of the model so that they can know whether the model is applicable to whatever they would like to test. Clients need formal statements of the question(s) the model is designed to answer, descriptions of the submodels and their organization within the model, information on the degree of testing performed on the model, and the rationale behind making any modifications throughout the long and iterative process that is the “modelling cycle”. So, several researchers have proposed and subsequently revised [49] a new standard format for the description of an IBM, TRANSPARENT and Comprehensive Ecological modelling documentation (TRACE) [113], which differs from the previously-proposed ODD protocol [47] in that TRACE is more comprehensive and more concerned with describing the development cycle and practical ability of a model. Furthermore, the ODD protocol can be used within TRACE as a means of describing the model’s implementation. TRACE complements the principle of “evaluation” [5], representing an urged evaluation and validation of a model throughout the development, application, and analysis of it. The current revision of TRACE intends to focus the developer on documenting the modelling process for the sake of ensuring quality and credibility throughout said process, as the originally proposed TRACE was less efficient and less specific regarding its goals. MacPherson and Gras [79] argue that there is too much of a focus on “evaluation” and that not all IBMs are “merely adjunctive tools”. More specifically, pragmatic models, focusing on a particular species or system usually with intent of making predictions in applied ecology, should undergo a more rigorous parameterization process using empirical data, be subject to evaluation, and be more stringently documented. Pragmatic models are often tied to conservation efforts or the management of delicate ecosystems, and so a model must be realistic enough to effectively predict how a specific (very complex) ecological system will behave. On the other hand, MacPherson and Gras argue that paradigmatic models are, in fact, experimental platforms. Though they must be realistic enough, in the general sense, there should be less of a focus on incorporating empirical data into the calibration or parameterization of them, as they are typically designed to answer rather general theoretical questions, the results of which we often have no means of historically validating due to the scale of interactions being emulated in the simula-

tion. Furthermore, they argue that paradigmatic models can lose generalizability by over-calibrating the model empirically. They propose a relaxed notion of model evaluation by removing the constraint of empirically calibrating a model; they instead insist that the calibration be reasonable, that is, consistent with general observations in nature.

Pragmatic models are those that aim to model a specific system or population, and most IBMs are pragmatic in nature [25]. de los Santos et al. [27], for instance, designed an IBM of a marine amphipod, *Gammarus locusta*, to assess the effect of long-term exposure to a chemical pollutant, aniline, on *G. locusta* populations. They used real life-history traits of *G. locusta* to parameterize the model, and observed significant negative impacts in individual survivorship and production of offspring with exposure to aniline. Other recent works in pragmatic modelling include a toxicological model for zebrafish [50], a model eliciting effects of climate change on population dynamics in European anchovies [104], a model for management of brown trout [33], and a model for motion of the blue mussel, *Mytilus edulis* [26].

As the naming convention suggests, paradigmatic modelling moves away from answering specific questions and instead aims to uncover the underlying causes of more generalized ecological or evolutionary phenomena [25]. Zaman et al. [132], for example, used Avida to show that parasite-host interactions increase the complexity and evolvability of digital organisms over a long time-frame. Avida has been used in several other recent works [32, 39, 71, 100]. Similar to Zaman et al. [132], Kvam et al. [70] also studied the complexity of the brain of a population of digital organisms, in this case Markov Brain agents. In contrast, they studied complexity in light of the problem-solving environment the agents were subject to. Olson et al. [99] used Markov Brain Agents as well, but instead they placed the agents into a toroidal world and observed changes in physical cluster tightness when subject to different types of predator attacks. Botta-Dukát and Czúcz [12] generated a spatially implicit IBM to simulate community compositions and tested the ability of five functional diversity indices. Functional diversity indices aim to determine the number of functionally different species in a community. Their simulation accounted for habitat filtering (suitability of an individual to a habitat—a means of local trait convergence) and trait-similarity-based competition for resources (a means of local trait divergence) in composing the simulated communities. With mechanisms causing individual trait divergence and convergence, they could effectively test the functional diversity indices for their ability to detect these two key assembly processes. They found trait divergence was difficult to detect for all the indices tested, whereas trait convergence was detectable by some indices. Uchmański [124] found, using an IBM, that dispersal mechanisms of individuals affect the persistence of metapopulations. In different runs of the simulation, individuals would disperse from their current habitat to another unoccupied neighboring habitat for different reasons (when one gains no resources resulting from competition, when competition yields insufficient resources to produce an offspring, random chance, or when no individuals in a habitat could reproduce). If individuals dispersed due to total loss of resources due to competition, the metapopulations persisted longest. Similarly, when individuals dispersed due to insufficient resources for reproduction, the metapopulations persisted longer

than by chance. If individuals waited until none in a habitat could reproduce, the metapopulations failed to persist longer than cases in which dispersal was random. Another recent paradigmatic IBM tested the effects of patch size and refuge abundance on the strength of predator-prey interactions and population dynamics [77]. They found that refuge availability decreased the interaction strength between prey and predators, which consequently improved the stability of populations. CDPOP [72] and its descendant CDMetaPOP [73] are both IBMs that use Mendelian inheritance with any number of alleles and loci to study the effects of a varying landscape of (nearly) any complexity on the genetic structure and composition of populations or metapopulations. Though natural selection does occur, individual fitness is also influenced by user-specified spatially explicit fitness values for each genotype that is selected upon.

EcoSim is a large-scale evolving predator-prey paradigmatic ecosystem simulation that can be used to perform studies in theoretical biology and ecology [43, 84]. It has been shown that EcoSim generates patterns as complex as those observed in real ecosystems [40]. Several studies have been done using EcoSim. Devaurs and Gras [28] have shown that the behavior of this model is realistic by comparing the species-abundance patterns observed in the simulation with real communities of species. Furthermore, chaotic behavior [40] with multi-fractal properties [41] of the system has been proved to be similar to that observed in real ecosystems [114], and Golestani, Gras, and Cristescu [43] have measured the effect of small geographic barriers on speciation in EcoSim. The effect of the spatial distribution of individuals on speciation has been investigated by Mashayekhi and Gras [83]. Khater et al. [61] demonstrated that introduction or removal of predators in an ecosystem can have widespread effects on the survival and evolution of prey by altering their genomes and behavior. Mashayekhi et al. [84] proved that the extinction mechanisms in EcoSim are similar to those of real communities. Lastly, a study by Gras et al. [46] used EcoSim to elicit the roles of natural selection and spatial isolation in the speciation process. They were able to unequivocally demonstrate that in order to observe genetic clusters (species), natural selection must be present. The number of individuals per species was much greater, species abundance distributions were far more even, the compactness and separation of genetic clusters were far greater, and hybrid production was far lower (after sufficient time had passed in the simulation) in runs where natural selection was present.

Real ecosystems are extremely complex systems with numerous interacting components and feedback loops. No paradigmatic model has all of the features of real ecosystems; consequently, these artificial systems are restricted to a small spectrum of possible questions to be answered. EcoSim was already quite complex and diverse in the types of questions it could answer, but we have added specific features to further improve its realism and applicability. Our objective is to propose to the community an improved simulation platform that models as many of the important features of real ecosystems as possible. Of course, not every significant feature of real ecosystems could be integrated into such a simulation platform. However, we have chosen a set of features that seem most important in modelling a stable, long-term evolutionary ecosystem and to provide the mechanisms needed to answer the largest

possible spectrum of important theoretical questions. The three most important features we have added to EcoSim are fertilization of soil via animal excretion, the ability of prey to defend against attacking predators (individually or cooperatively), and a female/male binary sex system with sexual reproduction. In previous iterations of EcoSim, individuals were of uniform sex and any two individuals of the same type (prey or predator) could attempt to reproduce.

There is a vast array of indirect impacts of herbivores on plant community features [6, 98]. Most importantly, herbivores affect the quantity and quality of organic matter returning to the soil [7, 8, 56, 126]. Generally, animal excreta facilitates decomposition through increasing soil microbial biomass [7, 34] and net Carbon (C) and Nitrogen (N) mineralization [35, 89]. Feces and urine also make it easier for plants to absorb, thereby increasing their growth rates [51]. Thus, herbivores are able to influence their own food supply [29, 54, 125] by producing negative feedback against the reduction of resources they consume. In order to include this complex feedback mechanism, we introduced a new concept to our simulated ecosystem called “fertilizer”, which models the effect of prey fertilizing their environment.

There is limited experimental evidence in the ecological literature regarding mobbing behavior as a kind of reciprocal altruism between heterospecifics. Krams et al. [67] and Krams et al. [68] report that breeding *Ficedula hypoleuca* (pied flycatchers) engage in mobbing behavior primarily with heterospecifics as a form of defense against predation. As Krams et al. [67] note, there is little empirical evidence for the existence of mobbing behavior as a form of reciprocal altruism. EcoSim could thus be used to test for mobbing behavior as a form of reciprocal defense in the presence of predation. In a related vein, an important unresolved debate in the biological literature is whether eusociality evolved via kin selection or group selection; Nowak et al. [96] claim that group selection rather than kin selection (inclusive fitness) combined with haplodiploidy theory is the best way to explain eusociality. They suggest that there may be no real relation between haplodiploidy and eusociality, and argue that inclusive fitness theory is not sufficiently general since it is a simple mathematical theory that has great limitations [96]. Furthermore, Nowak et al. [96] argue that there is no empirical confirmation of inclusive fitness theory. On the other hand, Marshall [82] and Abbot et al. [1] argue that recent evidence helps to support inclusive fitness theory. Since there is apparently an argumentative stalemate regarding whether kin selection or group selection drives evolution, EcoSim could help to resolve this debate by testing the hypothesis that kin selection explains the evolution of eusociality and altruism. Finally, another important issue in evolutionary theory is whether predation selects for morphological defenses in prey. Bollache et al. [14] argued that the main reason that the invasive amphipod *Gammarus roeseli* was eaten less than the native amphipod species *Gammarus pulex* was due to the presence of a spin on *G. roeseli*, as opposed to behavioral differences. EcoSim could be used to help resolve the debate regarding whether morphology or behavior is a key inducible defense against predators.

Typically, in sexually reproductive species in which sexual dimorphism exists, females are generally choosier than males when selecting mates. Compared to males, females typically invest far more resources (time and energy) into offspring. For

instance, females typically provide more parental care than males. Females also invest more in gametes for sexual reproduction; males produce the microgamete sperm, whereas females produce large, nutritious eggs. Moreover, unlike males, females only produce a limited number of eggs as long as they are reproductively active; therefore, there is more risk associated with mate choice [2]. To broaden the applicability and increase the realism of EcoSim, we introduced a model for sexual reproduction into the simulation. Previously, there was no categorization of individuals by sex; any individual could attempt reproduction with any other of the same type (prey with prey, predators with predators). Now, prey and predator individuals are divided into two groups, males and females. Furthermore, we have made significant modifications to reproduction mechanisms such as selection of mates, energy dynamics, and genetic recombination; these changes reflect the information-gathering and decision-making process that is mate choice [9]. These new improvements were aimed at unravelling some of the most controversial issues in behavioral ecology, such as the evolution of female preference.

In addition to presenting the new version of EcoSim following the updated 7-points Overview, Design concepts, and Details (ODD) standard protocol [47, 48], we present and discuss data from EcoSim in its default configuration. We also analyze the divergence of two sister species in EcoSim. We then present a sensitivity analysis on three parameters of EcoSim: the amount of energy spent per time step for prey and predators, the maximum amount of grass held in cells, and the initialization of newly added social concepts related to defense. The purpose of this sensitivity analysis was to show how sensitive or robust EcoSim is to these parameters. Finally, we present a case study of EcoSim's application; we determined the behavior and evolution of individuals under two conditions: reduced primary production (thereby increasing competition) and reduced energy expenditure. This study serves as an example of the types of study that are made possible by the EcoSim platform.

## 2 ODD Description of EcoSim

EcoSim is an individual-based ecosystem simulation [45, 85] for simulating 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 [84, 85]. 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 [47, 48]. 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>.

## 2.1 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; [66]) 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 predefined. Instead, fitness emerges from interactions between the model organisms and their biotic and abiotic environment.

## 2.2 Entities, State Variables, and Scales

### 2.2.1 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 newborn 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) that 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). 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).

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



**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 20,000 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

(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 [20], dependent on what the action is [11]. 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 [21]. In EcoSim, the size of each individual is modelled 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's body mass and their metabolic rate, which is best described by a 3/4 scaling exponent [53, 64, 65, 94, 102, 103, 107, 112, 116, 117]. Consequently, the metabolic rate of an individual in EcoSim is quantified through a power function of coefficient 3/4 on its MaxEnergy (Eqs. 1 and

2). Energy expenditure associated with movement is also modelled in EcoSim using the kinetic energy equation (KE), and here we use Strength as a proxy of mass ( $KE = mass \times speed^2$ , 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 [91, 92]. Individuals with a larger brain also require more energy, as the brain is an expensive organ in terms of specific chemical and thermoregulatory needs [31, 127]. Consequently, possessing a large brain leads to a heavier metabolic requirement [111]. 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 [115]. Therefore, we also include this parameter in calculating the energy spent by an individual. Taking these points into consideration, the energy spent by prey (1) and predators (2) at any time step is given by the following equations:

$$\begin{aligned}
 \text{Energy Spent by Prey} = & 0.8 \times \max((\text{NbArcs} - 100)^{0.75}, 1) \\
 & + \frac{(\text{Strength} \times \text{Speed}^2)}{10,000} + \left(\frac{\text{MaxEnergy}}{5.5}\right)^{0.75} \\
 & + (\text{Vision} \times 5.0)^{0.75} + (\text{MaxSpeed} \times 5)^{0.75} \\
 & + (\text{Defense} \times 100)^{0.75} + (\text{CoopDefense} \times 75)^{0.75} \\
 & + (\max(0.8 - \text{RepAge}))^{2.3}, \tag{1}
 \end{aligned}$$

$$\begin{aligned}
 \text{Energy Spent by Predator} = & (0.8 \times \max((\text{NbArcs} - 130)^{0.75}, 1)) \\
 & + \frac{(\text{Strength} \times \text{Speed}^2)}{11,000} + \left(\frac{\text{MaxEnergy}}{5.5}\right)^{0.75} \\
 & + (\text{Vision} \times 5.0)^{0.75} + (\text{MaxSpeed} \times 5)^{0.75} \\
 & + (\max(0.7 - \text{RepAge}))^{2.3}, \tag{2}
 \end{aligned}$$

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 (move to the closest prey in the vicinity, move to the cell with strongest prey, move to the cell with the greatest total prey strength, and move 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, search for food, socialize (move to the closest predator in the vicinity, move 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, after which its energy level and 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 that is its activation level (degree of stimulation) of its represented concept. Concepts can 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).

### 2.2.2 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).

### 2.2.3 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  $1000 \times 1000$  cells. The world is large enough that an individual moving in the same direction over the course of its entire life could not even cross half of it, 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 requirements (time and memory) of the simulation.

### 2.2.4 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).

## 2.3 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:
  - 1.1. Perceive environment
  - 1.2. Compute next action
  - 1.3. Increase Age
  - 1.4. Females that chose to Reproduce act in order of decreasing Strength (to simulate female choice in mate selection)
  - 1.5. Remaining prey act in order of decreasing Strength
  - 1.6. Update list of prey (as some may have died due to depletion of Energy or maximum Age)
2. For predator individuals:
  - 2.1. Perceive environment
  - 2.2. Compute next action
  - 2.3. Increase Age
  - 2.4. Females that chose to Reproduce act in order of decreasing Strength (to simulate female choice in mate selection)
  - 2.5. Remaining predators act in order of decreasing Strength
  - 2.6. 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
  - 7.1. Update Fertilizer level
  - 7.2. Update Grass level
  - 7.3. Update Meat level

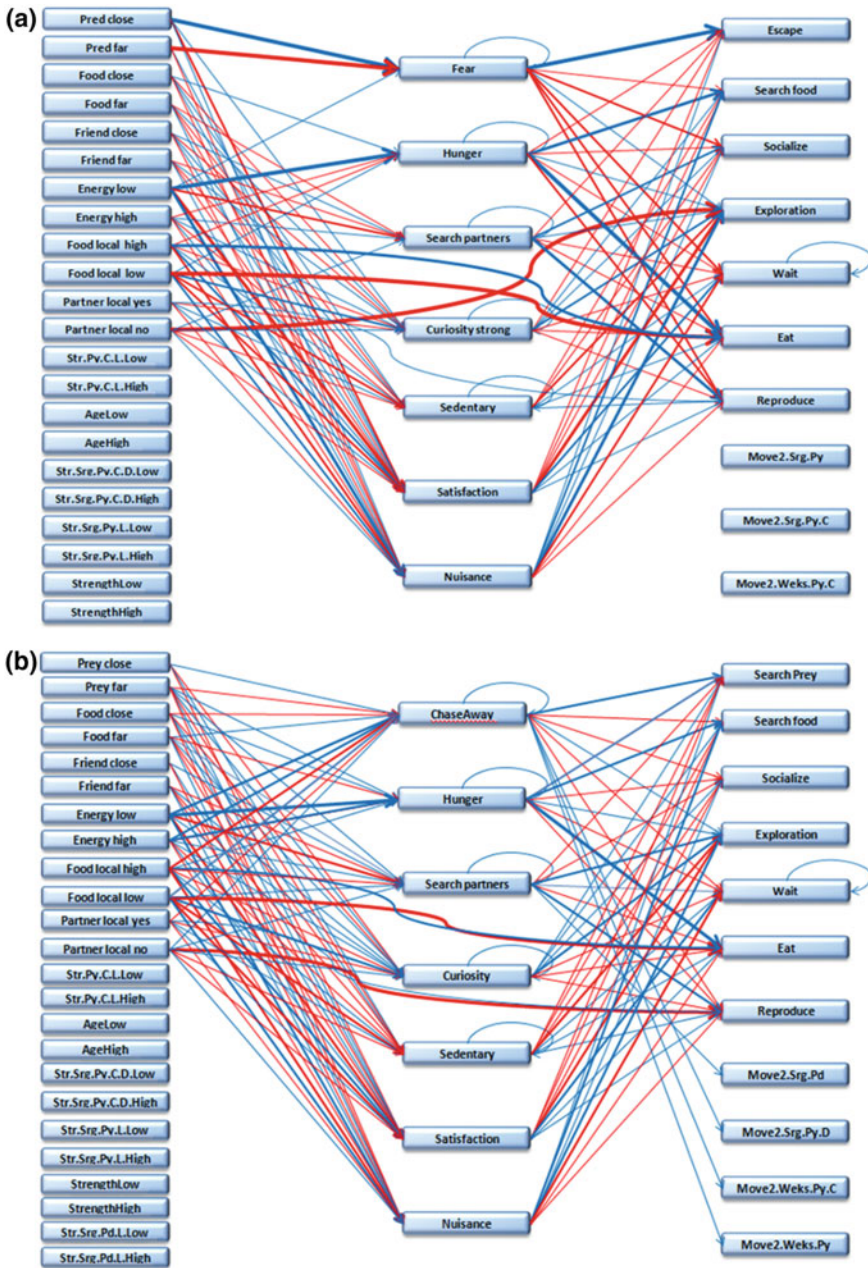
The complexity of the simulation algorithm is mostly linear with respect to the number of individuals. If we consider that there are  $N_1$  prey and  $N_2$  predators, then the complexity of parts 1 and 2 of the above algorithm, including the clustering algorithm used for speciation, will be  $O(N_1)$  and  $O(N_2)$ , respectively [4]. The sorting parts (parts 3 and 4) have a complexity of  $O(N_1 \log(N_1))$  and  $O(N_2 \log(N_2))$ , but are negligible in computational time so we will exclude them from the complexity computation. The complexity of parts 5 and 6 will be  $O(N_1 + N_2)$ . The virtual world of the simulation has  $1000 \times 1000$  cells, therefore the complexity of part 7 will be  $O(k = 1000 \times 1000)$ . As a result, the overall complexity of the algorithm is  $O(2N_1 + 2N_2 + k)$ , which is  $O(N = 2N_1 + 2N_2)$ . 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 20,000 time steps in 60 days.

## 2.4 Design Concepts

### 2.4.1 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 values that represent its physical attributes (see Table 1, inherited traits).

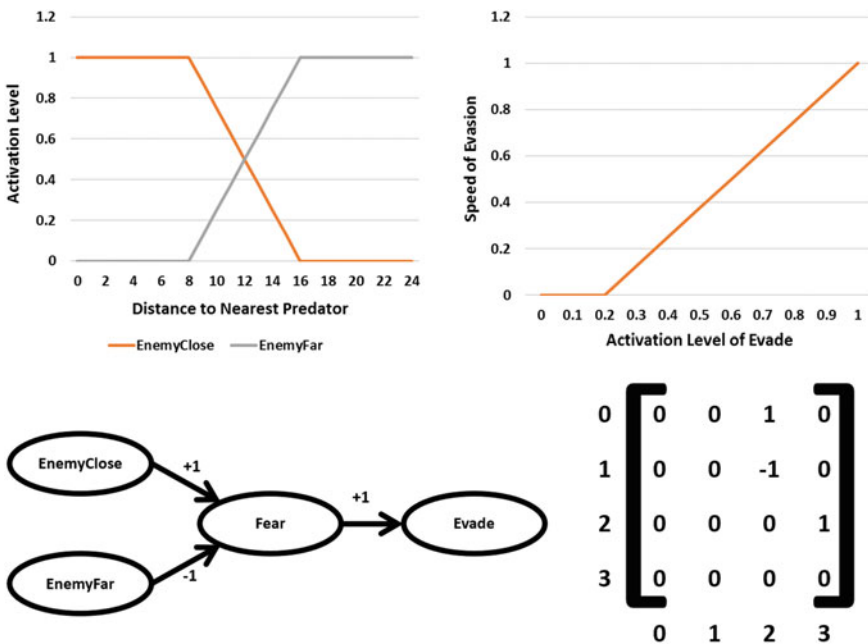
The behavioral model of each individual is encoded as an FCM [45] (Fig. 1). Formally, an FCM is a directed graph that contains a set of nodes  $C$  and a set of edges  $I$  (Fig. 1); [66]. Each node  $C_i$  represents a concept and each edge  $I_{ij}$  represents the influence of the concept  $C_i$  on the concept  $C_j$ . A positive weight associated with the edge  $I_{ij}$  corresponds to an excitation of the concept  $C_j$  from the concept  $C_i$ , whereas a negative weight represents inhibition. A zero value indicates that there is no influence of  $C_i$  on  $C_j$ . The edges of an FCM can be represented by an  $n \times n$  matrix,  $L$ , in which  $n$  is the number of concepts and  $L_{ij}$  is the influence of the concept  $C_i$  on the concept  $C_j$ . If  $L_{ij} = 0$ , there is no edge between  $C_i$  and  $C_j$ . 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 every one of an individual's nodes represent the individual's behavioral state. In each FCM, three kinds of concept 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



**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) with another (where the edge points to), and blue edges indicate positive association (excitation). The thickness of the edges represents the magnitude of the gene. The leftmost column of nodes is sensory concepts, the middle is internal concepts, and the rightmost is 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

a fuzzification of the information that 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).

We will illustrate the operation of the FCM with a simplified example prey FCM (Fig. 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



**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. The 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

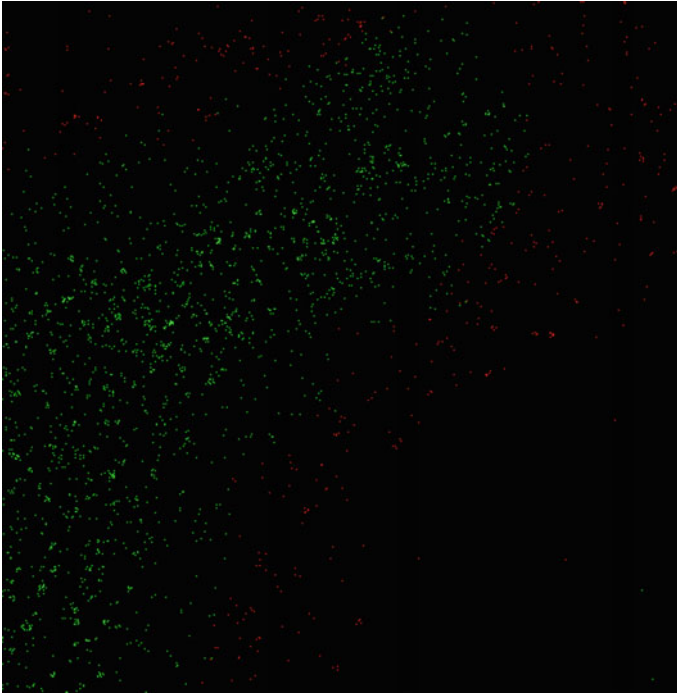
weights are the edge values from the behavioral genome. From our example, Fear has incident edges from EnemyClose and EnemyFar, thus we use edge weights from the behavioral genome for EnemyClose  $\rightarrow$  Fear and EnemyFar  $\rightarrow$  Fear to compute the weighted sum. The same computation is 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  $\rightarrow$  Evade), the corresponding genes have values of zero. However, as individuals evolve, new edges can be added and pre-existing edges could be removed.

### 2.4.2 Emergence

This representation of the behavioral model allows for 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 that 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 the way in which 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 ([42]; Fig. 3).





**Fig. 3** A cropped image of an EcoSim run at time step 20,000. Hungry predator individuals (red) chase fleeing prey individuals (green), one of the many contributory factors to the emergent high-level movement patterns we observe

### 2.4.3 Adaptation

The behavioral genome's 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 nonzero values at initialization. Each gene of the behavioural genome follows the continuum-of-alleles model [19] 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 the 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 differs 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 a step. For byte value  $k$ , its floating-point equivalent is  $\text{minimum} + (k \times \text{step})$ . 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 weighted 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 a probability of 0.001), removal of existing edges (with a probability of 0.0005), and changes in the weights associated with existing edges (with a 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 ( $\text{Age} > \text{MaxAgeRepAge}$ ). 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 [46].

$$ME_o = \begin{cases} \frac{5 \times ME_m + ME_f}{6}, & \text{if offspring is female} \\ \frac{5 \times ME_f + ME_m}{6}, & \text{if offspring is male} \end{cases} \quad (3)$$

#### 2.4.4 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 predefined explicit fitness-seeking process in the simulation; rather, fitness is a consequence of natural selection. Individuals who 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 [45, 46]. The fitness value is only computed for analysis of the results of the simulation and is not used in process during the simulation.

#### 2.4.5 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 lifetime. 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.

#### 2.4.6 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  $\text{Strength} \times (1 + \text{Defense})$  of prey in their cell, the distance to the cell in vision range with the highest sum of  $\text{prey Strength} \times (1 + \text{Defense})$ , and the maximum  $\text{strength} \times (1 + \text{Defense})$  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.

#### 2.4.7 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 that 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 [15]. 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 [15]. Competition in EcoSim, like in most ecosystems, is neither purely contest or scramble competition; elements of both forms of competition can be observed.

### 2.4.8 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,  $x_n$  and  $y_n$  (the  $x$  and  $y$  coordinates for the position of the  $n$ 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*. Furthermore, 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 into the grass diffusion model (see *Submodels* for elaboration). To understand the extent of stochasticity in EcoSim, Golestani and Gras [40] 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 are instead like those observed in complex biological systems [60].

## 2.4.9 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 60,000–1,000,000 prey and 2000–30,000 predators at any time step, depending on the parameterization of the run.

In EcoSim, it is necessary to compute the genetic distance between any two genomes of the same type (prey or predator) in order 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 [80] 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 predefined threshold for speciation, a 2-means clustering is performed [4], otherwise  $S$  stays unchanged.

To initialize the 2-means clustering process, one center is assigned to a random individual, denoted  $I_r$ , and the other center is assigned to the individual who is the most genetically different from  $I_r$ . 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.

#### 2.4.10 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 characteristics 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 the HDF5 format [123] with an average size of 6 gigabytes. Also, there is a possibility of storing all of the values of every variable in the current state of the simulation in a separate file, creating the possibility of restoring 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 of the data is stored in a compact special format, to facilitate storage and future analysis. There are also several utility programs that 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, to generate video of the world throughout a run or some portion of it, and to draw the FCM of the individuals.

#### 2.4.11 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 the 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 of 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

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

User-specified parameter	Used value
Number of prey	80,000
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

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 by 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.

## 2.5 Submodels

### 2.5.1 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 that 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 nonzero amount of grass. Fertilizer, a feature new to EcoSim, is derived from the excretions of individuals. AmountOfFertilizer, the amount of fertilizer in a cell, is proportional to the sum of maximum energy (MaxEnergy) of the prey and predators residing in that cell, limited to a total of 20,000. 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 amount of grass 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 in such a way 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 still limited 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.

## 2.5.2 Actions

For each movement action  $M$ , the movement speed is equal to  $\text{MaxSpeed} \times \text{ActivationLevel}(M)$ , thus the speed at which an individual moves during the action depends on its willingness to perform it. Movement speed is the straightline 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 predator's 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,  $\min(\text{MaxEnergy Energy}, \text{MeatUnits})$ , 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 defense capability, as well as cooperative defense, and use them in a battle against the predator [3].

Prey defense and cooperative defense is passive; prey defend automatically if they have a nonzero Defense value and are targeted by a predator, or if they have a nonzero 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 Defense and the Strength of the attacked prey;  $CPi.D$ ,  $CPi.CD$ , and  $CPi.S$  are the Defense, CoopDefense, 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 that are involved in a cooperative defense also lose some amount of Energy based on the strength of the predator ( $0.2 \times \text{PredatorStrength}/\text{NumberOfDefenders}$ ). 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.

$$P = AP \cdot D \times AP \cdot S + \sum_i (CP_i \cdot D \times CP_i \cdot CD \times CP_i \cdot S) \quad (4)$$

3. 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.
4. 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.
5. Exploring. A direction is computed randomly. The individual moves at its speed in this direction.
6. Resting. Nothing happens.
7. 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,  $\min(\text{MaxEnergy CurrentEnergy}, \text{EnergyUnits})$ , where EnergyUnits is the number of grass (meat) energy units in the cell. EnergyUnits is decreased by the amount consumed by the individual.
8. 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, the Y chromosome in male offspring is exclusively acquired from the father [52]. 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 that 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 of being male or female. Then, the initial Energy (Energy<sub>0</sub>) 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).

$$\text{Energy}_0 = \frac{ME_f \times SOB_f \times ME_m \times SOB_m}{100}. \quad (5)$$

Finally, the Energy of the two parents is decreased. The energy penalty for the mother,  $penalty_m$ , 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 subsequent pregnancies. The energy penalty for the father is based on Eq. (7).

$$penalty_m = \frac{SOB_m \times Energy \times 1.05}{SOB_m + SOB_f} + FPP \quad (6)$$

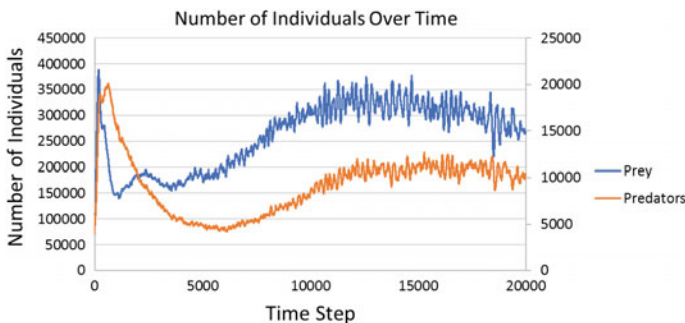
$$penalty_f = \frac{SOB_f \times Energy \times 1.05}{SOB_f + SOB_m}. \quad (7)$$

9. 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.
10. 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 defense against predators.
11. 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 a higher chance of success in competition with other prey individuals in accessing food or mates.
12. 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.
13. 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.
14. 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 defense by prey individuals.

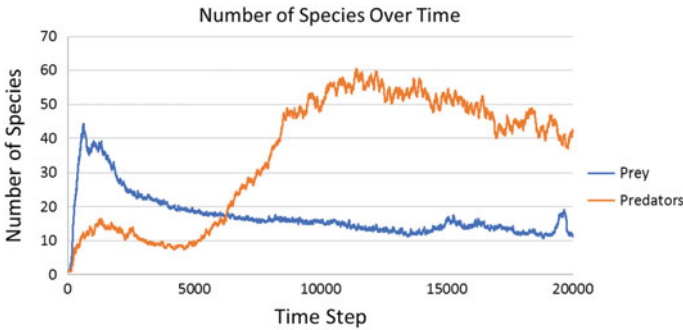
## 2.6 Ecological and Evolutionary Properties of EcoSim

Time-series data are generated automatically by EcoSim per time step, as explained above. We computed ten runs of EcoSim in the default configuration (which we hereby refer to as Default) to 20,000 time steps. Using external tools that have already existed, we computed the mean of several important measures for these ten runs. We computed the number of prey and predator individuals, the number of prey and predator species, the mean distance evolved of all female individuals, and three physical attributes for all female individuals (MaxEnergy, MaxSpeed, and Vision). Distance evolved is computed by first computing the mean genome for all individuals at a given time step and subsequently computing the genetic distance from this genome to the prey genome that the simulation was initialized with.

As expected, there was a dependency between number of prey and predators (Fig. 4). At initialization of the simulation, the number of prey is greater than the number of predators (80,000 and 4,000, respectively). Therefore, we tend to observe an early spike in the number of prey, which subsequently sharply declines when the number of predator individuals rises. The increasing number of prey provides a good chance for the predators to have access to more food, resulting in an increasing in their Energy and reproduction rate. The resulting increase in hunting by predators accompanied by local food resource shortages for prey decreases the number of prey, and consequently the number of predators, ultimately leading to stabilization of the system. A similar phenomenon occurs at finer spatial scales; local population explosions and extinctions yield fine-scaled fluctuations in numbers of individuals over time, with a time lag between the fluctuations in number of prey and predators. This dependence of predator population on prey population is known as the Lotka-Volterra model, as outlined in Berryman [10] and empirically corroborated by Piana et al. [105] where they fitted the model to a time series dataset of 16 species of neotropical fish that were classified as either predators or prey. These time series mostly stabilize with these small fluctuations, resulting in 268,871 prey (SD=80,804) and 10,388 predators (SD=2,613.4). As Britten et al. [16] observed, this stabilization



**Fig. 4** The number of prey (left y-axis) and predator (right y-axis) individuals in the world, over the course of the simulation

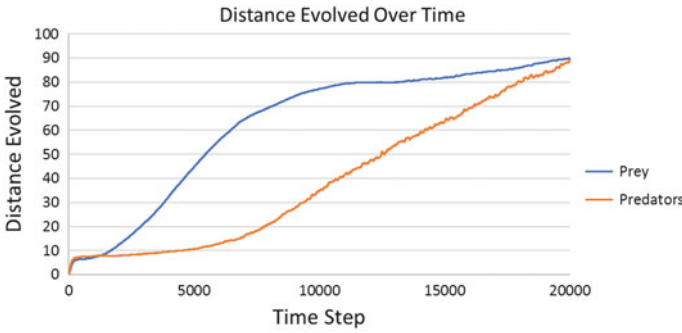


**Fig. 5** The number of prey and predator species throughout the course of the simulation

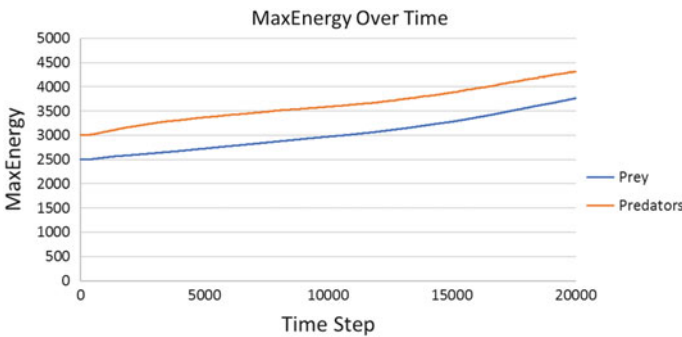
can be jeopardized if there is a sudden decline in predator species in such a predator-prey system.

The number of species more strongly correlated with the number of individuals for predators than for prey (Fig. 5). Generally, an increase in the number of individuals allows for a corresponding increase in variation within the gene pool, and this increased variation tends to lead to increased speciation [62]. However, with the number of prey individuals so high, the gene flow is also very high, which results in overall genetic convergence. Spatial separation in individuals reduces gene flow. With fewer predator individuals in the world, there is greater spatial separation overall amongst predators, providing a greater opportunity for the subpopulations to genetically differentiate and ultimately yield new species. As Hoskin et al. [57] argued, reduced gene flow in allopatry results in the gradual emergence of reproductive isolation, and subsequently new species; this has been observed in EcoSim as well [43].

The prey and predator distance evolved were comparable by the end of the simulation (Fig. 6). However, at the end of the simulation, the rate of predator evolution was greater than that of prey. In fact, nearly halfway through the simulation, the distance evolved for prey hit a plateau. This highlights an important distinction—that the prey (with such a high number of individuals) evolved rapidly but in a convergent manner whereas the predators evolved more slowly but with high differentiation across all individuals. As Brodie and Brodie [17], as well as Brodie et al. [18], observe, predators that pursue prey with multiple defenses will tend to adapt evolutionarily, which may in part explain the higher rate of evolution of predators versus prey. Two main factors are responsible for the convergent evolution in prey: the aforementioned high gene flow and the fact that natural selection occurs in EcoSim, since there is no predefined fitness function [46, 61]. The fitness landscape in EcoSim is dynamic overall; both the prey and predators evolve simultaneously and the world state is constantly changing. However, many aspects of the world remain constant, such as MaxGrass, the functions that govern energy expenditure of the individuals, and the rules that govern processes like reproduction. Thus, some genetic convergence should be expected—certain behavioral and physical genotypes will be desirable regardless of the world state at any given time step. The high genetic divergence



**Fig. 6** The distance evolved for prey and predators throughout the course of the simulation

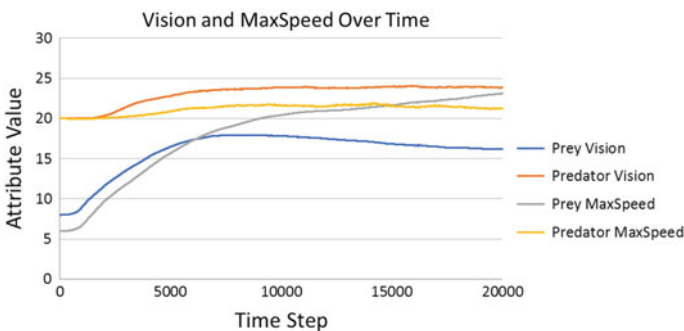


**Fig. 7** The evolution of MaxEnergy for prey and predators throughout the course of the simulation

accumulated early by the predators (apparent in the number of species over time) lead to faster overall evolution later in the simulation. Another factor contributory to the fast evolution of predators later in the simulation is that there is more potential for divergence in the predator behavioral genome; the prey behavioral genome has 663 elements, whereas that of predators has 756. It is inevitable that predators will eventually evolve in a more convergent manner as well; this is observable in the subtle decrease in predator evolutionary rate over time.

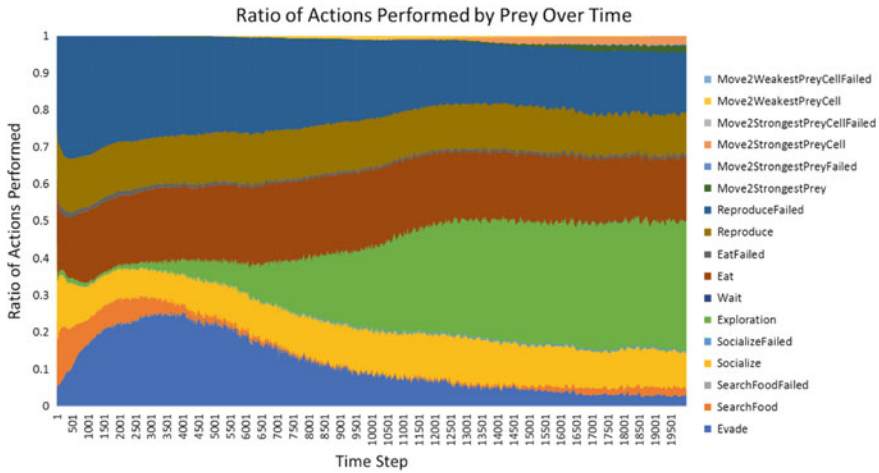
MaxEnergy evolved similarly for both prey and predators (Fig. 7). In both cases, it monotonically increased from the initial values of 2500 for prey and 3000 for predators to an average of 3763 (SD = 505.7) and 4310 (SD = 372.3), respectively. As Strength is related to MaxEnergy, this could represent a type of evolutionary arms race because of the possibility of prey fighting back against predators when they attack. Alternatively, a higher maximum energy capacity may be strictly beneficial for the individuals, because it allows individuals to survive longer between Eat actions. Moller [88] performed estimates of basal metabolism rate (BMR) of 76 bird species who were pursued by predators. The author reports that birds with longer flight initiation distances used to escape predators also had higher BMRs, from which he concludes that predation creates a selection pressure on species to develop higher

BMRs [88]. Thus, it is possible that the higher maximum energy capacity is necessary in individuals due to an increased BMR. Furthermore, the energy dynamics of each physical attribute is governed in part by the energy consumption functions for prey and predators. Thus, it is possible that with a more heavily penalized MaxEnergy, it might be less prone to such a runaway. Vision and MaxSpeed are related in that individuals must both perceive a resource (a mate, food, etc.) and be able to move to it in order to use it immediately. Otherwise, the individual will have to wait for at least one time step until it can use the resource it desires, which may be too late, depending on the state of the individual and the environment around it. Thus, we should expect that Vision and MaxSpeed evolve in a related and intuitive manner. Predator Vision and MaxSpeed appeared to be heavily related in the way we expected (Fig. 8). That is, both Vision and MaxSpeed evolved to slightly increase and then slightly decrease, nearly in unison, with Vision always greater than MaxSpeed. This is intuitive because it is particularly imperative for predators to perceive their resources; potential mates are far less abundant for predators and their food resources are constantly changing positions in the world. This observation has been empirically corroborated in a study of predatory bird species conducted by Garamszegi et al. [37], in which it was found that predatory species evolved increased visual acuity along with larger brains to detect prey. On the other hand, it is less important for prey to perceive their resources, but it is important for prey to move quickly to evade predators. Potential mates and food resources are far more abundant for prey, and their food resources are static in the world (unless a cell's grass is fully consumed before the prey can reach it). Furthermore, over time, we observed that prey tended to perform the Evade action decreasingly, while they increasingly performed Explore instead (Fig. 9). The directionality of the Explore action is randomly generated, and with the high prey density, it is possible that when they Explore, they can randomly discover mates or food resources while they simultaneously evade predators. If all prey in a particular wave performed Evade when faced with a predator, many of the prey individuals would move in a similar direction, which could increase competition for resources. On the other hand, increasingly performing Explore may be evidence of the evolution



**Fig. 8** The evolution of Vision and MaxSpeed for prey and predators throughout the course of the simulation





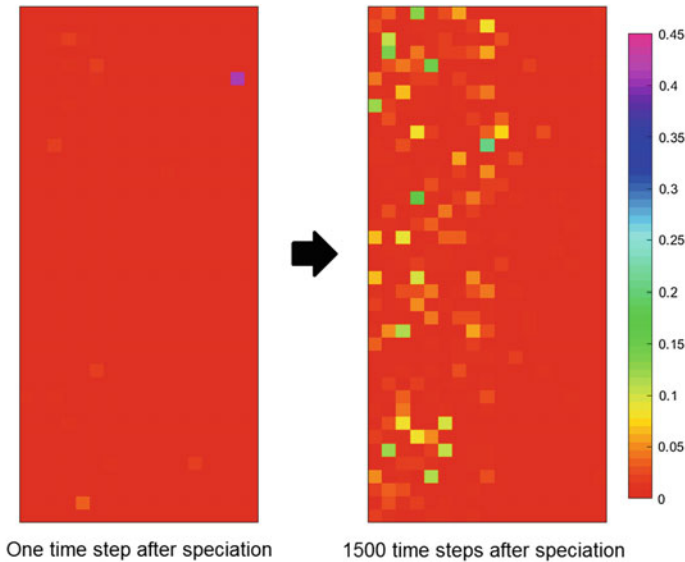
**Fig. 9** Selection of actions by prey over time. Prey evolved to Evade less and Explore more, while simultaneously reducing their reproduction failure rate (ReproduceFailed). Evolution of an increase in Move2StrongestPreyCell and Move2StrongestPrey is also observed

of altruism; if a small percentage of prey purposely sacrifice themselves by moving towards the wave of predators (using Explore rather than Evade), it keeps the wave of predators away from the highest-density prey regions.

### 2.7 Divergence of Sister Species

From a single Default EcoSim run, we found two sister species (species 1 and species 40) that coexisted for 1860 time steps. Species 40 was produced at time step 246 of this particular run and went extinct at time step 2106, while species 1 was produced at initialization and persisted to the end of the simulation. We analyzed divergence of the behavioral and physical genomes of these two species throughout their coexistence.

In EcoSim, depending on the genomes within a species, differentiation of very few genes can be sufficient to trigger a speciation. When species 40 was initially produced, only one gene in the behavioral genome showed a high degree of differentiation, though 1500 time steps later the species were highly diverged in other ways (Fig. 10). Interestingly, in this case, the allele that caused the initial speciation disappeared from species 40 over 1500 time steps. This indicates that although the appearance of this allele was sufficient to cause speciation, the allele was likely deleterious and was evolved out of the species over time. This was corroborated by the fact that the change that caused the initial speciation was an evolution of the mean value of the gene FriendFar→Move2StrongestPreyCell to 0.41 in species 40, which had a mean value of -0.00020 in species 1. With no friend nearby, attempting to move to the cell with the highest cumulative strength would likely be a waste of energy and an action. Furthermore, the genetic distance between behavioral genomes of

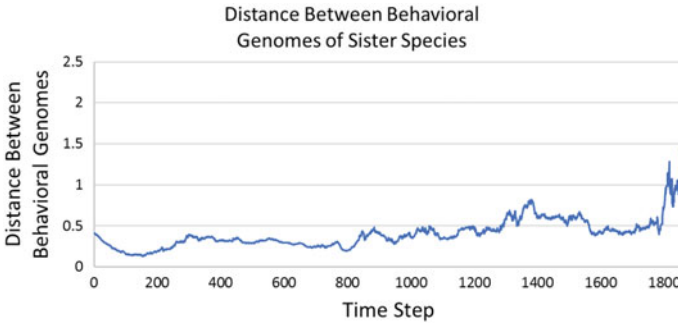


**Fig. 10** Divergence of behavior models of two sister species over 1500 time steps. Each square represents the absolute difference of a gene in the average behavioral genome of two sister species from a single run of EcoSim. Though differentiation of one gene was sufficient to cause the initial speciation (purple square in left heatmap), over time, the behavioral genomes diverged substantially

these two species declined over the first 175 time steps after speciation (due to the loss of the aforementioned allele in species 40) and then rose over the subsequent time steps due to the differentiation in the other behavioral genes (Fig. 11). Another factor contributing to the initial decline in genetic distance is low spatial separation (implying high gene flow) between the species shortly after the speciation event, with increased spatial separation and genetic divergence thereafter. EcoSim allows hybridization (reproduction between individuals of different species; see *Collectives, Reproducing* under *Submodels*), thus when two species are genetically similar enough and not spatially separated, their individuals can reproduce to form hybrid offspring. Being sister species generated very early in a run, the physical genomes between these species did not differentiate.

## 2.8 Sensitivity Analysis of EcoSim

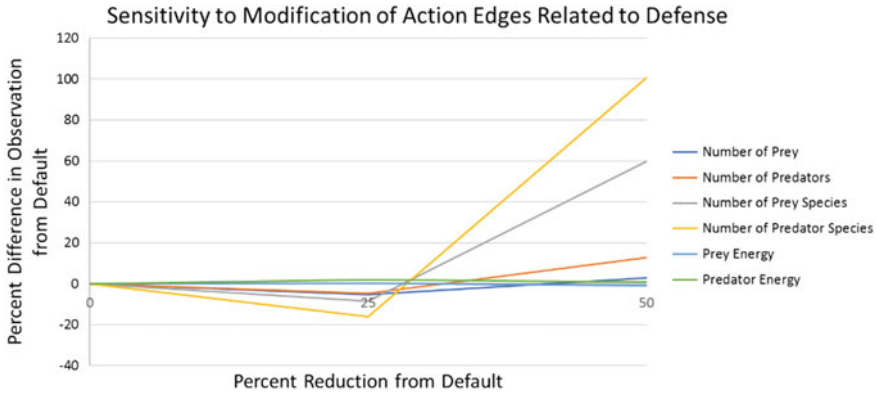
In addition to the ten Default EcoSim runs noted above, we computed ten runs each of EcoSim with the following modifications: reduction of initial social action edges related to defense by 25% of their default value (referred to hereon as RSE25), reduction of initial social action edges related to defense by 50% of their default value (referred to hereon as RSE50), reduction of energy spent by all individuals by 25% of



**Fig. 11** Genetic distance between behavioral genomes of sister species throughout their coexistence, computed as Euclidean distance between average behavioral genomes. After a slight decline in genetic distance due to the loss of a deleterious allele in the smaller species and hybridization along the interface of the two species, the behavioral genomes of the species diverged over time

the default (referred to hereon as RE25), reduction of energy spent by all individuals by 50% of the default value (referred to hereby as RE50), reduction of MaxGrass by 25% of the default value (referred to hereby as RMG25), and reduction of MaxGrass by 50% of the default value (referred to hereon as RMG50). For RSE25 and RSE50, the affected edges for prey were all edges incident to Move2StrongestPrey, Move2StrongestPreyCell, and Move2WeakestPreyCell. The affected edges in these runs for predators were all edges incident to Move2StrongestPredator, Move2StrongestPreyDistance, Move2WeakestPreyCell, and Move2WeakestPrey. For each of these runs, we computed the mean across ten runs and across time steps 5,000 through 6,000 for the following measures: number of prey and predator individuals, number of prey and predator species, mean energy level of all female prey individuals, and mean energy level for all female predator individuals. We computed these values over a window of 1,000 time steps, because many of the above measures show different behaviors at different scales. For instance, the number of prey or predator individuals at a very high scale may appear to follow the classic growth curve, with an initial lag period followed by a period of nearly linear growth that reduces in rate of increase as it approaches its asymptote (the carrying capacity of the system) and ultimately oscillates below the asymptote. At a smaller scale, however, many small cycles can typically be observed due to local population explosions and extinctions. For each treatment (reduction of energy spent, reduction of maximum grass, and reduction of social edges related to defense), we compared values of each observation to the respective values generated by Default EcoSim runs and determined the percent change in these observations. This allowed us to determine how sensitive or robust the system is to these changes, and it also allowed us to determine how these observations behaved relative to the different treatments (for example, to determine if a reduction in MaxGrass yields a linearly dependent reduction in number of prey individuals or number of prey species).

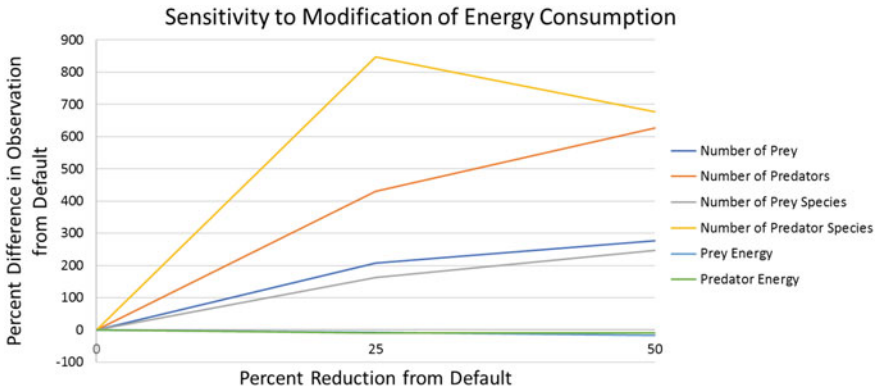
We expected that modifications in the action edges related to defense would yield nonlinear and nonmonotonic relationships to most of the dependent variables, as



**Fig. 12** Sensitivity of several variables to modification of action edges related to prey defense

we applied this modification to both prey and predators. None of the measures we computed were sensitive to these modifications ( $t$ -test  $p \geq 0.15$  in all cases), and the amounts of energy of prey and predator individuals were particularly insensitive. Interestingly, both prey and predator number of individuals and species declined slightly when these edges were reduced by 25%, if both increased when these edges were reduced by 50%, but insignificantly so (Fig. 12). Though the percent difference from Default runs was very high for some of these measures, the difference was statistically insignificant due to extremely high variance (only one run was responsible for these very high values).

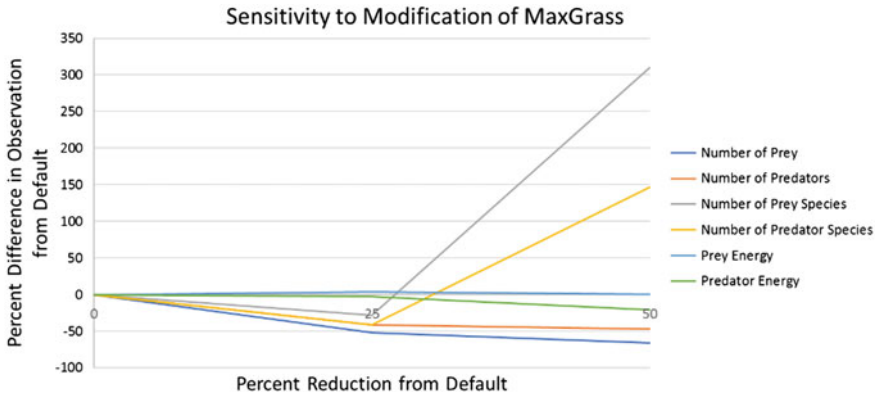
Modifications to the rate of Energy consumption of both prey and predators significantly impacted all of the variables we analyzed ( $t$ -test  $p \leq 0.0006$  in all cases, Fig. 13). The number of prey increased to 208% of the Default value with a 25% decrease in Energy consumption, and increased further to 277% of the Default value with a 50% decrease in Energy consumption. The number of predators followed a similar trend, increasing to 431 and 626% of the Default values, respectively. Both prey and predator numbers seemed affected by diminishing returns based on reduction of Energy consumption, most likely due to increased competition when Energy consumption was decreased. The effect of reduction of Energy consumption was stronger at higher trophic levels; the effect of Energy consumption on number of predators was almost double that on number of prey. Not surprisingly, the number of predator and prey species both increase significantly with reduction of Energy consumption, though the number of prey species closely followed the trend of number of prey individuals. The number of predator species, on the other hand, did not follow the trend of the number of predator individuals; there appeared to be a tipping point where decreasing Energy consumption actually decreased the number of predator species, despite their increasing number of individuals. This is due to the interplay between genetic variation across the population and gene flow; more individuals allows for more potential genetic variation (which should increase the number of species), but more individuals also increases gene flow (which should decrease the number of species). Decreasing the Energy consumption of predator and prey



**Fig. 13** Sensitivity of several variables to modification of Energy consumption per time step for both prey and predators

individuals actually decreased their mean Energy levels by 8–16%. The decreasing of Energy consumption provides the individuals with increased longevity and potential to reproduce, because their physical and behavioral traits are energetically less expensive to maintain. Thus, as we observed, the number of individuals increases drastically and disproportionately given the reduction in Energy consumption. With such a drastic increase in the number of individuals given the same food resource supply, competition strongly increased as well. Consequently, the individuals have a significantly lower Energy level.

Modifications to MaxGrass proportionally (and almost linearly) affected some variables while nonlinearly affecting other variables (Fig. 14). The differences between RMG25 and Default runs were almost all statistically significant ( $t$ -test  $p < 0.01$  for all comparisons, except predator number of species,  $p = 0.10$ , and predator energy,  $p = 0.33$ ). Similarly, differences between RMG50 and Default runs were mostly very statistically significant, yielding  $t$ -test  $p < 0.0001$  (except predator number of species, which was still significant, with  $p = 0.0015$ , and prey energy, which was not, with  $p = 0.78$ ). For instance, with a 25% and 50% reduction in MaxGrass, the number of prey individuals was reduced by 51.7% and 65.8%, respectively. Similarly, the number of predators were respectively reduced by 41.2% and 47.3%. With a 25% reduction in MaxGrass, both prey and predator number of species decreased (by 28.1% and 41.0%, respectively), while they both increased (by 309.9% and 146.3%, respectively) with a 50% reduction in MaxGrass. With only a 25% reduction in MaxGrass, it is possible that the reduction in number of prey and predators is sufficient to reduce the genetic variation across the populations while insufficient to reduce gene flow such that speciation increases. Thus, a net decrease in the number of species of each type was observed. Conversely, with a 50% reduction in MaxGrass, the number of individuals was so greatly reduced that gene flow between subpopulations was practically halted, which allowed for very high differentiation between spatially separated individuals, and consequently a high number of species. The vast difference in number of predator species given such a slight change



**Fig. 14** Sensitivity of several variables to modification of MaxGrass

in number of predator individuals between RMG25 and RMG50 runs could also be explained by increased fragmentation of prey subpopulations. The predators must follow the prey in order to survive, and spatially fragmented prey subpopulations should yield spatially fragmented predator subpopulations. Interestingly, prey and predator energy levels were largely unaffected by this modification, though predator energy was reduced by 20.6% in RMG50 runs. Overall, some aspects of the system are sensitive to MaxGrass and many others may be nonlinearly affected by modifications to it.

### 3 Case Study: Application of EcoSim to Study Behavior and Evolution Under Conditions of Reduced Primary Production and Reduced Energy Expenditure

The focus of this case study will be twofold: to investigate possible links between both intraspecific and interspecific competition for resources and evolution, as well as examine possible links between energy expenditure of organisms and evolution.

First, a number of studies have found evidence of a link between competition within and between species and the evolution of morphology, as well as the evolution of resource polymorphism and temporal variation. Pafilis et al. [101] maintain that, in general, resource availability and competition (and predation) drive the evolution of body size. They conducted an empirical study in which they showed that in the presence of a high number of breeding seabirds, there is an increase in lizard population densities, which in turn results in increased intraspecific competition for resources [101]. Pafilis et al. [101] report that the resultant increase in competition for resources leads to the evolution of large body sizes (gigantism) in a species of lizards (*Podarcis gaigeae*). Along the same lines, Svanback et al. [121], in an empirical study, report that a species of perch (*Perca fluviatilis*) and a species of roach

(*Rutilus rutilus*) that cohabitate two regions of a lake were deeper bodied in the littoral region versus individuals caught in the pelagic region, which they attributed to intraspecific competition. On the other hand, Grant and Grant [44] discovered that interspecific competition between two species of Darwin's finches (*Geospiza fortis* vs. *G. magnirostris*) resulted in the divergence of beak sizes.

In addition, Svanback et al. [121], cited above, found evidence of resource polymorphism in the fish and roach species, so that fish and roaches in the littoral region fed on different sorts of organisms versus their counterparts in the pelagic region. Svanback and Bolnick [120] studied a sympatric population of three-spine stickleback fish (*Gasterosteus aculeatus*) for which there was an increase in population density, thereby increasing intraspecific competition for prey. The result was diet variation between phenotypically different stickleback individuals so that some fish found alternative prey [120], although the authors attributed some of this resource polymorphism to phenotypic plasticity rather than to evolution. Marini et al. [81] demonstrated that interspecific competition between two species of mosquito (*Cx. pipiens* and *Ae. albopictus*) resulted in a shift in temporal dynamics for both species. The result is that the species tend to be in a common breeding site at different times to minimize overlap [81]. Strauss et al. [119] note that few studies have investigated the evolutionary effects of invasive species on native species. In reviewing studies on a variety of animal species, the authors conclude that, amongst other contexts (e.g., predation), invasive species as competitors drive evolution in native species [119].

Secondly, recent biological research has uncovered possible links between energy expenditure and animal morphology, as well as the rate of evolution. In a comprehensive literature review, Niven and Laughlin [95] report that the reduction of energy expenditure has driven the evolution of the morphology of sensory systems in a wide variety of vertebrate and invertebrate animal species. For example, animals that live on islands where there is limited energy due to scarce resources tend to lose some of their sensory systems, such as vision, in order to conserve energy [95]. In the same vein, Navarrette et al. [93] argue that the evolution of encephalization in humans is the result of the stabilization of energy inputs along with a redirection of energy from locomotion, reproduction and growth. Furthermore, Jasienska [59] hypothesizes that reproductive suppression in humans has evolved as a way of dealing with low energy. As Leonard and Ulijaszek [78] report, the role of energetics in the evolution of humans is an emerging domain.

Using a plethora of data relating to substitution rates for mitochondrial and nuclear genomes of a variety of vertebrate and invertebrate organisms, Gillooly et al. [38] argue that there is a direct link between the rate of energy transformation in metabolism and the rate of nucleotide substitution. In particular, they claim that smaller organisms (with a higher metabolic rate) evolve faster than larger organisms. Using a DNA-based phylogenetic analysis of 86 angiosperm plant sister species across environments with varying energy levels, Davies et al. [24] found that evolutionary rates are higher amongst populations in higher energy environments. According to the authors, many non-energetic variables such as geographical complexity and history contribute to species richness and rate of evolution in plant species, so that discerning the role of energetics with respect to these phenomena is an

important area of investigation. Finally, an empirical study conducted by Mönkkönen et al. [90] found that energy use in a variety of North American and European forest birds translated into species diversification.

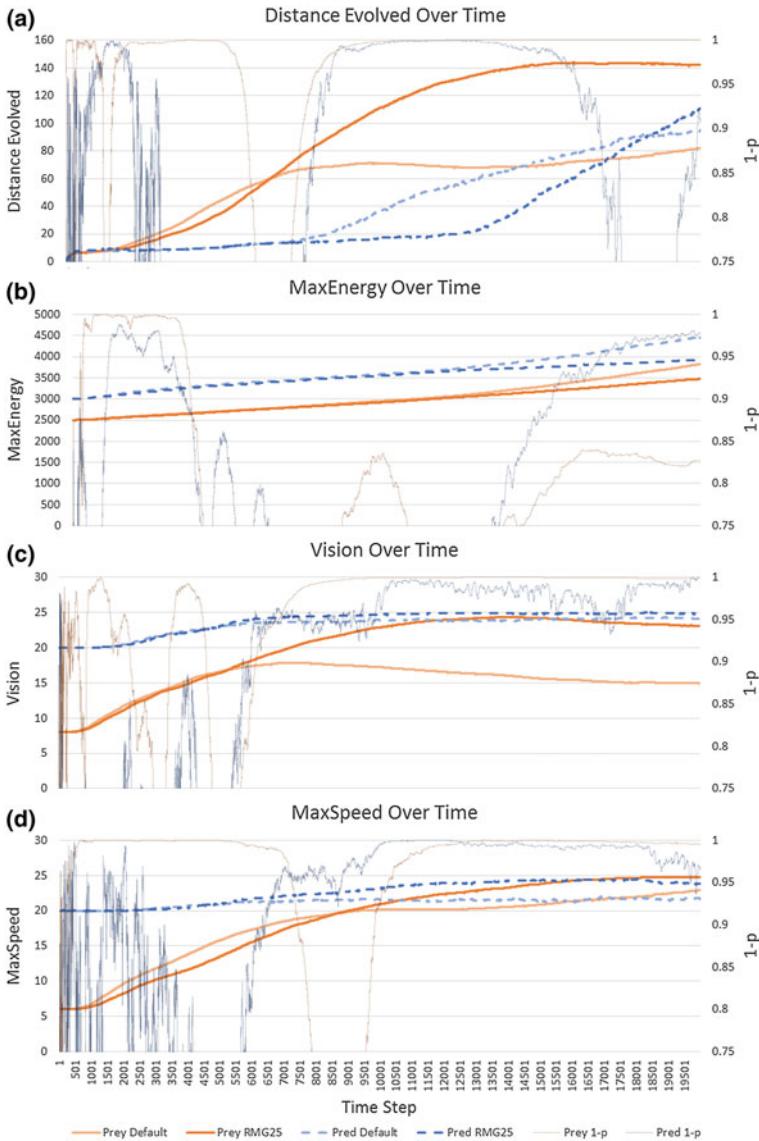
Besides shedding additional light on the connections between competition, energetics, and evolution, this study will help to address several open questions in ecology and evolution relating to these issues. First, our study will help to elucidate the effects of competition for limited resources on evolution. Secondly, our simulation study will help to determine the role of energetics in the evolution of morphology, which is regarded as an emerging domain by Leonard and Ulijaszek [78].

Using five runs each of the aforementioned Default, RMG25, and RE25 Eco-Sim variants, we aimed to determine differences in the way which individuals behave and evolve under conditions of reduced primary production (modelled by the RMG25 runs) and energy expenditure (modelled by the RE25 runs). Of the ten runs of each variant, we selected the five runs that were most progressed due to computational time constraints. To determine differences in behavior, we computed the mean percentage of individuals performing each action at each time step across the five runs of each type, and analyzed these time series data for differences over time. To determine differences in evolution of the behavioral genome, we compared distance evolved over time. Furthermore, we compared the evolution of physical traits such as vision range (Vision), maximum energy (MaxEnergy), and maximum speed (MaxSpeed). Since the RMG25 runs have lower amounts of grass (and consequently lower carrying capacities for prey and predators), they run very fast. Therefore, we analyzed the RMG25 runs to 20,000 time steps. The RE25 variant allows individuals to retain more energy and survive better, thus there are significantly more predators and prey in these runs. Consequently, they run slower, and we had to limit our analysis of RE25 runs to 10,000 time steps.

### ***3.1 Reduced Primary Production***

Both prey and predators evolved differently in several ways when primary production was reduced, compared to the Default scenario (Fig. 15). The amount of differentiation between the mean behavioral genome at a given time step and that at initialization (Distance Evolved) showed stark contrast between the two scenarios for prey starting at approximately 7000 time steps (Fig. 15a). Prior to that, prey living in high primary production evolved faster than those living in reduced primary production, and sometimes significantly so ( $t$ -test  $p < 0.05$ ). However, after 7000 time steps, the prey in an environment with low primary production evolved much faster ( $t$ -test  $p < 0.001$ ). The same phenomenon was observed for predators, however, the point at which those living in low primary production evolved further than those in high primary production came much later, at approximately 18,300 time steps. Friman et al. [36] report that the evolution of prey-predator interactions is driven by the availability of prey resources, although evolution of anti-predator defenses was greater in the presence of high resources. Along the same lines, Hiltunen et al.





**Fig. 15** Comparison of four measures related to evolution of prey and predator individuals between Default and RMG25 runs over time. Each measure uses the left y-axis while the  $t$ -test  $1 - p$  value uses the right axis.  $T$ -test  $1 - p$  value shows the significance of difference between Default and RMG25 runs for prey and predators separately. Distance evolved **a** is the genetic distance between behavioral genomes at initialization and the mean of all individuals at a given time step. MaxEnergy **(b)**, Vision **(c)**, and MaxSpeed **(d)** are physical properties determining the maximum energy capacity, vision range, and maximum movement speed of individuals, respectively. Values shown are the mean of all individuals alive at the given time step

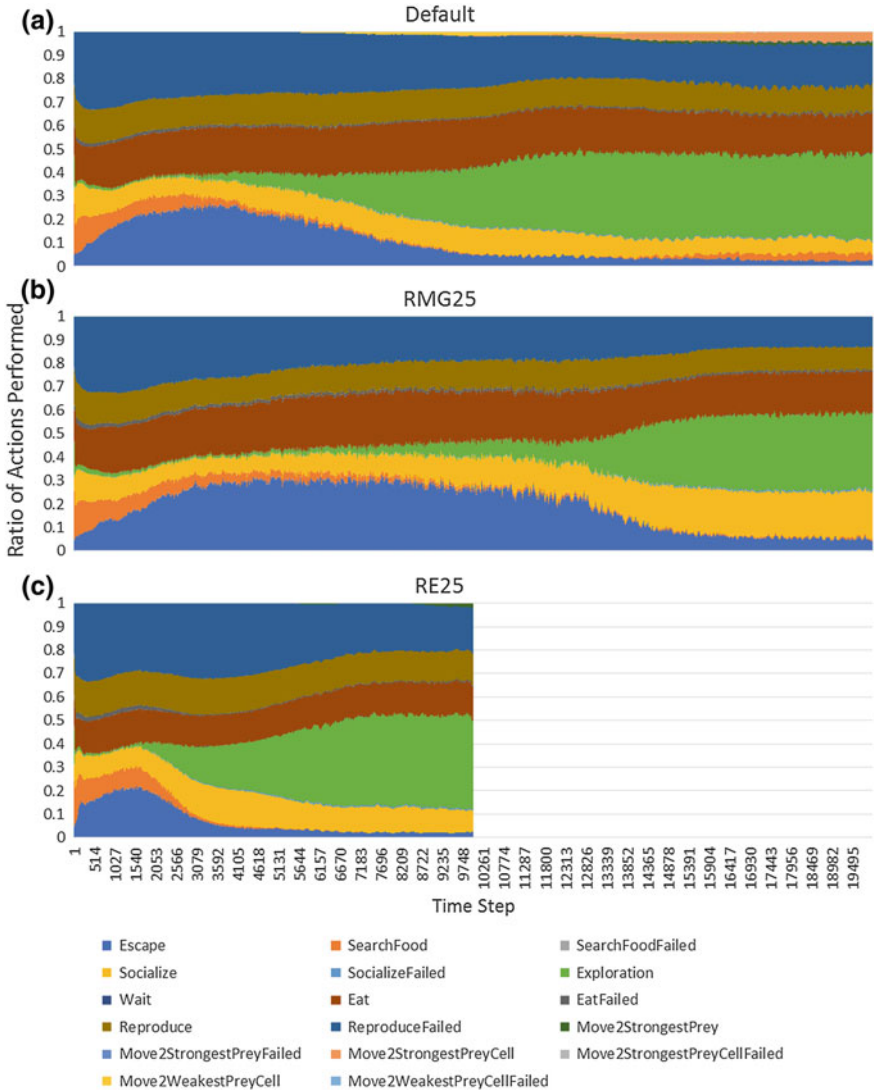
[55] report that in an experimental predator-prey system involving bacteria (*P. fluorescens*) and ciliates (*T. thermophila*), evolution of anti-predator defenses evolved at a higher rate in stable resources versus fluctuating resources. All of these results agree with what we found in our simulations. We have two main hypotheses as to why we observe these phenomena, and they are not mutually exclusive. First, this is a long-term evolutionary effect of differences in density. Reduced density of prey and predators when primary production is reduced caused a reduction in gene flow, which has been shown to increase evolutionary rates of populations. Secondly, as Distance Evolved is a measurement of evolutionary change from the initial populations, it is quite possible that the initial behavioral genome is simply more similar to the optimal genomes of the Default runs. Disputing this claim, the optimal genome is a moving target in EcoSim, as there is no fixed fitness function and the state of the simulation is highly dynamic. Furthermore, Distance Evolved is showing increasing trends in all cases, and it is impossible to determine whether it will ever equilibrate. Currently, we cannot force EcoSim to retain a constant density of prey or predators despite changing environmental conditions, which is a limitation in this particular situation. However, it is much more realistic, as in nature, the density of individuals is always dynamic and influenced by environmental conditions.

MaxEnergy displayed an increasing trend overall (Fig. 15b) and individuals in an environment with high primary production evolved a higher energy capacity—statistically significantly so in the case of predators and approaching statistical significance for prey. It is reasonable that individuals from an environment with high primary production evolve a higher energy capacity. Prey individuals can consume all of the Grass contents of a cell in a single Eat action, and each action is a highly valuable resource. Thus, it is highly beneficial to prey to obtain and retain as much Energy as possible when they do perform Eat. With a higher MaxEnergy, prey individuals can use their Eat actions more efficiently by storing more Energy per eat event. As Lewis and Kappler [76] observe, female lemurs (*Propithecus verreauxi verreauxi*) that inhabit seasonal environments will have higher body mass when there is an abundance of resources during the wet season, and during this time, they are more likely to reproduce and wean infant offspring. Furthermore, MaxEnergy influences Strength, as both are proxies for the size of the individual. A predator must have greater Strength than its prey target has Energy for a Hunt action to succeed. Thus, as prey MaxEnergy increases, that of the predators must as well. What we are observing is an evolutionary arms race between prey and predators, and the maximum amount of primary production in each cell significantly impacts the way in which this arms race occurs, as noted by Friman et al. [36].

Vision reached an equilibrium with high and low primary production for both predators and prey, except in the case of predators in low primary production, in which it evolved to its maximum value of 25 (Fig. 15c). For both predators and prey, after approximately 10,000 time steps, the difference in Vision between runs with high and low primary production was almost always statistically significant ( $t$ -test  $p < 0.05$ ) and individuals living in low primary production evolved higher Vision. This result shows that despite the Energy cost of maintaining Vision, there is a significant advantage to being able to perceive more potential resources (such

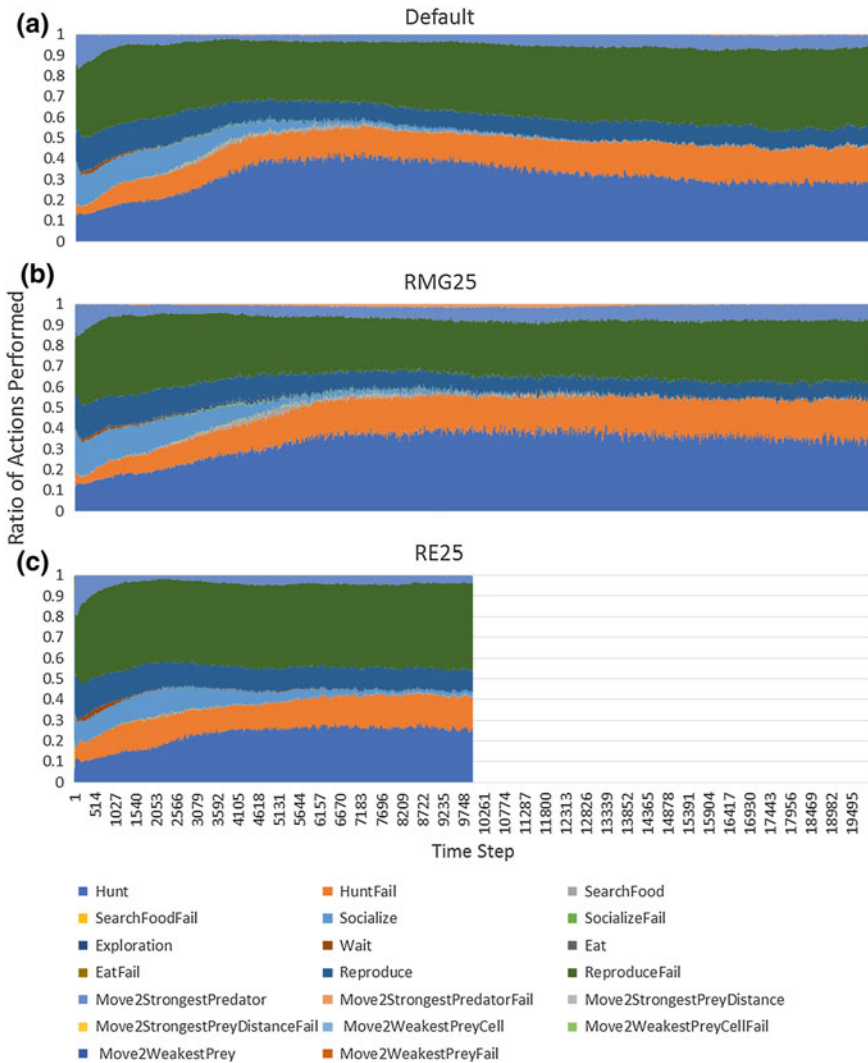
as mates and food) and competitors, particularly when food resources are scarcer. As Eklöf et al. [30] report, five species of insectivorous bats of the family Vespertilionidae developed different types and levels of visual acuity depending on the type of foraging they engaged in. Along similar lines, Potier et al. [106] observe that the visual abilities of two raptor species (*Parabuteo unicinctus* and *Milvus migrans*) differ according to their foraging activity. Reduced primary production effectively reduces the carrying capacity per cell, which increases the intensity of competition for resources within each cell. Thus, it is imperative to the survival of individuals to be able to obtain information about the locations of potential food and competitors so they can reduce their competition. In the same way, individuals evolve to move faster when primary production is reduced (Fig. 15d). Having a higher MaxSpeed aids in the dispersal of individuals, which serves to reduce competition amongst them. As stated earlier, MaxSpeed and Vision are highly related and tend to evolve together, because individuals can only move to positions with resources when they perceive these resources. Thus, the emergent pattern of evolution of MaxSpeed mirroring that of Vision is not surprising, and the difference between runs with high and low primary production were, again, mostly significant after time step 10,000. Similar to the evolution of MaxGrass, the evolution of both Vision and MaxSpeed may also represent an evolutionary arms race—a higher Vision range and MaxSpeed in prey means that they can perceive and evade potential threats more easily. We observed slight overall increases in both Vision and MaxSpeed in predators as well, despite the fact that these traits were already initialized to much higher values for predators.

Mirroring the differences in rate of behavioral evolution between the two EcoSim variants noted above, we observed many differences in the resultant behavior selections of the individuals (Fig. 16a, b—prey; Fig. 17a, b—predators). For prey, we observed significant differences in Reproduce and ReproduceFail. Overall, prey in an environment with high primary production both succeeded and failed to reproduce far more than those in an environment with low primary production, as they attempted to reproduce far more often ( $t$ -test  $p < 0.05$  for much of the time series). The reason for this is twofold: Reproduce is very costly in terms of Energy, and Reproduce requires that individuals are in the same cell. Due to the Energy cost of reproduction, when primary production is low, individuals reduce reproduction to save Energy. Furthermore, as Reproduce requires individuals to be in the same cell, with lower prey density, this is much harder to achieve when primary production is low. We observed insignificant differences in Eat success, but in an environment with reduced primary production, EatFail was significantly higher ( $t$ -test  $p < 0.05$  for most of the time series). This indicates that the prey were heavily affected by competition for food resources. Initially counterintuitively, we observed that prey Socialized significantly more often when primary production was reduced ( $t$ -test  $p < 0.05$  for most of the time series). This was counterintuitive because Socialize brings individuals together, and it was expected that prey would aim to reduce their competition with reduced primary production by reducing their Socialization. Furthermore, we observed insignificant differences in prey Compactness, the mean number of prey individuals per cell for all cells containing at least one prey individual (defined analogously for predators). However, with lower prey density, Socialize is an important mechanism for improving



**Fig. 16** Mean ratios of actions performed by prey in Default, RMG25, and RE25 EcoSim runs. Due to computational time constraints, RE25 runs were terminated at 10,000 time steps

reproduction success, as reproduction requires that mates be in the same cell. Because Compactness was not different despite significant differences in Socialize, it is likely that prey in RMG25 runs Socialize as a means to increase Reproduce success, and then disperse after in order to reduce subsequent competition. In fact, we found that actions aiding in dispersal (Escape, SearchForFood, and Explore) were performed 19% more often after Reproduction attempts in RMG25 runs than in Default runs,



**Fig. 17** Mean ratios of actions performed by predators in Default, RMG25, and RE25 EcoSim runs. Due to computational time constraints, RE25 runs were terminated at 10,000 time steps

and Reproduce was attempted after Socialize 21% more often in an RMG25 run than in a Default run. To determine this, we tracked all actions performed by all individuals born in time steps 20,000–20,010 for a single Default and RMG25 run.

Similar actions ratios overall were observed for predators between the two run types, but there was significantly more Reproduce success with high primary production for the same reasons for which we observed this phenomenon in prey (*t*-test  $p < 0.05$  for much of the time series). With many of the other actions yielding

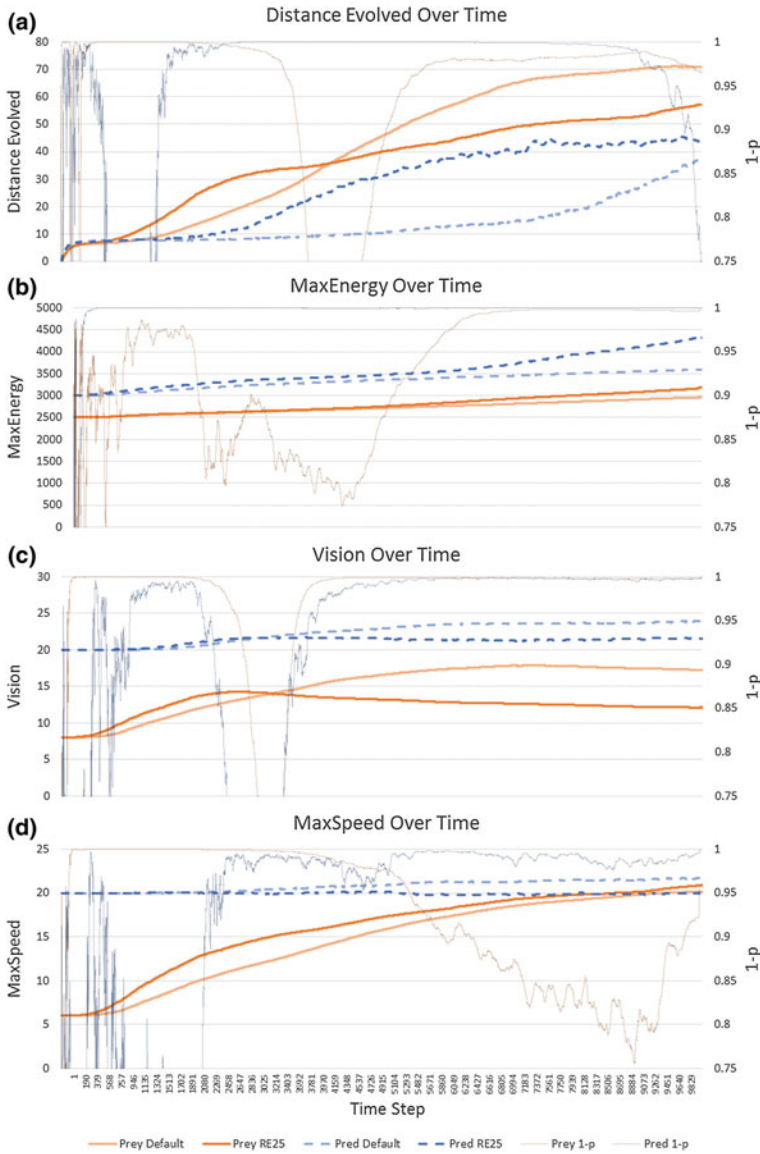
insignificant difference, the other time series affected by primary production was the ratio of Hunt actions performed. Predators must Hunt more with low primary production because prey are scarcer, they must take the opportunity to obtain Energy when the opportunity presents itself.

### 3.2 *Reduced Energy Expenditure*

Both prey and predators followed different evolutionary trajectories with reduced Energy expenditure when compared to Default EcoSim runs (Fig. 18). The behavioral genomes of prey with reduced Energy expenditure evolved faster than in Default runs prior to approximately 4000 time steps, which agrees with the experimental results obtained in Gillooly et al. [38], in which it was found that animals with lower energy expenditure evolved at a faster rate than animals with higher energy expenditure. However, after 4000 time steps we found that prey with reduced energy expenditure lagged behind in rate of evolution thereafter (Fig. 18a,  $t$ -test  $p < 0.05$  for most of the time series). Prior to 10,000 time steps, behavioral genomes of predators with reduced Energy expenditure evolved faster than their Default counterparts, which once again agrees with the results obtained in Gillooly et al. ([38], although near the end of the runs, it appeared inevitable that Default predators would ultimately overtake those in RE25 in terms of Distance Evolved (Fig. 18a,  $t$ -test  $p < 0.05$  until approximately 9500 time steps). The shapes of these curves bear strong resemblance to those of Distance Evolved when Default runs were compared to RMG25, however, here the roles are reversed. The common element between the two graphs is that the runs with significantly higher numbers of individuals exhibited faster evolution in prey and predators early in the run, only to be overtaken by the runs with lower number of individuals later on. This corroborates our speculations regarding the links between number of individuals, spatial separation of individuals, and gene flow.

Similarly, the shape of curves for MaxEnergy over time comparing Default and RE25 runs (Fig. 18b) are very similar to those comparing Default and RMG25 runs, though again, the roles are reversed (MaxEnergy in RE25 runs is greater than that in Default runs,  $t$ -test  $p < 0.05$  after 5600 time steps for prey,  $p < 0.001$  after 500 time steps for predators). Of all the determinants of Energy expenditure, MaxEnergy (a proxy of the size of the individual) plays the strongest role for both prey and predator individuals, as it is penalized directly in the Energy functions and also indirectly through the cost associated with Speed of movement in a given time step. Thus, as expected, individuals with reduced Energy expenditure per time step evolved to be larger, more rapidly.

Conversely, we did not entirely expect what we observed for evolution of Vision and MaxSpeed when comparing Default runs to RE25 (Fig. 18c, d), in light of the Energy costs associated with maintaining these features. We observed that individuals from Default EcoSim runs evolved greater Vision and MaxSpeed than their RE25 counterparts ( $t$ -test  $p < 0.05$  after 4000 time steps), in all cases except for MaxSpeed of prey. The results pertaining to visual acuity do, in fact, agree with empirical find-



**Fig. 18** Comparison of four measures related to evolution of prey and predator individuals between Default and RE25 runs over time. Each measure uses the left y-axis, while the  $t$ -test  $1 - p$  value uses the right axis. The  $T$ -test  $1 - p$  value shows the significance of the difference between Default and RE25 runs for prey and predators separately. Distance evolved **a** is the genetic distance between behavioral genomes at initialization and the mean of all individuals at a given time step. MaxEnergy **(b)**, Vision **(c)**, and MaxSpeed **(d)** are physical properties determining the maximum energy capacity, vision range, and maximum movement speed of individuals, respectively. Values shown are the mean of all individuals alive at the given time step

ings in the literature when we consider them in light of evolution of body size. Kiltie [63] found a positive correlation between body size and visual acuity across various species of birds, so that larger birds with higher energy expenditure exhibit higher visual acuity than smaller birds with lower energy expenditure. Moreover, Mech and Zollner [87] report a positive correlation between body size and perceptual range for various forest dwelling rodent species, including chipmunks, grey squirrels and fox squirrels. Finally, Rutowski, Gislen and Warrant [110] found that visual acuity increases with body size across four species of nymphalid butterfly. We expected that cheaper Energy costs associated with maintaining Vision and MaxSpeed would allow them to evolve to larger values, much like MaxEnergy. However, relatively, Vision and MaxSpeed play much smaller roles in determining the Energy expenditure of individuals per time step but crucial roles in determining the fitness of individuals. With reduced Energy consumption, the number of both prey and predator individuals was far greater than in Default runs. This result agrees with the empirical findings reported in McNab [86] with respect to a variety of vertebrate species inhabiting oceanic islands. Species with lower energy expenditure persist on oceanic islands by means of population increases, as opposed to species with higher energy expenditures [86]. As the number of individuals is much greater, so is the density of individuals, and thus finding mates is far less difficult. Furthermore, as individuals expend less Energy, they less often need to find food resources in order to survive. Thus, for both predators and prey, it is reasonable that, despite the cheaper cost of maintaining Vision and MaxSpeed, the importance of maintaining these features was overbearingly diminished as well in RE25 runs. The only anomaly is MaxSpeed of prey, however, at approximately 5000 time steps, the difference between the two run types was mostly insignificant, following a very similar trend to the earlier comparison regarding primary production. At approximately 9000 time steps in that comparison, MaxSpeed of RMG25 runs overtook that of Default runs. It is quite possible that in the long term, such a phenomenon would be observed here.

We observed several changes in behavior of prey (Fig. 16a, c) and predators (Fig. 17a, c) when their resource consumption was decreased. In prey, most notably, individuals in RE25 far more rapidly evolved a general loss in the ability to Evade predators and a reduction in Eat attempts, while only gaining in their frequency of Explore ( $t$ -test  $p < 0.05$  in all cases, for most of the runs). Ultimately, in Default runs, the loss of Evade occurs as well, but at a much later time ( $\sim 10,000$  time steps versus 5000 time steps), and Explore still occurred significantly less in the long term ( $t$ -test  $p < 0.05$  comparing Default time steps 16,000–20,000 against RE25 time steps 6000–10,000, for most of the time series). The rapid loss of the ability to Evade speaks to the futility in attempting to do so—in RE25 runs, the number of predators (and, accordingly, their density) was significantly greater ( $t$ -test  $p < 0.05$  for most of the duration of the runs), and thus performing Evade was insufficient in prolonging the lives of prey individuals. The reduction in prey Eat attempts was expected, again because the individuals require less Energy to persist. The remaining prey behaviors showed no deviation between the two EcoSim variants.

Predators in RE25 runs showed a significant reduction in frequency of Hunt when compared to Default runs ( $t$ -test  $p < 0.05$  for most of the time series), in accordance



with what was observed in prey. Like prey, the predators in RE25 required less Energy to survive, and thus evolved to spend fewer actions on obtaining Energy. Unlike prey, however, the predators of RE25 did not show an increase in Explore (which is sensible, as Explore has very little value to predators as it is). Instead, predators evolved to attempt Reproduction significantly more often in RE25 runs when compared to Default runs ( $t$ -test  $p < 0.05$  for most of the time series). Generally, as predators have much lower density, they also have a much harder time finding mates, and consequently, they tend to exhibit far more ReproduceFail than prey. In RE25 runs, with predator density greatly increased and Energy requirements slightly reduced, allocating more actions and Energy to Reproduction is necessary to improve their fitness. Thus, with the RE25 variant of EcoSim, both prey and predators get what they need to improve their fitness: the prey improve their longevity and the predators improve their fecundity through greater chance of Reproduction success.

## 4 Conclusion

We added many new features to EcoSim, improving the breadth and depth of questions it can now answer. The new features include new sensing and action concepts in the FCM of individuals, sexual reproduction, realistic feedback via fertilization of primary producers by consumers, and predator-prey combat, among others. In addition, new physical traits have been added to the behavioral genome, allowing different niches to emerge. Our results underline the importance of competition and energetics in evolution, and the great complexity that can emerge from relatively simplistic individuals. Our model reveals insights into the genetic mechanisms of niche adaptation, advances our understanding of both evolution and ecology, and allows us to address more complicated biological questions at resolutions varying from individual to whole communities. This is a major advantage of IBMs over empirical studies in the real world or other types of model; using IBMs, we are able to record anything we want at the resolution of the individual, something that would largely not be practical or possible otherwise. Of course, EcoSim and the general IBM approach has its drawbacks as well. Every IBM requires substantial simplification of the system it aims to replicate; as Box said regarding all scientific models, “All models are wrong but some are useful” [13]. Thus, the simplifications and assumptions made by an IBM must be understood before using it as an experimental platform, and conclusions made from use of the model must be considered in light of its assumptions and simplifications. For the same reason, it is sometimes difficult to generate new hypotheses using the IBM approach; researchers must ask themselves if the novelty of their conclusions is legitimate or, again, due to assumptions or simplifications of the model. Furthermore, many IBMs require substantial computing power, and EcoSim is no exception. Many IBMs, particularly those that would be considered pragmatic, require significant model tuning and validation to ensure legitimacy of the data they generate. Being at an early stage of the analysis of the new version of EcoSim, these preliminary results are promising and will lead to

some more dedicated studies on niche emergence, reproduction, ecology, and evolution. For instance, EcoSim is currently being used to perform exciting research on sexual selection, the evolution of communication (particularly, communication of fear), asexual versus sexual reproduction, and biological invasions.

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