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Building adaptive and flexible individual-based ecological models for a changing world via pattern-guided evolution

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Abstract

In a changing world, ecologists have an important role in examining the impacts of environmental changes, and formulating strategies for adapting to these changes, such as engineering sustainable ecosystems that are integrated with human society. Some ecological models supporting these processes need to model species’ adaptive responses to changing conditions. Individual-based models (IBMs) can be used to simulate intergenerational adaptation by implementing model organisms parameterized with structures analogous to genetic chromosomes. IBMs may be calibrated and validated using the pattern-oriented approach, in which model outputs are compared to field data patterns, generally at the end of each simulation. In some circumstances this approach may be limited and computationally expensive when applied to IBMs with adaptive mechanisms. This research explores an approach for using field data patterns, obtained from published research, to guide the evolution of model organisms within each model simulation. An adaptive IBM of an old-field ecosystem consisting of spiders, grasshoppers and plants was constructed using Repast Simphony to demonstrate the approach. The approach produced persistent ecosystem simulations matching aspects of field data patterns, and yielded populations of virtual organisms with phenotypic diversity. The approach produces flexible IBMs and may contribute towards improving model and data sharing within the ecological modelling community.

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1. Introduction

The role of the ecologist and environmental scientist is an important one in a changing world. Assessing and managing the impacts of environmental changes, as well as developing techniques for

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building adaptive, resilient, and sustainable ecosystems that are integrated with human society, such as those explored in the field of ecological engineering (described in [1]), present humanity with some of its greatest challenges. Ecological models to support these processes are likely to be diverse, including and expanding upon existing modelling approaches (summarized in [2]). Some of these models however, will undoubtedly need to simulate the adaptive responses of biological organisms to changing conditions.

Individual-based models (IBMs) have the capacity to model organism adaptation, both intergenerational (evolutionary) adaptation and adaptive behavioral responses that occur within the lifetime of individual organisms (discussed in [3]). IBMs model individual variability, heterogeneous distribution, local interactions and organism behaviors (described in [4]). Within an IBM, individual organism attributes and behaviors may be parameterized with inheritable ‘genetic’ structures, thus facilitating intergenerational adaptation via modeled reproductive life-cycles. This approach has been used to construct evolutionary IBMs for studying life-history and behavior evolution of various ecosystems, including those described in [5, 6].

IBMs may be developed and validated using the pattern-oriented modelling (POM) approach (described in [7]), whereby the model outputs are compared to known patterns, often sourced from field data. The process of calibrating the parameters of an IBM using the POM approach generally involves examining the final output of many simulation runs, and is generally limited by computational resources (discussed in [8]). IBMs with evolutionary mechanisms have been validated using the POM approach (in [6]). However, in many circumstances, evolutionary trajectories in simulated ecosystems are unlikely to result in final simulation outputs that reflect real-world pattern data (discussed in [9]), particularly without limiting the number or ranges of inheritable parameters. The POM approach may be especially limited for use with many IBMs that incorporate intergenerational adaptation.

This research explores an approach for using field data patterns to guide the evolution of model organisms within each model simulation, rather than comparing patterns to final model outputs of multiple simulations, as is typical of the POM approach. To demonstrate the pattern-guided evolution approach, an adaptive IBM of an old-field ecosystem located in Connecticut, USA was constructed, based on an IBM described in [10]. The model consisted of spider predators (*Pisaurina mira*), grasshopper prey (*Melanoplus femurrubrum*), and their plant habitat and food resource, represented simply as grass and herbs. As in [10], the model aims to replicate observed dietary shifts that grasshoppers tend to make in response to predation risk from spiders. The pattern-guided evolution approach provides, to the best of the authors’ knowledge, a novel method for developing IBMs that incorporate intergenerational adaptation, and whose outputs match field data patterns. The approach also yields populations of model organisms with parametric diversity, thereby reducing model rigidity, and potentially allowing model components to be reused in different models (as discussed in [11, 12]).

The next section presents an overview of the pattern-guided evolution method. Following that, Section 3 describes the model used to demonstrate the approach. Section 4 outlines the simulations performed with the demonstration model. The results from these simulations are presented in Section 5 and discussed in Section 6. Finally, Section 7 presents conclusions that have been made so far within the research, and explores possibilities for future research.
2. Method overview

The pattern-guided evolution method involved augmenting an individual-based model (IBM) with selective mechanisms for guiding the evolution of model organisms using field data patterns. To facilitate intergenerational adaptation, organism reproductive life-cycles were modeled. Inheritable organism attributes, including parameters that govern behaviors, were stored in evolutionary structures analogous to genetic chromosomes, and passed between generations via reproductive functionality that utilized genetic operators such as crossover (detailed in [13]). An additional model component for guiding evolution, denoted the gardener, was implemented to periodically remove individual organisms, their reproductive products (eggs), or local communities of organisms. Removal was conducted when entity or community properties excessively deviated from expected patterns, as derived from field experiment data and observations from published research. The organisms and eggs that remained after removal contributed to subsequent generations via reproductive functions. The method is summarized in Fig. 1.

3. Model description

The following sections describe the model following the ODD protocol for describing individual-based models (IBMs) outlined in [14, 15]. The model was constructed with the Repast Simphony agent-based modelling and simulation development toolkit (http://repast.sourceforge.net/).

3.1. Purpose

The purpose of the model was to demonstrate the proposed pattern-guided evolution method for developing an IBM that incorporates intergenerational adaptation, outlined in Section 2. An old-field ecosystem, consisting of grasshoppers, spiders, grass and herbs, was chosen as a suitable model domain. It was a simple, yet nontrivial, ecosystem to model, and has previously been modeled via an IBM based on field research (described in [10]). When applying the method with the modeled ecosystem, the aim was to evolve organisms with parameterized phenotypic diversity to facilitate intergenerational adaptation, whilst maintaining congruence with field data patterns and ecosystem observations. In particular, the model aimed to evolve adaptive feeding behaviors in grasshoppers in order to reproduce observed dietary shifts, that is, a reduction in the proportion of grass eaten, thus an increase in herb consumed, by grasshoppers when spiders are present (described in [10]).

3.2. Entities, state variables, and scales

The model consists of ecosystem entities representing the organisms and their reproductive products situated in a spatial grid-based environment. Additional non-situated entities, or agents, were constructed for performing seasonal tasks, imposing mortality, managing evolutionary structures, and performing selective activities for pattern-guided evolution.

3.2.1. Ecosystem entities

Entities specific to the ecosystem include grasshoppers, grasshopper egg pods, spiders, spider eggs, grass and herbs. The organisms were all modeled with sexual reproduction whereby the inheritable attributes of parent organisms, stored in genetic chromosomes, were combined using the genetic crossover operator to produce offspring chromosomes (detailed in [13]).
Grasshopper entities were modeled to convey their multi-stage lifecycle, metabolism, growth, reproduction, feeding, activity choices, movement, and danger avoidance behaviors. Much of this functionality was based on biomass consumption and assimilation as summarized in Fig. 2 (based on [16]).

Spider entities were modeled with simple constant growth, reproduction, movement, and hunting behavior. Their feeding and metabolism were not modeled, as their purpose in the model was to influence grasshopper behavior.

Grasshopper and spider entities both produced eggs, or multiple-egg pods in grasshopper cases, which were implemented as entities containing genetic chromosomes from both parents, and were hatched early in each simulated season.

Both plant types, grass and herbs, were implemented as entities that occupied single grid cells within the simulated environment. Plant entities were modeled with growth and reproduction.

Entity state variables, including inheritable gene parameters, are summarized in Tables 1 & 2. Many of these parameters were used in entity functionality, which are further described in Section 3.7.

3.2.2. Simulation environment

The simulated grid-based spatial environment was configured so that a single cell, which could contain one plant entity and multiple grasshoppers, spiders or eggs, scaled to a 10 cm square. The simulation results presented in this paper utilized a 50 by 50 grid (equivalent to a 25 square meter area).

Multiple ecosystem seasons were simulated to correspond to approximate seasonal life-spans of grasshoppers of up to 100 days (estimated from [17]). Each day consisted of 10 hours of grasshopper and spider activity (as per [10]) plus an additional 2 hours of sleep time for digestion. Each simulation step was equivalent to 15 minutes hence the simulations ran in 4800 step seasonal cycles.

3.2.3. Control agents

Non-situated entities, or agents, were constructed for controlling the simulated seasonal cycles, imposing mortality of grasshoppers and spiders, and managing evolutionary structures for intergenerational inheritance.
Table 1. State variables for grasshopper entities including inheritable gene parameters are listed below. Values and ranges are sourced, estimated or derived from the given references.

| State variable          | Description                                    | Genes   | Value/range | Unit   | References       |
|-------------------------|------------------------------------------------|---------|-------------|--------|------------------|
| Grasshopper             | Gender                                         | single  | m|f          |        |                  |
| Hatch length            | Initial length                                 | single  | 6-8         | mm     | [17, 18]         |
| Hatch mass              | Initial mass                                   | single  | 8-12        | mg     | [19]             |
| Adult length            | Maximum length at maturity                     | male    | 18-22       | mm     | [17, 20]         |
|                        |                                                | female  | 20-28       |        |                  |
| Adult mass to           | Mass divide length at maturity                 | male    | 11-17       | mg/mm  | [17, 18, 19, 20] |
| length ratio            |                                                | female  | 18-24       |        |                  |
| Crop size               | Fraction of wet body mass                      | male    | 0.070-0.086 |        | [20, 21, 22]     |
|                        |                                                | female  | 0.076-0.092 |        |                  |
| Feed rate               | Plant consumed as a fraction of body mass       | grass   | 0.06-0.12   | hour⁻¹ | [20, 23]         |
|                        |                                                | herb    | 0.06-0.15   |        |                  |
| Feed wastage           | Fraction of removed plant mass not consumed    | grass   | 0.55-0.75   |        | [16]             |
|                        |                                                | herb    | 0.65-0.85   |        |                  |
| Digestion rate         | Fraction of crop digested                      | single  | 0.30-0.38   | hour⁻¹ | [21]             |
| Plant assimilation      | Fraction of wet plant mass consumed            | grass   | 0.64-0.76   |        | [16, 21]         |
|                        |                                                | herb    | 0.54-0.65   |        |                  |
| Metabolic loss          | Fraction of body mass loss                     | single  | 0.10-0.17   | day⁻¹  | [16, 21]         |
| Egg investment          | Assimilated mass to produce an egg             | single  | 20-50       | mg/egg | [16, 21, 24, 25] |
| Clutch size             | Number of eggs per pod                         | single  | 15-25       | eggs/pod | [25] |
| Hunger threshold        | Feed when below fraction of crop               | single  | 0-1         |        |                  |
| Relocation rate         | Probability when not feeding                   | single  | 0-1         | per step |                  |
| Feed preference         | Grass feeding selection weight                 | single  | 0-1         |        |                  |
| Danger threshold        | Active until perceived danger level            | single  | 0-1         |        |                  |
| Forget rate             | Perceived danger level decrease rate           | single  | 0-1         | hour⁻¹  |                  |
| Safety preference       | Grass refuge selection weight                  | single  | 0-1         |        |                  |
| Length                  | Current length                                 | -       | 6-28        | mm     |                  |
| Wet mass                | Current body mass                              | -       | 8-672⁺       | mg     |                  |
| Crop mass               | Current crop content                           | -       | 0-62        | mg     |                  |
| Days old                | Days since hatched                             | -       | 0-91⁻       | days   |                  |
| Is pregnant?            | Is the grasshopper pregnant?                   | -       | yes/no      |        |                  |
| Egg number              | Current clutch eggs produced                   | -       | 0-25        | eggs   |                  |
| Danger level            | Current perceived danger level                 | -       | 0-1         |        |                  |
| Position                | Current grid coordinates                      | -       | (1-50,1-50) |        |                  |
Table 2. State variables for spider, grasshopper egg pods, spider eggs, and plant entities including inheritable gene parameters are listed below. Values and ranges are sourced, estimated or derived from the given references.

| State variable     | Description                        | Genes | Value/range | Unit   | References |
|-------------------|------------------------------------|-------|-------------|--------|------------|
| **Spider**        |                                    |       |             |        |            |
| Sex               | Gender single m|f            | single | 6-12 | mm      | [17]       |
| Initial length    | Hatch length single 6-12 mm         |       |             |        |            |
| Growth rate       | Constant growth rate 0.06-0.12 mm/day| single | 0.06-0.12 | mm/day | [17, 26]  |
| Relocation rate   | Relocation probability 0.0-0.5 per step | single | 0.0-0.5 | per step | [27]       |
| Capture skill     | Grasshopper capture skill 0.0-0.2 |       |             |        |            |
| Length            | Current length 6-18 mm              |       |             |        |            |
| Is still?         | Stationary last step? yes|no    |       | yes|no     |            |
| Position          | Current grid coordinates (1-50,1-50) |       |             |        |            |
| **Grasshopper egg pod** |                          |       |             |        |            |
| Mother            | Female parent chromosome all       |       |             |        |            |
| Father            | Male parent chromosome all         |       |             |        |            |
| Egg number        | Number of eggs in the pod 15-25 eggs |       |             |        | [25]       |
| Position          | Current grid coordinates (1-50,1-50) |       |             |        |            |
| **Spider egg**    |                                    |       |             |        |            |
| Mother            | Female parent chromosome all       |       |             |        |            |
| Father            | Male parent chromosome all         |       |             |        |            |
| Position          | Current grid coordinates (1-50,1-50) |       |             |        |            |
| **Plant (grass & herb)** |                          |       |             |        |            |
| Growth rate       | Intrinsic growth rate grass 0.04-0.14 day^-1 | grass | 0.04-0.14 | day^-1 | [28]       |
|                  | Shoot capacity Dry shoot carrying capacity herb 90-220 g/m^2 | grass | 90-220 | g/m^2 | [26, 27, 29, 30] |
|                  | Initial biomass Initial dry shoot biomass grass 2-24 g/m^2 | grass | 2-24 | g/m^2 | [31]       |
|                  | Root fraction Fraction of total biomass grass 0.45-0.70 | grass | 0.45-0.70 |        | [32, 33]  |
|                  | Shoot biomass Current dry shoot biomass - 20-2200 mg |       | - | 20-2200 | mg         |
|                  | Root biomass Current dry root biomass - 47-5133 mg |       | - | 47-5133 | mg         |
| Plant type        | Is the plant grass or herb? g|h |       | g|h     |            |
| Position          | Current grid coordinates (1-50,1-50) |       |             |        |            |

The seasonal controller performed tasks at the beginning and end of each simulated season. At the beginning of each season, surviving grasshopper eggs and a selection of spider eggs were hatched, and surviving perennial plants or new seedlings were set to their initial biomass. At the end of each season grasshoppers and spiders were removed and perennial plants entered their dormant phase.
The mortality controller performed daily removal of grasshoppers, based on staged mortality functions (see Section 3.7.7), and spiders at a constant rate. At the beginning of each season, over-winter mortality of grasshopper eggs was performed at a constant rate.

The evolution controller was used to manage populations of inheritable chromosomes for each organism type. Its tasks included creating initial chromosomes, saving and loading populations to and from files, and performing genetic crossover operations when creating child organisms. This controller utilized evolutionary structures and operators that were available via a library distributed with Repast Simphony.

State variables for the control agents are summarized in Table 3.

3.2.4. Gardener

The gardener (described in Section 2), a non-situated agent used to performed selective activities for pattern-guided evolution, periodically removed a limited number of individual entities, or local communities of organisms. Removal was performed when entity or community properties fell outside specified tolerated deviations from expected values, derived from published field experiment data (see Tables 5 & 6). Removal was stochastically weighted in accordance with deviations from expected values. Grasshopper removal was incorporated into daily mortality so as to maintain expected densities at various life-cycle stages. Grasshopper egg removal was also incorporated into inter-seasonal egg mortality. Community removal was performed by recording the deviations from data patterns of the properties of overlapping neighborhoods, centered at each cell, at various times during each season. At the end of each season, a stochastically weighted selection of cells (neighborhood centers) was cleared of all entities. This process generally produced patches of cleared cells, as illustrated in its simplified form in Fig. 1. Also at the end of each season, the gardener performed optional functionality for maintaining plant type coverage fractions across seasons by clearing additional cells to reinstate the expected coverage.

Gardener state variables are listed in Table 3. Global parameters, including selection pattern expected values and their tolerated deviations, used by the gardener are summarized in Tables 5 & 6.

3.3. Process overview and scheduling

An overview of the processes for the entities described in Section 3.2 in their scheduled order is presented in Fig. 3. The Repast Simphony simulation engine provided a synchronous, discrete-time, event simulation environment in which entity processes could be scheduled for specified time steps.

Grasshopper, spider and plant entities performed their chosen actions at each simulation step (equivalent to 15 minute intervals) concurrently (in random order).
Table 3. State variables for the control and gardener entities are listed below. Values and ranges are sourced, estimated or derived from the given references.

| State variable       | Description                                      | Genes | Value/range | Unit  | References |
|----------------------|--------------------------------------------------|-------|-------------|-------|------------|
| Seasonal controller  |                                                  |       | 1-51°       |       | [10, 17]   |
| Season               | Current season number                            | -     | 1-100       |       | [10, 17]   |
| Season day           | Current season day                               | -     | 1-100       |       | [10, 17]   |
| Hour of day          | Current hour within day                          | -     | 1-12        |       | [17]       |
| Trophic levels       | Current trophic levels                           | -     | 1-3         |       | [17]       |
| Mortality controller |                                                  |       | 0.01-0.12°  | day⁻¹ |            |
| Mortality rates      | Current grasshopper staged mortality             | -     | 0-2500°     |       | [17, 25, 26, 27, 34] |
| Stage numbers        | Grasshopper number at each stage                 | -     | 0-100°      |       | [17, 25, 27] |
| Current density      | Season grasshopper initial density               | -     | 0-100°      | no./m² | [17, 25, 27] |
| Previous density     | Season grasshopper initial density               | -     | 0-100°      | no./m² | [17, 25, 27] |
| Evolution controller |                                                  |       |             |       |            |
| Grasshopper pop.     | List of all grasshopper chromosomes             | all   |             |       |            |
| Spider pop.          | List of all spider chromosomes                   | all   |             |       |            |
| Grass pop.           | List of all grass chromosomes                    | all   |             |       |            |
| Herb pop.            | List of all herb chromosomes                     | all   |             |       |            |
| Gardener             |                                                  |       |             |       |            |
| Enabled?             | Is gardener currently enabled?                  | -     | yes|no        |       |            |
| Clearing enabled?    | Is clearing currently enabled?                  | -     | yes|no        |       |            |
| Mid season dev.      | Recorded plant biomass deviations               | -     |             |       |            |
| End season dev.      | Recorded plant biomass deviations               | -     |             |       |            |
| Density dev.         | Recorded grasshopper density deviations         | -     |             |       |            |
| Deaths dev.          | Recorded fraction of grasshopper deaths due to spiders deviations | -     |             |       |            |

3.4. Design concepts

This section outlines the design principles on which the model is founded.

3.4.1. Basic principles

The model was based on bioenergetics principles, particularly for grasshopper entities, for which the energy and mass requirements for organism function were considered. The model performed biomass transfers for grasshopper feeding, metabolism, growth, and reproduction, based on known biomass-energy equivalences (in [16, 21]). Generally these were implemented in the model using parameterized functions. Parameterized functions were also used for simulating organism behaviors. Most of these behavioral functions were stochastic in nature.

The pattern-oriented modelling (POM) approach was utilized by the selective guidance agent or gardener. When used with multiple patterns the approach may yield structurally realistic models (discussed in [7]).
Fig. 3. Overview of the model schedule including initialization, start & end of season tasks, grasshopper & spider daily mortality, gardener grasshopper & egg pod removal, gardener pattern deviation recording, gardener clearing, and key grasshopper, spider & plant processes.
The patterns used for guiding entity evolution included individual grasshopper maturity intervals, activity times, grass fraction consumed, egg clutch development intervals, and the number of egg pods laid per female, as well as ecosystem community properties, such as plant biomass at various times, adult grasshopper density, and spider induced grasshopper mortality. Values and references for these patterns are listed in Tables 5 & 6.

3.4.2. Emergence

The entities were designed with the aim of evolving them, albeit guided by the gardener, so that desired patterns emerge from individual entity processes & behaviors and interactions between entities. For example, grasshopper maturity intervals emerged from the feeding, growth & metabolism processes of individuals. Activity times emerged from activity choices that grasshoppers made. The grass fraction eaten emerged from grasshopper plant preference for feeding & safety and encounters with spiders (see Section 3.4.3). Egg clutch intervals emerged from metabolism & egg production properties, as did the number of egg pods laid by individual grasshoppers, which was also dependent on growth. Community based patterns also emerged as a result of interactions between individual entities as well as their individual properties. For example, individual plant biomass at various times within a season depended upon individual plant growth and grasshopper feeding, which was dependent on interactions with spiders.

3.4.3. Adaptation

Grasshopper entities were designed with adaptive behaviors for responding to spider presence. The behaviors aimed to reproduce field observations (from [17, 34]) in which spider presence resulted in lowered activity and a shift in grasshopper diet, reducing the amount of grass consumed, and increasing herb consumption. The mechanisms used to simulate these behaviors utilized entity memory (used in [35]) to maintain each grasshopper’s sense of perceived danger. This memory deteriorated over time at a constant forget rate.

Grasshoppers also periodically relocated based on their plant preferences, a mixture of feeding and safety preferences. When choosing a plant, these two preferences were weighted by a grasshopper’s sense of perceived danger, preferring safe plants when perceived as high and the more nutritious plants when it was low. Since the grasshoppers eat both types of plants, these mechanisms aimed to reproduce the observed diet shift patterns. Implementation details of these mechanisms are described in Section 3.7.3.

3.4.4. Sensing

In the model, grasshoppers could sense the plant types (grass or herb) of neighboring cells when choosing a relocation site. Grasshopper and spider entities both detected potential mates within the same cell. Spider entities also maintained a memory of mates encountered, so as to only mate once with each mate. Spider entities detected grasshoppers within the same cell. However, grasshoppers did not directly sense spider presence.

3.4.5. Interaction

Model entities interacted in numerous ways. Grasshopper entities fed upon, and hence removed biomass from, plants located on the same cell. Model grasshoppers and spiders both engaged in sexual reproduction with mates on the same cell. Spiders preyed on grasshoppers when detected in the same cell, resulting in either grasshopper death, or their escape which triggered their adaptive behaviors.

3.4.6. Stochasticity

Many model processes were stochastic in nature. Many initial model conditions, such as the initial proportion of plant types and the initial grasshopper density, were probabilistically determined. Entity
chromosomes were initially either randomly generated, or randomly selected from chromosomes optionally loaded from files. Seasonal plant replacement functionality utilized weighted (roulette-wheel) random selection for selecting parent plants. Mortality processes utilized random selection and initiated gardener activities that used weighted random selection. Grasshopper and spider entity cell relocation was stochastic, based on inherited rates. Grasshopper relocation was also based on weighted plant preferences. Spider predatory success was also based on a probability function.

3.4.7. Observation

The Repast Simphony environment provided utilities for monitoring simulations via runtime graphs and for data logging. Data collected and displayed at runtime for the model was numerous and included the individual inheritable attributes of all entities at each season. Daily grasshopper & spider numbers and grass & herb biomass were recorded. The end & mid season plant biomass of individual plants were recorded every 10 seasons. All seasonal population sizes were recorded. Individual & mean adult grasshopper maturity intervals, daily activity times, and grass fraction eaten were recorded on a specified season day, as was individual & mean clutch intervals and egg pod numbers produced by females. Numbers of entities removed and cells cleared by the gardener were also recorded each season. Some of the data collected is presented in the results in Section 5.

3.5. Initialization

Model initialization involved creating initial populations of ecosystem entities and scheduling control agent and gardener activities. Entities were created at densities specified via runtime parameters and randomly placed on the grid. Chromosomes of inheritable gene attributes were either randomly generated using configurable parameter ranges, or loaded from files when required. In many cases, gene parameters specified initial values for state variables (see Tables 1 & 2), such as initial biomass for plants, initial length for grasshoppers & spiders, and initial mass for grasshoppers. Other state variables were initialized using suitably realistic values, such as zero mass initially in grasshopper crops. Control agent and gardener activities were scheduled according to configuration parameters that could be adjusted at runtime, as were mortality rates, gardener expected pattern values & tolerated deviations, gardener clearing limit, and numerous other global parameters. Key initial values used in the simulations conducted for this research are listed in Tables 4, 5 & 6.

3.6. Input data

The model does not use input data to represent time-varying processes.

3.7. Submodels

In this section the submodels representing the processes outlined in Section 3.3 are described in more detail. The descriptions include how the submodels are parameterized with the entity state variables & inheritable attributes listed in Tables 1, 2, & 3, and the global parameters listed in Tables 4, 5 & 6.

3.7.1. Grasshopper feeding and metabolism

Grasshopper feeding and metabolism is summarized in Fig. 2 and is based on field studies reported in [16, 20- 23].
Table 4. Model global parameters and their initial values used in simulations conducted for this research. Values and ranges are sourced, estimated or derived from the given references.

| Parameter       | Description                                      | Value/range               | Unit/stage | References |
|-----------------|--------------------------------------------------|---------------------------|------------|------------|
| **Grasshopper** |                                                  |                           |            |            |
| Stages          | Number of life cycle stages                      | 6                         |            | [17]       |
| Pod density     | Initial egg pod density                          | 17                        | no./m²     | [17, 25, 27]|
| Hatch day       | Random hatch day of season                        | 9-17                      | day        | [17]       |
| Starvation time | Death if metabolism not met                       | 3                         | days       | [36]       |
| **Spider**      |                                                  |                           |            |            |
| Initial density | Applied at the start of each season               | 10                        | no./m²     | [17]       |
| Max. length     | Spider stops growing at length                    | 18                        | mm         | [17]       |
| **Plant**       |                                                  |                           |            |            |
| Initial grass fraction | Initial proportion of cells with grass | 0, 1, 0.4 |            | [23]       |
| Grass dry to wet | Ratio of wet/dry biomass                          | 1.64                      |            | [21]       |
| Herb dry to wet | Ratio of wet/dry biomass                          | 2.67                      |            | [21]       |
| Season survival | Probability of inter-seasonal survival            | 0.8                       |            |            |
| Seed range      | Initial Moore neighborhood                        | 1 (9 cells)               |            |            |
| Pollinate range | Initial Moore neighborhood                        | 2 (25 cells)              |            |            |
| Full size       | Fraction of capacity for full weighted reproductive selection | 0.8                      |            |            |
| **Seasonal controller** | Number of seasons to run | 1-51 | seasons | [10, 17] |
| Season days     | Number of days in a season                        | 100                       | days       | [10, 17]  |
| Day steps       | Simulation steps in a day                         | 48                        | steps      | [17]       |
| Day hours       | Hours in a simulation day                         | 12                        | hours      | [17]       |
| **Mortality controller** | Initial grasshopper density for linear function fitting | 90                      | no./m²     | [17, 25, 27]|
| Staged GH rates | Grasshopper daily mortality for each stage at the expected initial density | 0.077, 0.052, 0.036, 0.025, 0.017, 0.010 | stage-1, stage-2, stage-3, stage-4, stage-5, adult | [17, 25, 34], [26, 27] |
| Staged GH adjustments | Adjust grasshopper mortality rate per unit change in initial density between seasons | 0.00080, 0.00040, 0.00020, 0.00010, 0.00005, 0.00000 | stage-1, stage-2, stage-3, stage-4, stage-5, adult | [17, 25, 34], [26, 27] |
| GH egg mortality | Inter-seasonal egg mortality                      | 0.71                      |            | [25]       |
| Spider mortality | Constant daily mortality rate                     | 0.009                     |            | [17, 26]  |
Table 5. Model global parameters and their initial values used in simulations conducted for this research (continued). Values and ranges are sourced, estimated or derived from the given references.

| Parameter                          | Description                                                                 | Trophic levels | Value/range | Unit          | References |
|------------------------------------|----------------------------------------------------------------------------|----------------|--------------|---------------|------------|
| Grid                               |                                                                            | 1,2&3          | 50           | cells         | [26]       |
| Grid width                         | Number of cells wide                                                      |                | 50           | cells         |            |
| Grid height                        | Number of cells high                                                      |                | 50           | cells         |            |
| Grid scale                         | Grid cells per square meter                                               | 1,2&3          | 100          | cells/m²      |            |
| Evolution controller               |                                                                            | 1,2&3          | yes|no       | (for each)   |            |
| Load pop.                          | File load grasshopper, spider, grass, and/or herb chromosome population   |                |              |               |            |
| Save pop.                          | File save grasshopper, spider, grass, and/or herb chromosome population   | 1,2&3          | yes|no       | (for each)   |            |
| Gardener grasshopper removal       | Expected mature day                                                       | 2&3            | 45±16%       | days          | [25, 37]  |
| Expected activity                  | Expected daily activity time                                              | 2              | 375±25%      | min/day       | [34]       |
|                                   | 3                                                                          | 310±25%        |              |               |            |
| Expected grass eaten               | Expected fraction of grass eaten                                          | 2              | 0.89±40%     |               | [19, 23]  |
|                                   | 3                                                                          | 0.60±40%       |              |               |            |
| Mature day weight                  | Weight in removal criteria                                               | 2&3            | 0.6          |               |            |
| Activity weight                    | Weight in removal criteria                                               | 2&3            | 0.3          |               |            |
| Mature day weight                  | Weight in removal criteria                                               | 2&3            | 0.6          |               |            |
| Maturity rem. day                  | Removal after days old                                                   | 2&3            | 2            | days          |            |
| Activity rem. day                  | Removal after days old                                                   | 2&3            | 2            | days          |            |
| Grass eaten rem. day               | Removal after days old                                                   | 2&3            | 10           | days          |            |
| Gardener grasshopper egg pod removal| Exp. clutch interval                                                     | 2&3            | 20±50%       | days          | [24, 25]  |
| Exp. pod number                    | Egg pod number per female                                                | 2&3            | 2±110%       | pods          | [24, 25]  |
| Clutch interval weight             | Weight in removal criteria                                               | 2&3            | 0.8          |               |            |
| Pod number weight                  | Weight in removal criteria                                               | 2&3            | 0.2          |               |            |

The grasshopper entity consumes biomass at an inherited feed rate, specified as a fraction of its body mass per hour for the plant type, that is:

\[
\text{ConsumedMass} = \text{FeedRate} \cdot \text{BodyMass} \cdot \text{HoursFeeding}
\]  \hspace{1cm} (1)

More plant mass is removed than is consumed, the rest is wasted in accordance to an inherited feed wastage fraction:

\[
\text{PlantMassRemoved} = \frac{\text{ConsumedMass}}{\text{FeedWastage}}
\]  \hspace{1cm} (2)
Table 6. Model global parameters and their initial values used in simulations conducted for this research (continued). Values and ranges are sourced, estimated or derived from the given references.

| Parameter                              | Description                                                                 | Trophic levels | Value/range | Unit       | References |
|----------------------------------------|-----------------------------------------------------------------------------|----------------|-------------|------------|------------|
| Gardener community clearing            | Max. clearing Maximum fraction of cells cleared per season                   | 1,2&3         | 0.2         |            |            |
| Exp. end season grass                  | Expected end of season grass density with grass only (solo) and mixed grass & herbs | 1-solo        | 151±7.5%    | g/m²       | [26, 27]   |
|                                        |                                                                             | 2-solo        | 131±15%     |            | [29, 30]   |
|                                        |                                                                             | 2-mixed       | 99±30%      |            |            |
|                                        |                                                                             | 3-mixed       | 138±30%     |            |            |
| Exp. end season herb                   | Expected end of season herb density with herb only (solo) and mixed grass & herbs | 1-solo        | 112±7.5%    | g/m²       | [26, 27]   |
|                                        |                                                                             | 2-solo        | 85±22.5%    |            | [29, 30]   |
|                                        |                                                                             | 2-mixed       | 82±30%      |            |            |
|                                        |                                                                             | 3-mixed       | 72±30%      |            |            |
| Exp. mid season grass                  | Expected end of season grass density with grass only (solo)                 | 1-solo        | 104±15%     | g/m²       | [17]       |
|                                        |                                                                             | 2-solo        | 91±30%      |            |            |
| Exp. mid season herb                   | Expected end of season herb density with herb only (solo)                   | 1-solo        | 78±15%      | g/m²       | [17]       |
|                                        |                                                                             | 2-solo        | 59±45%      |            |            |
| Exp. GH density                        | Adult grasshopper density                                                  | 2&3           | 12±75%      | no./m²     | [26]       |
| Exp. spider deaths                     | Fraction of grasshopper deaths due to spiders                               | 3             | 0.3±60%     |            | [26, 27]   |
| End season weight                      | Weight in clearing criteria                                                | 1,2&3        | 0.8         |            |            |
| Mid season weight                      | Weight in clearing criteria                                                | 1&2           | 0.2         |            |            |
| GH density weight                      | Weight in clearing criteria (counteractive)                                | 2&3           | -0.2        |            |            |
| Spider deaths weight                   | Weight in clearing criteria                                                | 3             | 0.2         |            |            |
| Mid season recorded                    | Day deviations are recorded                                               | 1&2           | 50          |            | [17]       |
| GH density recorded                    | Day deviations are recorded                                               | 2&3           | 70          |            | [17, 25]   |

The consumed biomass is digested at an inherited rate specified as a fraction of the grasshopper’s crop capacity per hour:

$\text{DigestedMass} = \text{DigestionRate} \cdot \text{CropCapacity} \cdot \text{HoursDigesting}$  \hspace{1cm} (3)

where the crop capacity is calculated using the inherited crop size, expressed as a fraction of the body mass, hence:

$\text{CropCapacity} = \text{CropSize} \cdot \text{BodyMass}$ \hspace{1cm} (4)

The grasshopper continues feeding until its crop is full, after which it engages in other activities until its crop mass falls below a hunger threshold, expressed as a fraction of its crop capacity, hence:
\[ \text{CropMass} \prec \text{HungerThreshold} \cdot \text{CropCapacity} \Rightarrow \text{Hungry} = \text{True} \] (5)

A specified inherited fraction of the plant wet biomass digested is assimilated by the grasshopper:

\[ \text{Assimilate} \cdot d\text{Mass} = \text{DigestedMass} \cdot \text{PlantAssimilation} \] (6)

A portion of the assimilated mass is required for metabolic function, expressed as an inherited fraction of body mass loss per day. The remaining assimilated mass is then available for growth and reproduction:

\[ \text{AvailableAssimilated Mass} = \text{Assimilate} \cdot d\text{Mass} - \text{MetabolicLoss} \cdot \text{BodyMass} \cdot \text{TimeInDays} \] (7)

3.7.2. Grasshopper growth and reproduction

Grasshopper entity growth is based on the assimilated plant biomass after metabolic function costs. In the model, juvenile grasshoppers utilize the remaining available assimilated mass (as per Eq. 7) for growth, hence:

\[ \text{GrowthMassInJuveniles} = \text{AvailableAssimilated Mass} \] (8)

As the model grasshoppers gain assimilated mass, their lengths increase according to a logarithmic function:

\[ \text{Length} = (\text{AdultLength} - \text{HatchLength}) \cdot \frac{\log(\text{Mass}/\text{HatchMass})}{\log(\text{AdultMass}/\text{HatchMass})} + \text{HatchLength} \] (9)

where hatch length & mass and adult length are inherited attributes, and adult mass may be calculated using the inherited adult mass-to-length ratio. Eq. 9 was derived using mass and length values from field research in [17, 18, 19, 27].

The study grasshoppers (Melanoplus femurrubrum) undergo a multi-stage lifecycle with typically five juvenile in-star stages before maturing into adults [17]. The model assumes an approximate linear increase in length from hatch to adult lengths and the stage intervals are approximately evenly spaced during this time (as evident in [38]), hence the lifecycle stage can be calculated as follows:

\[ \text{CurrentStage} = \text{integer} \left( \frac{\text{NumberOfStages} - 1}{\text{AdultLength} - \text{HatchLength}} \cdot (\text{Length} - \text{HatchLength}) + 1 \right) \] (10)

where integer rounds the result down to the nearest integer value. Note that stage 6 refers to adult grasshoppers that have reached their maximum length.

Once they achieve their adult size, the model grasshoppers discontinue growth. Having achieved maturity, model adult grasshoppers may then mate at random, when opportunities arise, with members of the opposite sex located on the same grid cell. After mating, pregnant females utilize post-metabolic
assimilated mass (as per Eq. 7) to produce grasshopper eggs, each requiring assimilated mass determined by the inherited egg investment attribute, hence:

\[ \text{EggsProduced} = \frac{\text{AvailableAssimilatedMass}}{\text{EggInvestment}} \]  \hspace{1cm} (11)

Once a full clutch of eggs has been produced, as determined by the inherited clutch size, an egg pod is deposited on the current grid cell, and the female is again available for mating.

3.7.3. Grasshopper adaptive behavior

At each simulation time-step, when grasshopper entities are not feeding or engaged in reproductive behavior, they either rest or relocate to a neighboring grid cell (see Fig. 3). Resting and relocation choice functionality have been developed to model the adaptive behavior that grasshoppers have in response to predation risk from the modeled spider \((Pisaurina mira)\). Grasshoppers tend to shift their diet towards a greater proportion of herb and are less active when the spiders are present (as observed in [17, 34]). When a model grasshopper encounters a spider entity and escapes (via a random move to a neighboring cell), its perceived danger level is set to 1. The grasshopper will choose to be inactive (rest) while its danger level is above its inherited danger threshold:

\[ \text{DangerLevel} > \text{DangerThreshold} \Rightarrow \text{Inactive} = \text{True} \] \hspace{1cm} (12)

The danger level is decreased at its inherited forget rate (per hour) to a minimum of 0:

\[ \text{DangerLevel} = \text{DangerLevel} - \text{ForgetRate} \cdot \text{TimeInHours} \] \hspace{1cm} (13)

When the danger level is no longer above the threshold, the grasshopper resumes normal activity, and if it does not feed or reproduce then it may choose to relocate or rest. Relocation, rather than rest, is chosen with a probability specified by its inherited relocation rate. When choosing which cell to relocate to, preferences for the plants located at neighboring cells are calculated using the following function:

\[ \text{PlantPreference} = \text{FeedPreference} \cdot (1 - \text{DangerLevel}) + \text{SafetyPreference} \cdot \text{DangerLevel} \] \hspace{1cm} (14)

where feed and safety preferences are specified by inherited attributes for grass (herb preferences are \(1 - \text{GrassPreference}\) in both cases). The relocation cell is then chosen via a weighted (roulette-wheel) random selection based on each neighboring plant’s preference score (as per Eq. 14).

3.7.4. Spider growth and reproduction

Model spider entities undergo growth from their inherited initial length to the global maximum length at a constant inherited growth rate, specified in mm per day, hence:

\[ \text{Length} = \text{InitialLength} + \text{GrowthRate} \cdot \text{TimeInDays} \] \hspace{1cm} (15)
Spiders are assumed to be adults from the start of the simulation time, as adult spiders co-occur with grasshopper juveniles (as reported in [17]). Mating between spiders occurs at random when new mates encounter one-another in the same grid cell. Female spider entities lay a single egg immediately and avoid re-mating with the same mate. At the beginning of each season a random selection of spider eggs are hatched so as to begin with the same spider density as previous seasons.

3.7.5. Spider predatory behavior

The modeled spiders (Pisaurina mira) adopt a sit-and-wait predatory strategy, whereby they wait in stillness until their prey come within striking distance before attempting capture [27]. The spider was modeled with this strategy in mind. A capture attempt upon a grasshopper in the same cell can only be made in the current simulation step if the spider entity was inactive in the previous step. Experimental studies (in [17]) found that the modeled spiders could subdue prey up to 1.3 times their body size. Using this information and the spider capture rate experiments reported in [27], the following function was devised for estimating the spider capture rate, or probability, for each capture attempt on a grasshopper based on their lengths:

\[
\text{CaptureRate} = \left(1.4 - \frac{\text{GrasshopperLength}}{\text{SpiderLength}}\right) \cdot \text{CaptureSkill}
\]  

where capture skill is an inheritable spider attribute.

3.7.6. Plant growth and reproduction

The plant growth model was based on the logistic growth model presented in [28], modified to separate root and shoot biomass to enable plants to recover from over-consumption by grasshoppers. Growth depends on functional biomass, that is, combined shoot & root biomass in their expected proportions, as defined by the inheritable root fraction parameter, thus:

\[
\text{FunctionalBiomass} = \text{ShootBiomass} \left(1 + \frac{\text{RootFraction}}{1 - \text{RootFraction}}\right)
\]  

The modified growth function is therefore:

\[
\text{TotalGrowth} = \text{GrowthRate} \cdot \text{FunctionalBiomass} \cdot \left(1 - \frac{\text{TotalBiomass}}{\text{TotalCapacity}}\right)
\]

where the growth rate (scaled appropriately for the time interval) and capacity are inheritable parameters, and the biomass (shoot & root) is the current value. The total growth is distributed to the shoot and root biomass according to the following ratio (shoot : root):

\[
\left[\left(1 - \frac{\text{ShootBiomass}}{\text{ShootCapacity}}\right) \cdot (1 - \text{RootFraction})\right] \cdot \left[\left(1 - \frac{\text{RootBiomass}}{\text{RootCapacity}}\right) \cdot \text{RootFraction}\right]
\]  

(19)
An additional growth function allows the transference of biomass from the roots to the shoots, thus modelling perennial plant recovery from winter dormancy (described in [17]) or complete over-consumption of the shoots by herbivores. This function is as follows:

\[
\frac{\text{RootToShootBiomassTransfer}}{\text{GrowthRate}\cdot \text{Root Biomass}} = 1 - \frac{\text{ActualShootFraction}}{\text{ExpectedShootFraction}}
\]  

(20)

where the actual shoot fraction is the current fraction of total shoot and the expected shoot fraction utilizes the inherited root fraction parameter, that is: \(1 - \text{RootFraction}\).

Plant reproduction is managed by the season controller, so as to only replace dead plants when required. Replacement is achieved using seeds produced and pollinated by neighboring plants within specified ranges, which are expanded if no suitable plants are found (see Table 4).

3.7.7. Mortality
The daily mortality of grasshopper and spider entities was conducted by determining the number of individuals from each subpopulation that should be removed by applying a series of Bernoulli trials using the appropriate mortality rate and subpopulation size.

Grasshopper mortality applied a different mortality rate for each lifecycle stage (as do [39]). The staged mortality rates also changed for different initial grasshopper densities using linear functions. These were derived by fitting various density curves, using a homogenous population model across a season, to grasshopper densities at different stages estimated from field data in [17, 26, 27, 34]. The linear difference equation for the stage \(i\) grasshopper mortality rate for season \(j\) is as follows:

\[
\text{MortalityRate}_{i,j} = \text{MortalityRate}_{i,j-1} + \text{MortalityAdjust} \cdot \left( \text{InitialDensity}_{j} - \text{InitialDensity}_{j-1} \right)
\]

(21)

The process was initiated with mortality rates for the first season, the adjustments, and the expected initial grasshopper density for the first season, as listed in Table 4.

Spider mortality was applied at the constant rate listed in Table 4, estimated via trial simulations to concur with spider density data in [17, 26].

3.7.8. Gardener entity removal and community clearing
Both gardener entity removal and community clearing processes calculate, and record for future use where required, the fractional deviation from each expected pattern \(i\) for each entity or community \(j\), thus:

\[
\text{DeviationFromExpected}_{i,j} = \frac{\text{ActualValue}_{i,j} - \text{ExpectedValue}_{i}}{\text{ExpectedValue}_{i}}
\]

(22)

Prior to removal or clearing, each deviation is examined and compared with the tolerated range for the corresponding pattern, expressed in Tables 5 & 6 in the form \(\text{ExpectedValue} \pm \text{ToleratedDeviation}\%\). If the absolute value of the deviation is greater than tolerated deviation (as a fraction), the deviation excess is calculated for pattern \(i\) for entity or community \(j\) (otherwise it is set to zero), hence:
\[
|DeviatiomFromExpected_{i,j}| > ToleratedDeviation/100
\]

\[
\Rightarrow DeviationExcess_{i,j} = |DeviatiomFromExpected_{i,j}| - ToleratedDeviation/100
\]  

(23)

A weighted sum of pattern deviation excesses for each entity or community \( j \) is then calculated using the removal or clearing criteria weights for each pattern \( i \) of \( n \) patterns (see Tables 5 & 6), hence:

\[
SelectionWeight_{j} = \left[ \sum_{i=1}^{n} CriteriaWeight_{i} \cdot DeviationExcess_{i,j} \right]
\]  

(24)

The entities or communities are selected for removal or clearing, to a specified limit, via a weighted (roulette-wheel) random selection using the calculated selection weights. Taking the absolute value of the sum in Eq. 24 allows criteria weights to be negative for counteractive purposes, such as compensating for the impact that lower or higher than expected grasshopper densities would have on the plant biomass deviation from expected values (see Tables 5 & 6).

4. Simulation experiments

The simulation experiments conducted for this research are summarized in Table 7 and include control experiments, experiments with pattern-guidance, and validation experiments. All experiments utilized 10 replicate runs.

Control experiments were conducted with randomly initialized model grasshoppers, spiders, grass, and herbs, without the gardener evolution guidance.

The pattern-guided evolution experiments were conducted in multiple phases, beginning with one trophic level with each plant type alone (solo). Two trophic level experiments (with grasshoppers & plants) were then conducted. Populations of stable & viable grasshoppers were evolved, before including them in phase 2 experiments with each plant type (saved from phase 1), after which the grasshoppers were discarded. Two trophic level experiments were then conducted with mixed grass & herb (saved from phase 2), once again evolving grasshopper populations first. The final three trophic level phase included spiders, with grasshoppers, grass, and herbs saved from phase 3.

Validation experiments were conducted so as to make comparisons with field results (from [26]), which were reserved for this purpose, and were not used in the pattern formulation process. These experiments were conducted for each of the three trophic levels with mixed grass & herbs (1-level), plus grasshoppers (2-level), and finally also with spiders (3-level), each of which were loaded from the population files saved at the end of phase 4 of the pattern-guided experiments.

5. Results

A selection of results from the simulation experiments described in Section 4 is presented in this section. Firstly, results that examine the population dynamics of the simulations are presented. Selected results from the validation experiments are then presented, along with the corresponding field data from published research for comparison. Lastly, the final distributions of model entity inheritable attributes are presented to illustrate the parametric diversity generated by the pattern-guided evolution approach.
### Table 7. Overview of the simulations conducted including evolution without pattern-guidance (control), multi-phase pattern-guided evolution, and validation runs using the final evolved populations from phase 4.

| Simulation experiments | Control | Phase 1 | Phase 2 | Phase 3 | Phase 4 | Valid. |
|------------------------|---------|---------|---------|---------|---------|-------|
| Number of runs         | 10      | 10      | 10      | 10      | 10      | 10×3  |
| Simulation seasons     | 21      | 51      | 51      | 51      | 51      | 21    |
| Gardener active        | no      | yes     | yes     | yes     | yes     | yes   | no    |
| Trophic levels         | 3       | 1       | 1       | 2       | 2       | 2     | 3     | 1,2,3 |

| Entities included      |         |         |         |         |         |       |
|------------------------|---------|---------|---------|---------|---------|-------|
| Grasshoppers           | R       | -       | R,S L   | L       | R,S L   | L,S   | L,2,3 |
| Spiders                | R       | -       | -       | -       | -       | -     | R,S L |
| Grass                  | R       | R,S L   | -       | L       | L,S     | L     | L,S   | L,1,2,3 |
| Herbs                  | R       | -       | R,S L   | -       | L       | L,S   | L     | L,S   | L,1,2,3 |

(Key: R = random, L = load from file, S=save to file; Validation loads appropriate trophic levels)

| Selective patterns applied |         |         |         |         |         |       |
|-----------------------------|---------|---------|---------|---------|---------|-------|
| Individual entities         |         |         |         |         |         |       |
| Mature day                  | -       | -       | 45      | 45      | 45      | 45    | -     |
| Activity                    | -       | -       | 375     | 375     | 375     | 375   | 310   | -     |
| Grass eaten                 | -       | -       | 60%     | -       | 89%     | 89%   | 60%   | -     |
| Clutch interval             | -       | -       | 20      | 20      | 20      | 20    | 20    | -     |
| Pod number                  | -       | -       | 2       | 2       | 2       | 2     | 2     | -     |
| Entity communities          |         |         |         |         |         |       |
| End season plant            | -       | solo    | solo    | solo    | mixed   | mixed | -     |
| Mid season plant            | -       | solo    | solo    | solo    | -       | -     | -     |
| Grasshopper density         | -       | -       | -       | 12      | 12      | 12    | -     |
| Deaths via spiders          | -       | -       | -       | -       | -       | -     | 30%   |

(Key: Pattern value used, or solo/mixed biomass pattern for trophic level from Table 4)

### 5.1. Population dynamics

Results presented in Fig. 4 illustrate the population dynamics of typical sample simulation runs with three trophic level ecosystems (grasshoppers, spiders & plants) evolved with and without pattern-guidance.

The decline in model grass observed in the control experiments was most likely due to the tendency for the grasshopper entities to evolve a feed preference for grass. The mean inheritable attribute for feed preference (for grass) in the final control season was 0.75±0.17 (1 standard deviation, n = 2666).

Declines, albeit slower, in either plant type were typically observed with pattern guidance; however the gardener optional functionality to maintain constant plant type coverage fractions (see Section 3.2.4) was utilized, so as to evolve grasshopper entities in a relatively constant mixed plant environment.
Grasshopper populations tended to climb and develop boom-and-bust cycles in the control experiments. Grasshopper populations were generally more stable in the pattern-guided simulations, and thus more likely to persist over multiple generations.

Spider populations were stable in both simulation sets, as the seasonal controller initialized a constant spider density at the beginning of each season.

5.2. Validation results

Published research and the corresponding results from validation simulation experiments are presented for comparison in Table 8 and Fig. 5.

Table 8 presents the published data (with source references) for the grasshopper properties that were considered in gardener individual entity removal and the corresponding mean results from the validation simulations.

Figure 5 presents end of season biomasses of grass & herbs from published field experiments (from [26]) for one to three trophic level ecosystems, and their corresponding mean values from the validation experiments.

5.3. Inheritable entity attributes

Presented in Fig. 6 are the final distributions of grasshopper, spider, grass, and herb entity inheritable attributes at the end of the multi-phase simulations using pattern-guided evolution. Some inheritable attributes, or genes, evolved towards narrow ranges, whereas others remained spread across their initial ranges (presented on each graph). Some genes tended towards the upper or lower limits of the parameter ranges.
Table 8. A comparison of grasshopper properties sourced from published data with mean values (±1 standard deviations, n = 3000) obtained from the validation simulations at two and three trophic levels.

| Grasshopper pattern | Published data | Validation simulations | Unit | References |
|---------------------|----------------|------------------------|------|------------|
|                     | 2-level        | 3-level                |      |            |
| Mature day          | 36-49          | 36-49                  | 41±2 | 43±2       | days | [25, 37] |
| Activity            | 375            | 310                    | 359±18 | 334±17 | min/day | [34] |
| Grass eaten         | 0.89           | 0.60                   | 0.78±0.06 | 0.60±0.08 | |
| Clutch interval     | 10-30          | 10-30                  | 10.0±1.5 | 10.2±1.5 | days | [24, 25] |
| Pod number          | 0-4+           | 0-4+                   | 2.9±1.5 | 2.7±1.3 | pods/female | [24, 25] |

6. Discussion

In this section the observations of the simulation experiments are discussed. Implications of the observed simulation population dynamics are examined. The congruence and divergence of the validation results from expected field data patterns is then analyzed. Finally, the validity and appropriateness of inheritable parameterized, or phenotypic, model diversity is examined.

6.1. Simulation stability and persistence

With the gardener functionality enabled, the model evolved with stable and persistent population dynamics. Evolution without pattern-guidance, and without other gardener functions for maintaining a balanced mix of plants, was observed to be unstable in all ten replicate runs. This instability was likely due to the observed tendency for grasshopper entities to evolve properties for unrealistically high growth and reproduction without pattern-guidance, given the range of values within the inherited parameters. This observation suggests that without restricting the initial parameter ranges, and therefore the full potential for parametric diversity, entities would probably never evolve by chance toward realistic patterns. Hence it would be very unlikely, at least for this type of ecosystem model, for the usual pattern-oriented approach of applying pattern-based selection at the end of each simulation, to produce realistic entities with the same degree of parametric diversity as the pattern-guided approach presented here.

6.2. Congruence with field data

The results in Table 8 relating to grasshopper entity properties suggest that the individual selection technique was mostly effective in keeping grasshopper properties within tolerated deviations from their expected values. However, properties that related to growth and metabolism, such as mature day and clutch interval, tended to evolve towards the lower ends of the specified tolerance intervals, since lower values generally resulted in higher representation in subsequent generations. Offsetting the gardener expected value pattern to compensate for this trend resulted in reasonable mature day values (note the difference in values between Table 5 and Table 8).

Properties relating to grasshopper behavioral responses to spider presence, such as grass fraction eaten and activity, exhibited a similar trend between trophic levels, but not to the same degree as the field data. This may have been due to a lack of narrow guidance in evolving the inheritable attributes that governed adaptive behavior. Pattern guidance in later simulation stages tended to undo congruence with patterns achieved in earlier stages.
Fig. 5. A comparison of end of season biomass for each of the three trophic levels, between field data from [26] and the mean biomass obtained from the validation simulations.

For example, the mean grass fraction eaten was in agreement with the expected value at the end of phase 3, mostly as a result of an appropriately evolved feed preference attribute distribution. The pattern-guidance in phase 4 ideally would have maintained this distribution and evolved the distribution of the safety preference and danger attributes to accommodate the diet shift in response to spiders. However, although the safety and danger attributes were evolved to some degree in phase 4, the feed preference distribution was shifted towards the lower end of its range, resulting in lower than expected grass fraction eaten values for two trophic levels in the validation runs (see Table 8).

End of season biomass was the major pattern utilized for gardener community clearing during the pattern-guided evolution process. Ideally this functionality would have guided plant evolution towards appropriate capacity and growth parameters for matching expected biomasses at each trophic level, given grasshopper feeding and diet shift behavior. The published field data presented with the simulation results in Fig. 5 illustrates the expected degree of plant response to grasshopper feeding and diet shift. The validation simulation data did not reproduce this pattern with the expected degree of change in biomass. This may have been partly due to a lower than expected diet shift in grasshoppers. Although it may also suggest that the plant growth rate distributions were too high in the final simulation phases, thereby reducing the impact that grasshopper entity feeding had on final plant biomasses. Also, the biomasses in the one trophic level experiments were lower than expected, especially for herbs. This was likely due to lower than expected plant capacity distributions, particularly for herbs (see Fig. 6). In the final simulation phases, the capacity distributions, which were approximately centered at their expected values in the early simulation phases, had shifted to lower values. The combination of lower than expected plant capacities, and high growth rates may explain much of the discrepancy between field data and simulation results evident in Fig. 5. Generally, the community pattern-guidance strategy, by utilizing expected biomass alone, was not sophisticated enough to select only the plants with appropriate capacity and growth to match the expected impacts of grasshopper feeding and diet shift. Instead, plants with lower than expected capacity and high growth rates were evolved, resulting in lower than expected feeding impact.

Another factor that may partially explain the discrepancy between field data and simulation results for end of season biomasses is the impact that herbivores in real systems may have on plant competition for space. By utilizing a fixed-grid spatial environment, the model did not consider spatial competition between plants. This research explored mechanisms for modelling competition between plants in a grid-based environment, but these features were insufficiently developed at the time of writing for inclusion in this paper.
6.3. Phenotypic diversity

The pattern-guided evolution approach utilized in the model simulations generated inheritable entity attributes with parametric, or phenotypic, diversity. The generated inheritable attribute distributions (illustrated in Fig. 6) were diverse in spread and positioning. Of particular interest and perhaps concern, are those attributes that evolved towards the upper or lower limits of their parameter ranges. Grasshopper metabolic loss rate & herb assimilation rate attributes and both plant root fractions may have shifted towards unrealistic values, and may consequently lack congruence with field data. This may suggest that there are factors that constrain these organism properties in real ecosystems which have not been included in the model. Hence it may not always be appropriate to implement some entity attributes with the full range of values observed in field data. Without modelling all the necessary constraints, some entity attributes are likely to evolve towards values which, albeit give them maximum reproductive advantage, are unrealistic. This trend towards edge-of-range values for some attributes is likely to worsen if the saved model entities are used in models without pattern guidance, especially when long simulation intervals are required.

The spider relocation rate attribute also evolved to the upper limit of its parameter range. This was likely due to the reproductive advantage that movement gave to spiders for encountering mates at random. A reproductive advantage for grasshopper capture was not implemented in the modeled spiders, but rather left to the pattern guidance mechanisms. Hence the advantage of remaining still, given the sit-and-wait strategy implementation, was not reflected in the evolution of the relocation rate. Ideally this rate would
have evolved to reflect the compromise needed to find mates, yet remain still often enough for predatory success. This may suggest that the pattern-guided mechanisms for achieving this aim were deficient or inadequately focused. Alternatively the spider capture skill values may have been too high, thereby reducing the need for model spiders to remain as still as often as they do in real systems.

7. Conclusion

The research presented in this paper described the pattern-guided evolution approach for developing individual-based models (IBMs) with realistically parameterized phenotypic diversity. Model entities with phenotypic diversity facilitate the modelling of intergenerational adaptation, and may be useful, if not necessary in some cases, for modelling changing environments.

The pattern-guided evolution approach was demonstrated using an IBM of an old-field ecosystem consisting of grasshoppers, spiders, grass, and herb entities. Model simulations utilizing the approach were conducted and produced stable and persistent population dynamics. In contrast, simulations conducted without pattern guidance produced unstable population dynamics and evolved entities with unrealistic properties. The entities produced with pattern-guided evolution were observed to have parameterized diversity and properties with values mostly within the tolerated ranges specified by the guidance patterns, sourced from published research. In some cases however, entity attributes and properties evolved towards the lower or upper limits of the specified ranges, suggesting that realistic constraints for limiting these properties were absent in the model.

The model aimed to reproduce the observed effects of changes in grasshopper feeding and activity in response to spider predation. To some degree the simulations reproduced these effects, but generally not with the same degree of change observed in published field research. This suggests that the pattern-guidance strategies used may not have been sophisticated enough to guide the evolutionary trajectory of entities and their communities in the intended manner.

Future research may further explore more sophisticated strategies for pattern-guided selection, as well as more involved multi-phase simulation sequences, each focusing on the guided evolution of specific aspects of individual entity properties and community interactions. It may also be useful to investigate strategies for determining appropriate entity attribute ranges (or parametric diversity) given various model limitations, and for different modelling purposes, especially when long simulations are intended. Further investigation into the long-term evolutionary stability of the entities produced by this research could be conducted. An exploration of strategies for implementing plant spatial competition also may be addressed for this research.

It is hoped that the ongoing research presented in this paper will contribute towards the development of flexible ecological models that support the challenges faced in a changing world, and encourage collaborative model sharing within the ecological modelling and broader scientific community.

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Model

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