ODD Model Description

This is an agent based model built in Netlogo 5.3.1 designed to replicate the model of evolving learning strategies in Rendell et al (2010). In particular, this model allows observers to investigate the ecological conditions under which social and asocial learning strategies spread more readily within a population, the impact that these various conditions have on mean fitness of individuals in a population, and how spatially explicit, local interactions affect this dynamic. Each agent in this model is represented by a single, immobile patch following a set of basic rules, and through stochastic interactions with state variables and one another, they simulate emergent, dynamic learning outcomes that affect fitness and reproduction. This model description follows the ODD protocol for describing agent-based models (Railsback & Grimm 2012).

Purpose

The purpose of this model is to test: (1) the effect of a spatially explicit, dynamic environment on the mean fitness and reproductive success of pure strategy social and asocial learners, and (2) test the effect of introducing mixed strategy social learners into spatially explicit, dynamic environments with varying levels of harshness and spatial variation. These questions are raised in an effort to find conditions that resolve Rogers' Paradox, the analytic finding that frequency-dependent mean fitness among social learners is only advantageous at low frequencies because they are essentially informational freeriders (i.e., they derive benefit from and contribute no added mean fitness to populations of asocial learners - see Rogers 1988).

Entities, state variables and scales

This model consists of 6400 patches in a toroidal population. Each represents a single individual executing a behavior in response to its local (i.e., patch-owned) environmental state, resulting in a fitness value during each time step that dictates the likelihood of reproduction.

Each time step reflects approximately one generation. During a time step, the environmental state of each individual's particular patch is represented by a value *s*, and the behavior of the individual within a given patch is represented by *b*. These values are specific to their own patches. The s values can take on any number between 1 and *Ns* (Ns is number of environmental states possible), and b values can take on this same range of values. The number of possible environmental state values (Ns) are organized in a "ring structure," meaning that there are no high or low values (e.g., if Ns = 10, then counting "up" from 8 would look like: 9, 10, 1, 2, and so on). Ns can be any value between 2 and 1000 in this model.

The error term (*Sb*) is a result of how close an individual's behavior (b) comes to matching its environmental state value (s), such that:

For all abs(s - b) <= Ns / 2:
Sb = abs(s - b)

For all abs(s - b) > Ns / 2:
Sb = Ns - abs(s - b)

This allows for the error term to reflect a magnitude of distance between b and s values while maintaining the ring structure of environmental state values. The error term of a behavior in its environmental context is magnified by the environmental harshness (global slider variable called *harshness*), which can take on values between 1.1 and 5. The error term when considering harshness is:

harshness ^ Sb

The acquisition of b values is contingent on heritable learning strategies (*genotype*), which can be values [0, 1, 2, 3] and correspond to learner strategies: asocial = 0, social = 1, conditional = 2 and critical = 3 (the latter two are only relevant when mixed strategies are introduced, defined by an on/off switch in the interface set to *add-mixed-strategies?* = true). The genotype of each entity also influences which learning costs are to be deducted from potential fitness. Costs of learning (*cost*) is a patch variable that is set at each time step according to the method by which behavior is acquired. For example, if a patch copies its b value from another patch, then its cost is set to *C-social* (cost of social learning; global slider value). Conversely, if a patch learns s values asocially, then it takes on a cost of *C-asocial* (cost of asocial learning; global slider value).

An individual with a genotype = 0 (asocial) will always learn about s values asocially and will incur cost = C-asocial at each time step. Individuals with genotype = 1 (social) will always learn about s values socially and will incur cost = C-social at each time step. When add-mixed? = true (i.e., mixed strategies are introduced), genotype = 2 (conditional) will default to asocial learning at cost = C-asocial, but if pr-asocial < 1 (which is typically the case in mixed strategy conditions) and the resulting b value is not equal to s, then it will switch to copying the b value of another patch and incur cost = C-social. Conversely, genotype = 3 (critical) will default to socially copying b from another patch at cost = C-social, but if the result does not equal s it will switch to asocially learning s at cost = C-asocial.

The probability of coming up with a "correct" b value while learning asocially is defined by *pr-asocial-learning*. This is typically set to 1.0 (i.e., 100% asocial learning accuracy) in pure strategy settings. Because pr-asocial is a probability value, it can only be set (on its global slider) between 0-1. In mixed strategy conditions, it only deviates from pr-asocial = 1 to differentiate the acquisition methods and fitness outcomes of asocial and conditional learners. C-social and C-asocial are also values between 0-1, and are typically set such that C-asocial > C-social (C-social is usually ~0.0; see below for initialization values).

The copying of other patches has a “reach” (i.e., how far away can an individual see while copying another b value?) determined by the *learning-type* chooser in the interface. *Local* learning-type means that individuals can only copy b values from neighboring patches, while *global* learning-type means that individuals can copy b values from any patch in the torus.

The relationship between the harshness-relevant error term, cost and fitness (*W*) is updated at each time step, defined by the equation:

W = (1 / (harshness ^ Sb)) - cost

A “perfect” potential W value with neither error nor cost would be 1, and all negative W values are coded to reset to a lower limit of zero. The W value takes on only values between 0-1 because it defines the probability of reproduction (which occurs asexually in this model) and dispersal at a given time step.

The dispersal of individual offspring results in the displacement of an individual of another patch. The end result of this is another patch taking on the genotype value of the dispersing patch. In the global condition of the *dispersal-type* chooser, this displaced/new offspring patch is any patch in the torus. In the local condition, it is a neighboring patch only. The mutation rate is coded in at 0.0008, so with probability 0.0008 at each dispersal event, the offspring genotype value will take on a random number (0 or 1 in pure strategy conditions, 0-3 in mixed strategy conditions) instead of making a copy of its parent.

The dynamics of environmental state in this model have two settings in the *environment-type* chooser. The temporal environment-type sets the s values of each patch to the same random number between 1 and Ns in lockstep, with probability *Ps* (probability of state change, a global slider with possible values 0-1). The spatiotemporal environment-type sets the s value of each patch to different numbers between 1 and Ns independently, each with probability Ps at a given time step. The randomness of change in the spatiotemporal condition is determined by the “spatial-corr?” switch. If spatial-corr? = true, then each spatiotemporal patch change will move one step (s = s + 1; or s = s - 1) toward the average of its surrounding state values. If spatial-corr? = false, then each changing patch will pick an s value between 1 and Ns, randomly and independently of other patches. If spatial-corr? = true in the temporal condition, the model will give a user error and stop running. This is because temporal environment types are perfectly spatially correlated already, and is featured in the model to prevent long and unnecessary BehaviorSpace runs through redundant parameter spaces.

Finally, the *center?* variable is a patch-only boolean variable which is kept false at all patches except for a randomly selected one during each time step. The patch with center? = true is to be the center of a homogeneous perturbation event, the size of which follows a power law equation:

Radius = 8*R^(-1/6), where R is a randomly selected number from a uniform distribution between 0-1.

The perturbation event only occurs once per time step during the spatiotemporal environment-type setting, and does not occur during the temporal environment-type setting. It is worth noting that the Pn value is an approximation used by Rendell et al (2010) to track the homogeneity of the environmental state values across space (or what they call “effectively autocorrelation… with a spatial ‘lag’ of one cell”). It is the probability that a given patch in the torus has a neighbor with the same s value as its own.

Process overview and scheduling

This model goes through the following order at each time step: environmental updates, learning behavioral responses, updating fitness values, and with probability of the resulting fitness value (W), dispersal may or may not occur.

The environmental state values update concurrently depending on the environment-type setting. If this is temporal, then all s values change with probability Ps, and if it is spatiotemporal then each patch s value changes with probability Ps, in accordance with its spatial-corr? setting. In the spatiotemporal setting, all center? values are reset to false before one random patch is set to center? = true. The *perturbation-event* command is then called, and a perturbation event occurs with the center? = true patch at the center.

After the environmental state has been established, each patch is asked to learn their environment by calling the *learn-env* command, where they acquire a b value (socially or asocially, depending on genotype) and get assigned a cost. After this, fitness is assessed by calling the *update-fitness* command, which runs through the fitness equation described above and assigns an updated W value to each patch.

All patches are then asked to (reproduce and) disperse based on their fitness value by calling the *disperse* command with probability W. When this has concluded, the *color-update* command is called to update each patch color according to genotype. Pn values are then updated, and if the time step is within the final 250 ticks of the simulation, then the mean W and mean proportion of each genotype are each added to their own respective lists before the list means are updated (see below under Observations).

Design concepts

Basic principles

The basic principle addressed by this model is the underlying evolutionary game theoretic concept of asocial and social learning among pure strategy learners in a dynamic environment. This model is conceptually rooted in the fundamental relationship between environment state, organism behavior in the context of that environmental state, and the impact that this behavior has on fitness. A basic assumption of this model, then, is the abstract and uncontroversial notion that organisms “correctly” responding to their environmental state are more likely to have higher fitness outcomes than those who do not. Two learning strategies explored in in depth with this model are asocial and social learning.

Within a population of asocial learners, individuals independently track environmental states while incurring a cost. Assuming a relatively low rate of error, the mean fitness of asocial learners is almost entirely a result of learning cost because their informed behavior is likely to be in accordance with their environmental state, so they are unlikely to be penalized for incorrect behaviors.

Social learners, on the other hand, indiscriminately copy other individuals’ behaviors at little to no cost because they bypass environment tracking efforts. When a small number of social learners is introduced into a population of asocial learners, they have a high probability of cheaply copying high quality, up-to-date information from an asocial learner, resulting in a relatively substantial fitness advantage. The fitness of social learners, however, is frequency-dependent. When the proportion of social learners increases, asocial learners are displaced and fewer environment-tracking individuals are feeding relevant information to social learners. In an extreme case, a population of only social learners would effectively have zero fitness because they would have no means of tracking their dynamic environmental conditions. Thus, as an invasion of social learners spreads, the probability increases that a given social learner will copy lower quality, potentially outdated information from another social learner.

Emergence

The emergent result of the frequency-dependent payoff structure between social and asocial learners is the basis for Rogers’ Paradox. The fitness advantage among social learners leads to their spread in a population, and this spread leads to a decrease in their fitness until a polymorphic equilibrium is reached. At this equilibrium, the mean fitness among the population is equivalent to the original mean fitness among only asocial learners (assuming the same costs and environmental conditions in each scenario). This is considered a paradox because of the commonly held assertion that culture enhances fitness.

This model demonstrates the emergence of polymorphic equilibria reached among learning strategies in various environmental conditions. Moreover, it also demonstrates the emergence of mean fitness effects associated with these equilibria across ecological conditions, which may result above or below the Rogers' paradox "threshold" (mean W = 1 - C-asocial). Mean fitnesses above the threshold indicate a resolution of Rogers' paradox. The basic rules underlying these emergent properties are simple heritable learning rules associated with different costs. The effectiveness of asocial learning rules is fixed (pr-asocial), but the effectiveness of social learning rules is inversely related to the emergent increase of social learners. This feedback essentially drives mean fitness downward.

This is particularly distinct in the local learning and dispersal condition, in which many small clusters of social learners form as a result of higher social learner fitness in contact zones with asocial learners (i.e., cluster edges) and lower social learner fitness inside the clusters. This local condition phenomenon accommodates a more widespread invasion of social learners, with an overall lower mean fitness (see Collectives for brief discussion on this phenomenon).

In mixed strategy simulations, the expected utilities of conditional and critical learners are equivalent when social and asocial learning are equally effective, harshness is medium to low, and asocial costs are low. By spatially varying the environment in these conditions, social learning becomes less effective and conditional learners emerge as the dominant portion of the population until a pivotal asocial cost is reached. The increase of asocial costs in low harshness settings results in the prevalence of random social learning, which is a robust result because penalties for error are low and asocial costs are avoided. This scenario raises mean fitness, resolving Rogers' paradox. In most other harshness and environmental stability settings, critical social learners prevail and similarly, they resolve Rogers' paradox because they only incur asocial costs when necessary, and raise mean fitness across a range of harshness and asocial cost parameter spaces. These emergent trends in demography and mean fitness are informative results of simple learning strategies with different costs, environmental harshness, and spatial stability levels in environmental state.

Adaptation

Individuals adapt to state values by unthinkingly employing different heritable strategies. Because these strategies are inherited and influence individual fitness, the adaptation of a given learning strategy type is the result of most individuals' reproductive success with that strategy. In other words, in a given set of environmental conditions, individuals are actively adapting to the environment by learning to behave correctly, in the most fitness-enhancing way possible. This results in the emergence of an evolutionarily adaptive learning strategy, particular to the given set of environmental conditions, as a result of continued existence for some learning types (and extinction for others).

Objectives

The individuals in patches have an objective to correctly assess (i.e., learn about) and respond to their environmental state. Those doing so successfully are more likely to reproduce, meaning that the goal-directed nature of individuals "solving" or successfully learning their environmental state is an effect of the underlying rules. The objective, then is for an individual to maximize its fitness and reproduce at a higher rate than other individuals.

Learning

Learning is the central phenomenon investigated in this model. Individuals in this simulation are learning the environmental states of their patches with different strategies, which results in different fitness outcomes. Strategies which are better at acquiring the correct state information in a given environment, and responding appropriately, are more likely to reproduce and invade the population. Strategies which incur too many costs and incorrect responses are more likely to be driven to extinction. The success of learning, then, is contingent on expected utility for this evolutionary game theoretic model, where utility is reproductive success in a finite environment.

Prediction

Individuals learn the environment in order to predict the correct behavior to execute, though a simplifying assumption of this model is that individuals are predicting the correct behaviors based on the state that they are learning. Because behavioral responses and learned state are inextricably linked in this model, prediction is an assumption (but not an ability with varying competences). In other words, prediction is tacitly suggested by adaptive traits such as behavioral responses to state.

Sensing

Individuals are assumed to sense the environmental state when they have asocial learning capacities. Those with social learning capacities are assumed to sense the behavioral responses to environmental state of other individuals, either globally or locally (depending on the learning type condition). If this condition is global, then social learners can sense the behaviors of others across the entire World. Social learners in the local condition can sense only the behaviors of their neighbors (in a Moore neighborhood). Individuals neither "know" nor have to know the fitness consequences of their behaviors, because this is selected for based on differential fitness outcomes.

Interaction

In an instance of social learning, the model's agents interact by copying the behavior of other agents. In instances of asocial learning, there is no active interaction on the asocial learners' part with other agents, but another socially learning agent may be copying the behavior of the asocial learner. During the reproductive and dispersal stage of each time step, the most significant interaction between agents takes place, because the result of dispersing offspring into a finite number of patches necessarily results in the displacement of many individuals of the previous generation by incoming offspring. The competition between agents, then, is for continued existence in this model.

Stochasticity

The genotypes of individuals at initialization, along with their state values, are assigned randomly. The simulation also relies on stochasticity for resetting environmental states (including perturbation events, both in size and location), along with the existence of an environmental change in the first place. It is also used for copying the behavior of social learners, because an individual learning socially selects a random patch in its learning scope (based on condition). While fitness updates are a non-random result of random states and behavioral outcomes, the value of fitness itself also serves as a probability against which randomly drawn numbers between 0-1 are compared at each time step. This determines the dispersal of offspring, which results in the displacement of a random neighbor (or patch, depending on dispersal condition). This displacement is truly stochastic in that it does not take the displaced individual’s fitness, age, learning strategy, etc. into account. The mutation rate at mu = 0.0008 also allows for some stochasticity, in that transmission of learning strategy may sometimes result in errors.

Collectives

Strategies in this model are distinguished by how behaviors are learned and dictated by the heritable genotypes in this model. There is no other overt top-down force or cooperation rules that establish collectives in this model; they are always a bottom-up, emergent property. In the spatially explicit conditions (i.e., local learning and dispersal), the clustering of social learners is perhaps the most readily apparent instance of collective formation in this model. This is the simple result of environmental changes, because in the event of a state change, social learners in close contact with asocial learners are more likely to copy up-to-date information. On the other hand, social learners inside the middle of the collective are receiving this information by means of a copying cascade, but individuals further from the cluster edges are receiving increasingly outdated information. This is damaging to the fitness of individuals inside large clusters of social learners, and seems to favor smaller clusters of social learners maximizing their “surface area” (i.e., collective contact with asocial learners). This emergent process alone seems to be responsible for the social learner clustering in spatially explicit conditions.

Observation

The data collected were mean fitnesses in the population, proportion of social learners, and (if applicable) proportions of conditional and critical learners (W-mean, s-mean, cond-mean and crit-mean, respectively). These were all taken from the mean values of the last 250 time steps of a 2000 time step simulation, which was done by compiling lists for each of these values during time steps 1750-2000, updating the mean of these lists in each time step, and collecting the final value at the last time step. The plots coded on the interface included mean fitness across time and mean proportion of learning types across time, which allows the observer to track these relevant data visually during a simulation. Furthermore, informative plots in the interface include spatial autocorrelation (i.e., homogeneity of environmental state), which plots the Pn value across time, and mean environmental state across time. The former is for observing how conducive to social learning the environment is at a given time (low stability undermines the effectiveness of social learning), and the latter is for detecting sudden shifts in environmental states. This often can coincide with and account for either sudden demographic shifts in the proportion of learners plot, sudden changes in mean fitness, or both.

Inititialization

For the pure strategy conditions replicating the model of Rendell et al (Figures 1A and 1B), the spatially explicit condition is initialized at Ns=1000, Ps=0.1, harshness=2, environment-type=temporal (meaning that spatial-corr? is not applicable and thus set to false), pr-asocial-learning=1.0, C-social=0.0, add-mixed-strategies?=false, and both dispersal-condition and learning-type are set to local. This condition varies C-asocial from 0.01 to 0.7 in increments of 0.01, with 20 experiments at each C-asocial value. The global condition, which replicates previous mathematical analyses of Rogers' paradox without a spatially explicit component, is a replication of the spatially explicit condition but with dispersal-condition and learning-type set to global.

In the mixed strategy conditions, the simulation is initialized at Ns=10, Ps=0.1, environment-type=temporal (meaning that spatial-corr? is not applicable and still set to false), pr-asocial-learning=0.5, C-social=0.02, add-mixed-strategies?=true, and both dispersal-condition and learning-type are set to local. This condition varies C-asocial from 0.01 to 0.7 in increments of 0.01 (20 runs at each C-asocial value), under three different harshness conditions (harshness = 1.1, 2 and 5). This simulation was repeated with the same settings, but environment-type was set to spatiotemporal and spatial-corr? was set to true. This was to repeat the first mixed strategy simulation, but after weakening the effectiveness of social learning.

Submodels

perturbation-event

This occurs at each time step among spatially varying environmental states, resulting in homogeneous, circular clusters of environmental states that follow the power law equation:

Radius = 8*R^(-1/6)

After a center? = true patch has been selected already, a random-float number (0-1) is assigned to R, and the radius is calculated thereafter. All patches within that radius of the randomly selected center patch are then asked to change their environmental state to a random s value between 1 and Ns.

color-update

This is for visualizing the demographic changes among different strategy types. If genotype = 0 (asocial) then patch color is blue, if genotype = 1 (asocial) then patch color is yellow, if genotype = 2 (conditional) then patch color is orange and if genotype = 3 (critical) then patch color is red. Patch color turns black if genotypes deviate by going above 3, which is unlikely but a visual failsafe nonetheless.

learn-env

This is the command where individuals learn their environment. Asocial, social, conditional and critical learners if identified by their genotype first. For asocial learners, behavior is set to state number based on the probability of asocial learner success. If asocial learning does fail (which is only possible when pr-asocial < 1), then behavior is set to a random number. In either case, cost is set to C-asocial. Social learners set their behaviors to that of another patch (in the torus for global learning-type, and in their immediate Moore neighborhood for the local learning-type), and then set their cost to C-social.

If this command is called for a conditional learner, then it will run through the asocial learning procedure as described above. If the resulting behavior does not equal the state value, then it will run through the social procedure as described above. Conversely, if this command is called for a critical learner then it will run through the social learning procedure as described above, and if the resulting behavior does not equal the state value, it will run through the asocial procedure as described above.

update-fitness

The error term Sb is set according the accuracy of behavior relative to state, such that:

For all abs(s - b) <= Ns / 2:
Sb = abs(s - b)

For all abs(s - b) > Ns / 2:
Sb = Ns - abs(s - b)

Fitness is then updated by the equation outlined by Rendell et al (2010):

W = (1 / (harshness ^ Sb)) - cost

To maintain the [0, 1] boundaries of W in this model, if W < 0 then W is reset to zero.

disperse

If a patch is selected to execute the disperse command (the probability of which was based on its fitness, as discussed), then it will first determine if it is leaving a mutation or a copy of itself. In the rare event ($pr < 0.0008$) that it is a mutation, it will ask another patch to set its genotype to a random number (0-1 if add-mixed?=false, 0-3 if add-mixed?=true). In most cases, when it is leaving a copy of itself, it will ask another patch to change its genotype to the genotype of itself.

This procedure is spelled out in the disperse command twice, because in the local dispersal condition it is asking a neighboring patch to change its genotype, and in the global dispersal condition it is asking any random patch in the torus to change its genotype (but the procedures are otherwise identical).