

#### Please cite the Published Version

Edmonds, Bruce (2019) A Socio-Ecological Test Bed. Ecological Complexity, 40 (Part B). p. 100741. ISSN 1476-945X

DOI: https://doi.org/10.1016/j.ecocom.2018.10.003

Publisher: Elsevier

Version: Accepted Version

Downloaded from: https://e-space.mmu.ac.uk/621979/

Usage rights: Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Additional Information: Accepted manuscript, copyright Elsevier.

#### Enquiries:

If you have questions about this document, contact openresearch@mmu.ac.uk. Please include the URL of the record in e-space. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.mmu.ac.uk/library/using-the-library/policies-and-guidelines)

# A Socio-Ecological Test Bed

Bruce Edmonds bruce@edmonds.name Centre for Policy Modelling, Manchester Metropolitan University, Aytoun Campus, Oxford Road, Manchester M15 6BH, UK.

# Abstract

A test bed simulation is described, composed of an individual-based simulation where species co-evolve on a 2D grid. This can generate, in a bottom-up manner, complex ecosystems of individuals. This test bed is designed so that the kind of ecological complexity observed is exhibited in order to be able to assess the longer-term complex dynamics that might occur if humans with different cultural characteristics are introduced. This is compared to Hubbell's 'Neutral Theory'. A sensitivity analysis is shown. Then an example where "human agents" are introduced half way into the simulation is described. A comprehensive exploration of the impact of introducing 'human-like' agents is beyond the scope of this paper, but some indicative results shown, showing both the high impact humans have, but also some of the complexity of the human-ecosystem interaction.

# **1** Introduction

The evidence is overwhelming that, many times, humans have destroyed the ecologies they inhabited to their own and other species detriment – sometimes causing whole settlements or civilizations to disappear. Examples include the Mayan civilization where it seems that a combination of increasing climatic aridity, demands of agriculture and societal conflicts lead to an abandonment of their impressive step temples in the jungle (Turner & Sabloff 2012). However, you look at it, humans have a profound effect upon the ecosystems they come into contact with, even to the extent that (as some have argued) we are in the middle of the sixth great extinction event – the 'Anthropocene' (Crutzen 2002).

However, *how* humans will effect a particular ecosystem is not always clear – sometimes it seems that a balance between humans and the rest of the ecosystem is established, but at other times, the arrival of humans can only be described as catastrophic. The difference in these cases is not in the biology of the particular humans, but due to their different cultures (in the widest sense of methods of social organisation, technologies, traditions etc.). In biological terms, the genetic difference between the Inuit and the Norse was small but their cultures were "worlds apart". Eventually, the Norse had to abandon their settlements in Greenland, whilst the Inuit succeeded<sup>1</sup> (Diamond 2004). The combination of an ecological and a social system is called a socio-ecological system (SES). Being composed of two very complex systems means that SES are very hard to understand, where both society and the ecology co-adapt in a dynamic and often chaotic manner<sup>2</sup>. The challenge of understanding the long-term outcomes from the interaction of the social and ecological complexities is severe, yet that is what is needed if we are to adapt our society for long-term survival.

There have been many agent-based simulations addressing the interaction of man with the environment, going back (at least) to 1994 (Bousquet, Cambier & Morand 1994) – see (Bousquet & Le Page 1994) for a review. Individual-based ecological models go back even further (Grimm 1999). However to fully address this challenge we need to have a multi-agent model concerning human decision making and social interaction combined with an individual-based model of an ecology that more fully reflects the dynamism and complexity of real

<sup>&</sup>lt;sup>1</sup> To be exact it was the fourth wave of Inuit that succeeded in gaining a living around the shores of Greenland. <sup>2</sup> In the sense of sensitive dependence on initial conditions.

ecologies. Up to now, models of humans interacting with their environment have had either a relatively simple model of human interaction or a simple model of the ecosystem they are embedded in (for example a systems dynamic model concerning a single resource such as water of a particular species of fish). As is stated in (Deffuant & al. 2012):

"...The more serious shortcomings of existing modelling techniques, however, are of a structural nature: the failure to adequately capture nonlinear feedbacks within resource and environmental systems and between human societies and these systems." (p. 523)

This paper describes a test bed wherein these nonlinear feedbacks can be examined and better understood. It aims to go beyond simple interactions to start to represent the complex co-adaption that can occur over long time scales and a variety of niches.

## 1.1 A Specification for a Socio-Ecological Test Bed

In order to be able to capture the fuller complexities of the interaction of a society with an ecology, the humans and their society have to be fully embedded within that ecology, in terms of time, space and nutrition. That is the following:

- a) The environment needs to include space, so that there can be a differentiation in terms of niches and the possibility of spatial migration between locations
- b) The environment needs to include habitats with different characteristics, for example deserts (which can not sustain much life) and natural barriers to migration
- c) Complex food webs of species need to be able to develop within each habitat either extracting resources from the environment or other individuals (predation)
- d) New species need to be able to evolve in response to the pressure of the environment, other species and humans
- e) When agents representing humans are introduced, they need to be embedded within these habitats, needing to use/eat other species to enable their own survival

## **1.2** Assessment of the State of the Overall Ecology

The basic strategy is to be able to assess the state of the ecologies in the simulation after a relatively long period of time. For example, with or without human agents being introduced after a period. The assessment of the final state of the simulation could be done in a variety of ways, e.g.:

- Measuring the diversity of the ecology, for example the average genetic difference between non-human individuals, as in (de Aguiar et al. 2009).
- The species-number distribution how many species are there with a population of at least 2<sup>*n*</sup>, where *n* varies the "Species Abundance Distribution" of (Eldridge 2000).
- The number of trophic layers that have survived for a period of time since the injection of human agents, shown by the distribution of trophic layers.
- The health of the society of any "human" agents, in terms of the number of surviving humans and its variability over time.

Measures such as these can be brought together to assess the sustainability/health of the SES as a whole. The state of the whole SES is a complex matter to establish and requires a multilevel and multi-aspect assessment to understand its evolution. Given that, we have a complex simulation with individual humans and other organisms explicitly represented (rather than abstracted away), we are able to apply a whole range of measurements.

Runs starting with the same ecological starting point, but with contrasting social or cultural characteristics can then be used to asses the range of outcomes that can result from the "cultures" and how often each kind of outcome might occur.

# 2 The Test bed

This is a synchronous individual-based simulation. Entities – plants, herbivores and predators – are represented as individual objects. They inhabit one of a number of patches arranged in a 2D pattern that makes up the world. Each patch is well mixed so that interactions within that

patch are random, but there is a probability that each individual can migrate to one of the four neighbouring patches each tick via a diffusion process. The world is wrapped vertically and horizontally. Each patch and individual has a binary bit-string that represents its characteristics, their lengths determined by parameters. There is a basic energy economy: each simulation tick, energy is injected into the world and divided equally between patches, which drives the ecology. Whether an individual can extract energy from a patch or predate upon another is determined by both of their bit-strings and a fixed random interaction matrix, described below. The bit-string of any individual is passed to any progeny but there is a probability that one of the bits of these bits is flipped at birth. The world is illustrated in Figure 1.



Figure 1. An illustration of the grid of 2D patches, in this case an 8x8 grid. Plants are small stars, herbivores and higher predators are circles (the more they have eaten the bigger they are displayed up to a maximum size,). Different colours indicate different species but not all species are visually distinguishable in this and similar illustrations<sup>3</sup>.

Key to this simulation is understanding how it is determined whether individuals can extract energy from a patch or predate upon another. This method is adapted from that in (Caldarelli et al. 1998). A random interaction matrix with the dimensions of the length of individuals' bitstrings is generated at the start of a simulation. It is filled with normally distributed random floating-point numbers (mean 0, standard deviation 1/3)<sup>4</sup>. This interaction matrix determines which entity can eat another entity in the following manner (see Figure 2 for an illustration):

- 1. The non-zero bits of the predator select the columns of the matrix; the non-zero bits of the potential prey select the rows.
- 2. The intersection of the selected rows and columns determine a set of numbers, these are summed.
- 3. If the sum is greater than zero the predator can eat the prey, in which case the prey dies and the predator gains a percentage of its energy value the rest is lost.

A more mathematical account of this calculation can be found in the appendix.

<sup>&</sup>lt;sup>3</sup> The space of possible bit-strings is *much* larger than the space of distinguishable colours. Thus colour is illustrative of genetic difference (similar colour is a fallible indicator of similar bit string), but many differences will not be discernable.

<sup>&</sup>lt;sup>4</sup> This could be forced to be anti-symmetric but in the runs here, it is not. Forcing the matrix to be anti-symmetric slightly simplifies the possible interactions but (in all the variants I have observed) does not substantially change them. Various ways of generating this matrix have been tried but does not make any discernable difference to the overall results, although it is possible that certain matrices could have a substantial influence on the outcomes.



Figure 2. The use of the interaction matrix to determine predation as well as energy extraction from a patch to give its relative fitness.

The interaction matrix is a proxy for the complex affordances between species. It does not directly represent anything in particular. Its essential features are that it allows for co-evolutionary 'arms races' to occur. It allows for a sufficiently large space of possible ways of interaction, and applied in different models has lead to the development of realistic looking food webs (McKane 2004). Clearly, we do not know which matrix would correspond to any given observed ecosystem without a painstaking mapping process, which is why the runs here are done with a random selection of matrices and summary results presented.

Essentially the same process is used to determine which entities can extract energy directly from the environment, except that the part of the prey is taken by the patch with its bit-string (padded with zeros to reach the appropriate length). In this case, only those with scores greater than zero get any of the patch's energy. The patch's energy is divided between all qualifying individuals in proportion to their score against the patch. This scheme has the consequence that no individuals can extract energy from a patch with a bit-string of all zeros. Thus, all the simulations reported below will have some patches that act as "deserts", that is patches where individuals cannot extract any energy from the environment (although they may pass through the patch using previously stored energy or predate upon other individuals there).

This interaction scheme allows complex food webs to develop, for example via a genetic "armsrace" between predator species and prey species, since it allows for adaption with respect to another specific species. In other words, the fitness of an individual is not an absolute number but relative to the environment dependent on whether it extracts energy from this, or another species. (Caldarelli et al. 1998) showed that this kind of scheme can be used to evolve complex ecologies with plausible characteristics including food webs with similar network characteristics to observed food webs.

At the start of the simulation, the random interaction matrix is generated. Each patch is allocated a random bit-string with the given number of bits, padded out with zeros to make it the same length as individuals' bit-strings. The "environmental complexity" is the number of significant characteristics that patches have – the number of bits in their bit-string. Bit-strings of length 2 allow for 4 types of patch, of length 3 8 types etc.<sup>5</sup>. The simulation starts with no individuals.

<sup>&</sup>lt;sup>5</sup> Due to the fact that a patch with a zero-length bit string would be equivalent to having a bit-string of all zeros and hence a desert, only environmental complexities starting at length 1 or above are explored.

Each tick<sup>6</sup> following processes occur in the following order:

- 1. **Input energy**. A fixed amount of energy is added to the model, equally divided between all the patches.
- 2. **Death**. A life tax is subtracted from all individuals<sup>7</sup>; if their total energy is less than zero they are removed from the simulation. Their age is incremented.
- 3. **Initial seeding.** (In the initial phase), until a viable population<sup>8</sup> is established, a new individual with randomly generated characteristics is introduced with a given probability.
- 4. Energy extraction from patch. The energy stored in a patch is divided among the individuals on that patch that have a positive score when their bit-string is evaluated, using the interaction as described above (against the patch's bit-string) in proportion to their relative fitness, at the simulation's efficiency rate.
- 5. **Predation**. In a random sequence, each individual is randomly paired with a number of others on the patch, given by the parameter "eating tries". If it has a positive dominance score against the other, the other is removed from the simulation and the individual gains a fixed proportion of its energy, given by the "efficiency" parameter. Individuals are not allowed to predate upon members of their own species.
- 6. **Maximum Store**. Individuals can only retain so much energy, so any above the maximum level set (by a parameter) is discarded.
- 7. **Birth**. If an individual has a level of energy above that determined by the "reproducelevel" parameter, it gives birth to a new entity with the same bit-string as itself, with a probability of mutation. The new entity has an energy level of 1, which is subtracted from the energy of the parent.
- 8. **Migration**. With a probability determined by the "migration" parameter, the individual is moved to one of the neighbouring 4 patches (the world being "wrapped" top and bottom).
- 9. Statistics. Various statistics concerning the model are calculated.

The simulation ends after a given number of ticks. At the end, the diversity of the ecology is calculated; this is the average hamming distance between all bit-strings in the ecology<sup>9</sup>, called "pi-t", following (de Aguiar et al. 2009). This is a better measure of diversity than the number of species since it is not disproportionately influenced by the existence of almost extinct species.

Notable features of this set-up are:

- It can produce ecologies with plausible food webs.
- The fundamental interactions in the model, those that constitute the food chain, are emergent and can continually change in both time and space.
- The model creates endogenous shocks on its own, with new species appearing to sometimes-catastrophic effect on the existing food chains, affecting them radically in terms of their constituent species, their relative abundances and even the predation links.
- Mutation and migration happen in parallel, so that new species often appear before previous species have been completely spread over the space – states that could be interpreted as being in "equilibrium" are rarely observed, unless the ecology is nonviable or is dominated by a single species.

## Level of Realism

The model presented is not intended to be descriptively accurate in every detail but rather is an abstract model with key characteristics that make it suitable as an ecological test bed. In

<sup>&</sup>lt;sup>6</sup> Time is abstract here and not scaled to any particular observable interval.

<sup>&</sup>lt;sup>7</sup> Called 'maintenance' in the Marr-Pirt models (Kooijman, 2010).

<sup>&</sup>lt;sup>8</sup> This is simply when the number of individuals reaches a certain minimum size.

<sup>&</sup>lt;sup>9</sup> In fact, this is approximated by using a random sample of 10,000 possible pairs between individuals if there are more possible pairs than this in the population (more than 142 individuals), otherwise the calculation can take too long.

modelling terms, it aims to be used as a kind of 'risk-analysis' – a way of exploring some of the complex ways in which ecologies could fail or succeed<sup>10</sup>. The criteria it seeks to achieve are those listed in the "Specification" section above. Thus, the model is not 'realistic' in many respects, but is just a model with a particular purpose (Edmonds 2017). In particular, the model is not realistic in the following ways:

- Particular families of organisms are not represented (viruses, fungi etc.) rather different kinds are allowed to emerge in the evolutionary process. Thus, 'alternative' biological histories are generated. In this model, the interaction matrix is the proxy for the various complex ways in which organisms can interact rather than all these ways being explicitly represented.
- Reproduction is asexual. Though it would be easy to add in sexual reproduction, I have not done so here. Consequently, a species is not well defined in this model version<sup>11</sup>. Thus, when I talk about a 'species' in the text below I mean a collection of entities with the same genome.
- In the model, there is the possibility that a patche may have an all zero set of characteristics. This means that no entity can extract energy from it. This does not mean they instantly die, because entities might have stored energy and pass through this patch before they run out. Although it is debatable that there are any places in the world where no organisms can survive, there are certainly places where not many do. Thus, given the granularity of the simulation (the limited number of kinds of patch and the numbers of species) this is acceptable.
- Time scales in such models are particularly tricky. This is an abstract model for the purposes of risk-analysis and is thus designed to be the simplest to satisfy criteria (a)-(e) above. One of the factors here is being able to do enough runs over sufficient time for some of the subtle longer-term emergent risks to be identified. Clearly, this would involve trials with a variety of time scales with respect to different processes (mutation, movement, reproduction, etc.). This is future work beyond the scope of this paper.

# **3** Typical Behaviour of the Basic Simulation

There are four different ecological kinds of outcome observed in this model: (1) a non-viable outcome where nothing thrives or reproduces, defined as being fewer than 10 individuals in the whole space, (2) a situation where one, or two, plant species dominate, (3) a plant ecology, not case 1 or 2, with no herbivores or higher predators and, (4) a mixed ecology like case 3 but with herbivores and higher predators. Thus although the division is somewhat arbitrary, it very clearly distinguishes four cases between observed simulation trajectories. Furthermore, these four kinds tend to persist for many simulation ticks so that each can be meaningfully identified. These are each described with outcomes from a typical run below. Many of the later results will be in terms of the occurrences of each of these four types.

Each description is accompanied with three figures: on the left is a visualisation of the patches and individuals, the colours of the background patches indicate their bit-string, plants are indicated by a small star, individuals higher up the food-chain are indicated by a circle whose size is related to how many other individuals they have eaten; in the centre is a graph of the number of species over time; and on the right is a graph showing the number of individuals of each trophic level on a shifted log scale.

## 3.1 Non-Viable Ecology

Here species do not manage to extract any energy from the environment, so any introduced species quickly starve with no reproduction. There is only ever one individual since only when one dies is a new random one is introduced into the simulation.

<sup>&</sup>lt;sup>10</sup> In the sense of diversity and survival (including our own).

<sup>&</sup>lt;sup>11</sup> In contrast to (de Aguiar et al. 2009)



Figure 3. Typical Non-Viable Ecology: (left) the world state, (centre) Number of Species, (right) Log (1 + Number of Individuals) at each trophic level

## 3.2 Dominant Species Ecology

Here one, or a few, species dominate. The dominant species is both a plant and a predator, eating any new other species that appear. Thus, occasionally individuals are classified as belonging to a higher order trophic level, although no other species manages to achieve a long-term survival. Very occasionally two or three dominant species occur, each destroying the others that wander into the patches they dominate.



Figure 4. Typical Dominant Species Ecology: (left) the world state, (centre) Number of Species, (right) Log (1 + Number of Individuals) at each trophic level

## 3.3 Rich Plant Ecology

In this case a rich plant ecology develops where many different species compete as to their efficiency in extracting energy from the different kinds of patch, and are resistant to potential herbivores who, if introduced, simply starve. In terms of the number of individuals, this state often produces the greatest number of species and the highest population (in terms of number of individuals). Species only gradually replace older ones as they marginally out-compete them in terms of energy extraction.



Figure 5. Typical Herbivore Ecology: (left) the world state, (centre) Number of Species, (right) Log (1 + Number of Individuals) at each trophic level

## 3.4 Mixed Ecology

In the last case, successful herbivores and higher predators evolve to produce a highly dynamic ecology. There is a continual "arms race" both in terms of bit-string evolution as well as over the space of patches. There are typically far fewer species than in the rich plant ecologies since many plant species are wiped out<sup>12</sup>. This typically results in a power law in numbers of

<sup>&</sup>lt;sup>12</sup> Although it is received wisdom that adding a trophic level increases diversity at lower levels, the evidence is not clear. When a new predator is introduced some species are eliminated, and when an established predator is removed this can disrupt an ecosystem. However comparing the situation with and without a predator in the longer-term is different to these cases of sudden change and difficult to compare empirically.

individuals at each trophic level with an order of magnitude between the prevalence of each layer. Here you get a more constant replacement of older species as found in (Drossel et al 2001).



Figure 6. Typical Mixed Ecology: (left) the world state, (centre) Number of Species, (right) Log (1 + Number of Individuals) at each trophic level

A longer and more detailed graph of the number of species over time shows the advent of higher trophic levels. In such a run, it can take a long time for the first successful plant to be discovered, followed by an explosion of other kinds of plant due to mutation. The number of species generally increases (but may flatten out due to competition for resources) until the first herbivore appears. This causes a decrease in the diversity of plants as the herbivores consume all the plants that are vulnerable to them, before the plants evolve to survive in the face of this new threat. The same pattern then re-occurs until the first herbivore predator appears, etc. This sequence is illustrated in Figure 7. The distribution of the trophic levels at the end of this run is shown in Figure 8.



Figure 7.The number of species in a single run with the advent of higher trophic levels labelled with arrows (green for plants, blue for herbivores, red for carnivores).



Figure 8. The number of individuals at each trophic level at the end of the run shown in Figure 7.

# 4 Sensitivity Analysis of Basic Ecological Model

Each individual run of this simulation can give very different results starting from the same parameter values. Partly this depends on the different interaction matrices generated for each run and partly on the happenstance of mutation and movement within the world. Summaries of such runs for different parameter values may thus be misleading as averaging may give a false picture of the collection of trajectories. Thus for each parameter I show both the average effect on diversity over all the runs (the charts on the left below indicating a 95% spread) and a count of how many runs end up in each of the four states defined above (the bar-charts on the right)<sup>13</sup>. For each of these there were 25 runs of 1000 ticks for each parameter value. Where the results are less interesting I have relegated the respective graphs to Appendix II.



Figure 9. Effect of Energy Input on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

The greater the amount of energy that is put into the system, the greater the diversity that results (Figure 9), however the response to more energy is non-linear as larger populations support more predators, which can have the effect of reducing the diversity. Generally, the higher the input energy, the less frequent does a pure plant ecology result.



Figure 10. Effect of Migration Rate on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

A zero rate of migration means that each patch is isolated, so this severely restricts the diversity and ensures small populations. Above that the higher the migration rate, the lower the diversity since patches act less like semi-isolate demes and more like a total well-mixed population, with all species competing against each other (Figure 10).

<sup>&</sup>lt;sup>13</sup> Tests of statistical significance are not appropriate for analyzing the output of simulation runs. Statistical significance is used to rule out the possibility that apparent differences in figures are due to random variation, here we know the simulations are different (different settings are being compared). One can obtain any desired level of significance simply by running the simulations for long enough, even if they are the same simulations with different random seeds.



Figure 11. Effect of Mutation Rate on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

A zero mutation rate means that nothing can evolve, so that there is, at most, one species. Above that, a higher mutation rate implies a higher diversity and fewer cases of a "non-viable" ecology (Figure 11).



Figure 12. An illustration of the number of species and their types over longer runs, red=plant, blue=mixed

Figure 12 shows 5 independent runs of the model over 10,000 simulation ticks with a lower mutation rate of 0.001. The first two runs are dominated by plant ecologies with occasional periods of higher trophic levels appearing, the second two are the reverse and remain mixed ecologies for the majority of the time, though mixed ecologies are not as stable as plant ecologies. The last is dominated by a single species and remains so with very short-lived appearance of herbivores. These longer runs illustrate the long-term robustness of the four types of ecology in this model. In the top two runs illustrated in Figure 12 a rich plant ecology dominates, sustaining large numbers of individuals, with occasional short-lived intrusions of herbivores. In the next two runs a mixed ecology dominates with occasional periods when herbivores disappear. The bottom run shows the stability of the situation when one species dominates, effectively preventing any others appearing.

# 5 Comparison with Hubbell's Neutral Model

Hubbell (2001) proposed a very simple mathematical model of species distribution focussing on the effects of demographic stochasticity and dispersal limitation. In this model local extinctions are balanced by immigration from a 'metacommunity' – a resource of individuals

composed of many species. Although not descriptively realistic of the biological processes involved, this does seem to match many sets of biological data, especially for the distributions of plants in ecologies. In particular, this theory predicts the shapes of the 'species-area curve' (a log-log scatter graph of the number of species vs the area that these species were counted over) and the 'species-abundance distribution' (represented in (Hubbell 2001) by a histogram of the log of the relative species abundance ranked in order of this abundance, and a histogram of the number of species against the log to base 2 of species abundance).

As a partial check on the model's correctness, a version of the simulation presented here with only plants and with random migration was run and the outcomes after 5000 simulation ticks analysed. Three different distributions of the outcomes were measured following those used by Hubbell (2001): a scatter plot of the number of species vs. area, a histogram of the relative species abundance (with the species ranked from most abundant downwards), and a histogram of the number of species at increasing levels of abundance. The graphs that resulted from these were remarkably consistent across runs, with very little variation in levels and none in terms of the overall shape of the distributions. Figure 13 shows these graphs for the first four independent runs. These match up remarkably well to those discovered by Hubbell (2001) in his empirical work, with the exception of the upper half of the species vs. area scatterplots (corresponding to a continental scale), but then the model was not tested on very large scales where the size of the space is much bigger than the average species range, so this would be expected.



Figure 13. Species vs. Area, Relative Species Abundance and Species Abundance Distributions for 4 independent runs

# 6 Adding 'Human' Agents

To simulate the impact of humans upon the basic ecology we inject 'human agents" into the model once a basic ecology has had a chance to establish itself. This method embeds the impact of humans *within* the model, rather than as an exterior intervention. It allows the dynamics of the participant individuals of an ecology to be explored as a whole system. Thus enabling the identification of dynamics that might not be manifest from examining that of the ecological system or human system alone, or by connecting models of an ecology and human system via simple connection (e.g. only the numbers of each influencing the other).

There are clearly many different characteristics one could endow these human agents with, depending on what aspect of human culture and abilities one wanted to assess. The point of this paper is not to make any kind of comprehensive attempt at such an assessment, but to merely given an example of the approach and the possibilities. However, what is essential to this approach is that the human agents are embedded within the simulation and have to participate in the food chain just as other entities.

## 6.1 Method

The agents representing humans share many aspects of the entities in the basic ecological model.

- They have a similar bit-string of characteristics representing their abilities and these are assessed against other species in the same manner as before using the interaction matrix.
- They inhabit the grid of patches and can migrate to neighbouring patches as other entities.
- They have a similar energy economy as other entities.
- To survive they have to successfully predate upon other entities. They may be predated upon by other entities.

However, there are important differences. In this set of experiments, the human agents have the following basic characteristics.

- They are not allowed to extract energy directly from a patch, even if their bit-string would allow this (they are not a plant), but have to eat plants and other entities within their reach to survive.
- Their bit-string is not genetic, but rather represents a set of skills that can be changed during a lifetime. Change in the bit-string does not particularly occur at birth since these skills are passed to children during training, but rather there is a relatively high rate of continual change in their characteristics throughout the life of human individuals.
- They can learn from nearby other humans on the same patch as themselves. This is realised as a probability to look at a set number of other random humans on the same patch, and if those have more energy than they do, they copy a random bit from them.
- The rate of change of their bit-strings is higher than that of other entities, since it represents a cognitive rather than genetic process.
- They arrive in the simulation as a diverse group of individuals on the same patch. If they die out another group is introduced after a period.
- Some of their parameters are also different: they have a max age of 100, a higher threshold for reproduction (20), and a higher default ability to store energy (30).
- In some of the runs reported below their migration rate is different from that for other entities allowing the exploration of the effect of the relative rate of migration rates.

These agents are not just another predator; they are not restricted to a genetic mutation rate at the same rate of their prey but can adapt far more quickly and then share these adaptions with their peers. In this way, they change the pattern of evolutionary competition and, *if they survive*, can easily dominate the ecosystem. These agents might be interpreted as representing

hunter-gatherer nomads who indiscriminately eat what happens to be around before moving  $on^{14}$ .

## 6.2 Results

Here we deliberately give results at a number of different levels and using a number of different methods. The outcomes are complex and any one measure of the whole picture is necessarily partial. In a sense, the whole state of the ecology is the outcome; however this is hard to directly understand, so some abstraction or measurement from this is desirable.

### 6.2.1 Some Typical Trajectories

There seem to be a variety of different kinds of trajectory possible once human individuals have been introduced into the model.

One possibility is that humans do not manage to predate upon any existing organisms and rapidly die out. In this case, they have little impact upon the ecology. Another is that they predate only upon a thin top layer of herbivores/predators and then die out after they have eliminated any of those around themselves. This has the effect of a temporary depression in the numbers of these, which recover as soon as the human individuals have gone. These are not illustrated since they are obvious.

A third, more catastrophic possibility is that the humans predate upon all the entities in the simulation, allowing a population explosion that eventually results in the consumption of all other entities in the world, after which the human agents gradually starve. This is the sequence illustrated in Figure 14, with the human agents depicted as having faces.



Figure 14. A sequence of world snapshots of an invasion of humans into a plant ecology with fast migration, causing self-extinction due to elimination of plants followed by starvation

A fourth possibility is that some kind of spatial predator-prey dynamics emerge for a while between humans and other entities. An illustration of this is in Figure 15. Here "waves" of humans develop, consuming all in their path but in such a pattern that new clumps of entities develop in the patches they have disappeared from (due to the previous elimination of food). This is a spatial "cat and mouse" situation, which depends upon the humans not spreading

<sup>&</sup>lt;sup>14</sup> Movement is not coordinated, but a random diffusion process. However, those moving to locations where other species have been depleted tend not to survive, whilst those who go to locations with resources survive, so movement looks like it is coordinated.

evenly but leaving patches and those patches being able to be seeded by other entities thriving for a short time there.



Figure 15. A sequence of world snapshots with slower migration with humans eating all resources as they go, but new plants re-growing after they have left

A graph of their numbers may look like classic predator-prey dynamics such as in Figure 16, although this apparently simple summary might not reflect what is happening within a more complex spatial dynamic.



Figure 16. Number of humans (red) and plants (blue) in a single run of the simulation starting from a rich plant ecology, from the point at which humans were introduced.

There are, of course, more complex mixes of dynamics where the pattern is not so distinguishable to the eye.

#### 6.2.2 Sensitivity of model with and without humans

The first set of results is a series of runs where the ecology is allowed to evolve without humans for 1000 ticks, as described above, and then in half the runs people are injected as a diverse group of 50 people into one patch. If the people die out then after 100 ticks, giving the ecology a chance to recover, another batch of people is injected. If there are any existing people then no new people are injected from the outside. The simulation continues to time 2000, when the statistics are calculated: the kind of ecology that it is at this point (assessed by

what, apart from human agents, is there) and the measure of diversity (*pi-t*). This is done 25 times for each parameter value with humans and 25 times without.



Figure 17. The differential effect of the arrival of humans, or not, with diversity of landscape (left) by proportion of ecology types, red=plant, blue=mixed, purple=single species, green=nonviable (right - lower row with humans, upper row without) by diversity of ecology, blue=with humans, red=without

In Figure 17 we look at the effect of the presence of humans in environments of different complexities, measured by number of bits that patches have (which exponentially affects the number of different patch types). Humans have a general depressing effect upon the ecological diversity. Without humans, increasing environmental complexity means fewer cases of plant ecologies, but with humans the incidence of plant ecologies increases with environmental complexity. Whilst environmental complexity increases the proportion of mixed ecologies without people but is roughly constant with people.



Figure 18. The differential effect of the arrival of humans, or not, with migration rate (left) by proportion of ecology types, red=plant, blue=mixed, purple=single species, green=non-viable (right - lower row with humans, upper row without) by diversity of ecology, blue=with humans, red=without

In Figure 18 we look at the effect of different migration rates (the same for entities and humans). As before a zero migration rate is catastrophic for the survival of most species because entities and humans never spread beyond a single patch. Without humans, the migration rate does not have much effect on the occurrence of ecology types, but with humans increasing migration rate results in more non-viable ecologies at the expense of mixed ecologies.



Figure 19. The differential effect of the arrival of humans, or not, with availability of energy (left) by proportion of ecology types, red=plant, blue=mixed, purple=single species, green=nonviable (right - lower row with humans, upper row without) by diversity of ecology, blue=with humans, red=without

Figure 19 shows the differential effect of the amount of energy being input into the system (the food rate). Without humans, an increase in energy allows for more diversity and a greater occurrence of mixed ecologies and fewer plant and single species ecologies. With humans, increasing energy results in a greater proportion of mixed ecologies but also many more non-viable states, due to the human population growing faster than the ecology and wiping out their own food supply.

#### 6.2.3 A Larger Random Sample of Runs with Human Agents

4,478 runs of the simulation, starting from a blank ecology at tick zero with humans entering at tick 1000, running the simulation on to tick 2000 were performed with parameters set at random from given ranges, world dimensions from {2x2, 3x3,... 10x10}; number of patch types from {2, 4, 8, ..., 32}; migration rate from {0, 0.0025, 0.005,..., 0.02}; energy input rate from {50, 100, ..., 500}; innovation rate from {0, 0.05, 0.1,...,0.2} and learning rate from {0, 0.1}. The purpose of this is to enable the exploration of factors not in a 'thin' slice of parameter sampling but over a wide variety of settings, as would be the case in observed ecologies. Thus, these results are less like a controlled experiment and more like observing a large number of occurring cases to look for trends, as might happen with field data. In other words, these results correspond to observed data which might display more of the natural variety that empirical data might contain (covering a wider range of cases).



Figure 20. Overall change in ecological diversity with humans being introduced with (left) migration rate and (right) energy input into the system.

Figure 20 shows the overall change in diversity across all final states analysed by migration rate and amount of energy available to the system. Increasing migration rate has the effect of decreasing diversity due to more mixing but also faster spread of humans to patches with other entities on them. A greater amount of energy input does result in a higher level of average diversity but with a greater spread of outcomes as energy increases.



Figure 21. Proportion of different ecological outcomes with humans for different migration probabilities and food rates, red=plant, blue=mixed, purple=single species, green=non-viable

Figure 21 splits the results according to rate of migration and the input energy (the food rate), with the proportion of each kind of outcome displayed. There is a greater proportion of single species outcomes for low rates of energy input and input energy. For low mutation rates increasing the energy available increases the proportion of mixed ecologies, but for high mutation rates more energy increases the proportion of non-viable outcomes.



Figure 22. Number of species/variants of people (horizontal axes) and other entities (vertical axes), red=plant, blue=mixed, purple=single species, green=non-viable

Figure 22 is a scatter plot of all outcomes in terms of ecology diversity and then number of variants/species. In terms of diversity there are all levels of diversity in the human bit-strings whilst the ecological diversity is limited to smaller levels, the presence of people severely depresses ecological diversity (up to a maximum carrying capacity for people). When the number of variants among human agents is plotted against number of species, we see that

one rarely gets a high number of variants at the same time as a high number of species – species and variants seem to be mutually exclusive.

### 6.3 Starting from a given Ecological State

Here, three contrasting ecological states were "saved": a rich plant ecology, a single species plant ecology, and a mixed ecology with all trophic levels. This means that runs starting from these have the same interaction matrix and the same initial state of entities (species, populations, distribution etc.). Then two sets of simulation runs were one where migration rates for entities and humans were varied systematically and one where innovation rates for humans and mutation rates for entities were varied. 25 simulations starting at the same ecological state where done for each parameter up to 2000 ticks, ecology was "frozen" at 1000 ticks, and the type of ecology stored. These results are now discussed.



Figure 23. Starting from a Plant Ecology the effects of innovation rate/mutation rate (left) and people migration rate/entity migration rate (right), red=plant, blue=mixed, purple=single species, green=non-viable

Figure 23 shows the outcomes starting from the same plant ecology. Unsurprisingly plant ecologies still tended to dominate after 1000 ticks. Higher mutation rates and lower innovation rates resulted in more mixed ecologies resulting. When the migration rate of people was less than or equal to that of other entities more mixed and single species ecologies resulted. A higher proportion of non-viable states occurred with low levels of entity mutation and high levels of human migration.



Figure 24. Starting from a Mixed Ecology the effects of innovation rate/mutation rate (left) and people migration rate/entity migration rate (right), red=plant, blue=mixed, purple=single species, green=non-viable

Figure 24 shows the outcomes starting from the same mixed ecology. Again, mixed ecologies still tended to dominate after the arrival of people. Low levels of entity mutation or high levels

of entity migration resulted in a greater proportion of plant ecologies. Again high rates of people migration resulted in a greater proportion of non-viable states, but this time a low level of entity mutation did not result in many non-viable states.



Figure 25. Starting from a Single Species Ecology the effects of innovation rate/mutation rate (left) and people migration rate/entity migration rate (right), red=plant, blue=mixed, purple=single species, green=non-viable

Figure 25 shows the outcomes starting from the same single plant species ecology. Here a high level of entity mutation resulted in the appearance of mixed ecologies and high levels of either entity or people migration resulted in the appearance of more plant ecologies. High levels of both entity and people migration rates resulted in a higher proportion of non-viable states.

Consistently, regardless of the starting ecological state, a high rate of people migration resulted in a greater proportion of non-viable states and higher mutation rates results in more mixed states. However, the effects of varying these parameters were also different depending upon the ecological state that the simulation started from. Both rich plant and mixed states were more resistant to being altered into a different state, in other words more resilient to the impact upon humans (in terms of type).

# 7 Discussion of Results

In this model, the human individuals had a profound, but sometimes complex, effect upon the ecologies they entered.

In terms of straightforward effects, there was the following. They uniformly reduced ecological diversity, causing a greater proportion of non-viable states and far fewer mixed ecologies since they directly competed with herbivores and higher predators. They often caused their own disappearance as they wiped out the species they depended upon for sustenance. High levels of migration reduce diversity (Figure 18, Figure 21, Figure 30, Figure 23, Figure 24 and Figure 25). The greater the migration rate between patches the less they act as separate demes, which afford some protection of the diversity.

In terms of more subtle and context-dependent effects, there were the following. The presence of human individuals flattened the effect of increasing environmental complexity. So whereas increasing the number of patch types would result in an increase in environmental complexity, in the presence of humans this effect is almost eliminated (Figure 17). The presence of humans also changes the impact of increasing energy input into the environment, from increasing mixed states, decreasing single species, and decreasing plant-only states, to increasing non-viable states, decreasing single species states, (Figure 18). Species diversity is somewhat of a short-term protection against the arrival of humans since each group of humans might not be able to predate upon all kinds of species simultaneously, leaving certain species less affected. Higher mutation rates among non-human entities ensure a higher supply of new species to the world and hence tend to result in more diversity, a greater proportion of

mixed ecologies and no non-viable ecologies (Figure 23, Figure 24 and Figure 25). Since each mixed patch is usually dominated by humans or other entities and not both for extended periods of times (Figure 30 in Appendix II).

In terms of starting from each of three different kinds of ecology with humans being injected we had the following results.

Richer plant ecologies (Figure 23) tended to remain so for medium/low mutation rates, and lower migration rates (both entity and human). For high mutation rates, they often evolved into mixed ecologies even in the presence of humans. High migration rates meant the simulations could evolve into any of the states. Low mutation rates or high people migration rates also meant a proportion became non-viable.

Mixed ecologies (Figure 24) were also fairly stable, tending to remain almost entirely for high migration rates for both humans and entities. Low mutation rates or high entity migration rates increased the tendency to result in a plant-only state.

Single species states (Figure 25) were the most vulnerable to change and less so the higher the mutation rate and migration rates. For high mutation rates, they had a strong tendency to result in a mixed ecology, for medium/high migration rates they tended to result in a plant or non-viable state.

These results indicate that transition probabilities between ecological states would be highly dependent upon factors such as mutation and migrations rates. Mixed ecologies seem to be facilitated by high mutation probabilities – allowing ecologies to better adapt to changing humans (sometimes avoiding their predation) – and/or low migration rates of people and other entities, whereas in situations of low mutation rates a lower innovation rate helped. Non-viable states most often arose from high people migration rates, and from low mutation rates when starting from a plant ecology.

# 8 General Discussion

In any complex system where change is endogenously embedded, it will be hard to identify "the" cause of any particular outcome. As pointed out before (Edmonds 1999) such simulations, and presumably many systems that we observe, are subject to the phenomena of "causal spread" (Wheeler and Clark 1999) whereby the further you trace the formal causes of any outcome back in simulation time via the firing of individual simulation rules, the set of causes can spread to include almost all entities and settings of the simulation. This is particularly hard when systemic change is endogenised, rather than applied from the outside as a parameter change or extra process.

One response to such complexity is to seek to simplify the model so that it can be rigorously understood. Clearly, there is a tension between a wish for rigour (which, almost always, implies simplicity) and relevance (which almost always implies complication). This issue has been discussed elsewhere (Edmonds and Moss 2005). However, in the case of wishing to explore some of the ways in which a system can fail, especially when one wishes to explore complex routes to failure – where it will be infeasible to track the complex web of interactions mentally – one should err on the side of complication. This is becuase it often better to suffer a few false alarms – where one has identified a trajectory that, in fact, was harmless – rather than miss a possible danger. This explains the approach taken in this paper, since I am not concerned with predicting the *probable* but rather to capture and understand the *possible*.

In particular it is no good hoping for clean universal laws from complex evolutionary systems. Both ecological systems and social systems are well known for displaying highly contextdependent patterns of behaviour (Edmonds 2012a). Accepting this does not mean that one has abandoned solid science, but rather has accepted the complexity (Edmonds 2012b). A far more insidious, and I would argue less productive, strategy is to limit oneself to using simple computational models that give an illusion of generality because they can be analogically applied to many situations. Analogies are very valuable for suggesting new insights but they are not falsifiable. Complex, specific and contingent but formal models with definite referents are amenable to inspection, critique and confrontation with evidence. Thus, they hold out the possibility of participating in the development of observation and understanding, slowly bootstrapping understanding over time (Edmonds 2010). I hope that the approaches and models described herein can be part of such a process.

Here it has been necessary to impose some level of interpretation upon the results to help understand the outcomes and be able to draw some conclusions from them (in the form of characterising and then counting kinds of outcome)<sup>15</sup>. It was necessary to go beyond simple relationships of changing parameters and measuring outcomes, since these necessarily were averages over a wide range of actual trajectories (even when limited to a single set of parameter settings). Rather some of the more telling outcomes were gained by being less general and looking at more specific outcomes, for example by starting the simulation at a particular "frozen" state and looking at a particular projection of a larger space of possible outcomes (as in Figure 23, Figure 24 and Figure 25). In this case, the interpretations were drawn from observations of the simulations as a whole and not linked to the kind of systemic change engineered into them.

One direction that this work implies is the increased use of careful data-mining techniques in order to do more systematic explorations of the complex space of outcomes that such models generate. This is an example of the strategy of "staging" the abstraction process from complex systems and maybe allowing a clustering and division of the analysis into different phases as appropriate (Edmonds 2012b).

Clearly, there is a lot of scope for further exploration and development of these kinds of model. Indeed the paper has only had room to describe some of the facilities and features of the actual simulation code<sup>16</sup>. Future possible developments include: exploring much larger simulations in terms of number of individuals, patches and time horizons; adapting the settings and arrangement of the simulation to be more representative of a particular ecology; an exploration of more sophisticated kinds of humans such as those that emerge separate groups using tag-like mechanisms (Holland 1993, Hales 2000); simulating more static farmers and hunters that have a fixed base but range further afield for prey.

# 9 Conclusions

An individual-based meta-population model of an ecology has been exhibited that has allowed for the exploration of some possible complex impacts of humans.

It instantiated in a computer simulation the following phenomena (and thus made them amenable to exploration):

- that humans generally can significantly reduce ecological diversity, with a particular impact upon higher trophic levels;
- that nomadic patterns of resource usage by humans can destroy the ecology they depend upon;
- that higher levels of migration can help destabilise ecologies and help reduce diversity;
- that the presence of humans may nullify the advantages of environmental diversity, becoming themselves the key environmental factor.

<sup>&</sup>lt;sup>15</sup> See (Terán 2004) for a discussion of such levels.

<sup>&</sup>lt;sup>16</sup> However, some of these features are simply to check that we have not just engineered in the results inadvertently by adding noise of various kinds, initializing the model in different ways, allowing comparisons with null cases etc.

It also suggested the following hypotheses concerning how people might impact upon such ecologies, namely:

- that the presence of human agents may have a varied impact upon different niches, perturbing some of these significantly (increasing as well as decreasing diversity in different cases);
- that human agents may modify the effect of different levels of available energy facilitating the development of non-viable ecologies even in high energy situations;
- that the kind of ecological state one is in changes the outcomes one might expect from it under different circumstances (e.g. migration rates);
- that catastrophic non-viable ecological states might be more likely in the presence of human agents when there is a high degree of movement of people and entities and fewer sources of environmental diversity.

Finally, the very different transition probabilities and wirings between states in different settings casts doubt on the efficacy of simple state-based or system dynamics models to capture the possible routes to ecosystem failure.

# Acknowledgements

This research was partially supported by the Engineering and Physical Sciences Research Council [grant number EP/H02171X/1]. Many thanks to Emma Norling (who first worked on these kinds of models at the CfPM), all those I have discussed this and previous versions of this model with, including those at the Manchester Complexity Seminar (especially Alan McKane), those at the iEMSs conference in 2012, those at the Lorentz Workshop on "Cross-Scale Resilience in Socio-Ecological Simulations" in 2017, as well as: Nanda Wijermans, Gert Jan Hofstede, Eline de Jong, Nick Gotts, Ruth Meyer, George van Voorn and Gary Polhill.

# Appendix I – More Details of the Simulation

## **Platform and Code**

The model code and ODD documentation (without human agents) can be found in (Edmonds 2014).

## **Simulation Lineage**

The simulation here can be seen as an descendent of (Norling et al. 2008). It uses a variety of the interaction matrix described in (Caldarelli et al 1998). It relates to the ecological model described in (Edmonds 2013) but this version has only one type of basic resource.

### **Dominance Calculation**

If the potential predator bit-string is represented by column vector  $\boldsymbol{p} = [p_1, p_2, ..., p_n]$ , the potential prey (or patch) bit-string is represented by vector  $\boldsymbol{y} = [y_1, y_2, ..., y_n]$  and the interaction matrix by  $\boldsymbol{M}$  with entries  $m_{i,j}$  then  $s = \sum_{i:p_i=1,j:y_j=1} m_{i,j}$  is calculated, or  $s = \sum_{i:p_i=1,j:y_j=1} m_{i,j}$ 

y.(M.p). In the case of a potential predator-prey interaction predation (between individuals that are randomly paired within a patch) occurs if s > 0 and in the case of individual patch interaction, the individual will receive a share in the energy of the patch in proportion to s if s > 0 (along side all other such individuals).

## Parameters

### In the Basic Ecological Model

The parameters of the basic ecological model are as follows, with their default values in square brackets. Note that not all of these are explored in the paper, but simply left at their default values, which are given by the value in square brackets.

- gene-size: [100 bits] the number of bits in an individual's gene
- **num-env-chars**: [3 bits] the number of, effective, bits in the characteristics of a patch, functions similar to an individual's gene
- **migration-prob**: [0.01] the probability that any individual will move to another patch each tick
- mut-prob: [0.01] the probability that a newly born individual will have its gene mutated
- **food-rate**: [500 energy units] how much energy is put into the world each tick, evenly divided among patches
- **efficiency**: [0.9] what proportion of energy of something eaten goes to predator, or to herbivore from patch
- **reproduce-level**: [3 energy units] if an individual's energy gets to this point it gives birth once, new-born's energy being then subtracted from it
- **eating-tries**: [2] each tick each individual tries to eat this number of others on the same patch, but this only happens if they dominate them via the interaction matrix
- max-age: [80 ticks] if > 0 individuals die when they reach this age in simulation ticks, otherwise no age ceiling
- **max-store**: [20 energy units] if > 0 this is the upper bound on what energy individuals can accumulate, rest is lost to system
- max-time: [1000 ticks] if > 0 the time at which the simulation is halted

The following are included for completeness but are not varied in the simulation runs reported.

- **life-tax**: [0.25 energy units] how much energy subtracted from each individual each tick, dies if energy is 0 or below,
- **init-energy**: [1 energy unit] the energy of a newborn, this is subtracted from the parent at birth,
- **init-new-species-prob**: [0.01] probability of a new individual with a random genome being introduced each tick
- **stop-new-species-once-established?**: [true] if set stops new individuals with new genomes being introduced into the simulation once a viable population is established
- initial-species-variety: [0] 0/1: if 0 simulation starts with a single individual, if this is not successful relies on a new individual being introduced via init-new-species-prob, if 1 starts with a full population with random genes
- rand-death-prob: [0.02] the probability an individual randomly dies each tick
- **anti-sym-mat?**: [false] forces the interaction matrix generated at start to be anti-symmetric
- **migrate-near?:** [true] if true then individuals migrate, if they do, to a neighbouring patch if false to a random other patch
- **allow-cannibals?**: [false] if true individuals of the same species can eat each other, if not can only eat those of another species
- **neutral?**: [false] if true then all individuals on a patch get the same amount of energy from the patch regardless of their bit-string, otherwise they have to dominate the patch via the interaction matrix to extract energy,

### In the Extended Mode with Human Agents

- **init-variety**: [1] whether humans enter as a diverse of set of individuals (1) or a homogeneous set (0)
- **tol-on?**: [false] whether the tag-based tolerance system is turned on (allowing the emergence of subgroups) or off (in which case learning and sharing can happen with any humans in the same patch, that is tags are ignored)
- **max-age-people**: [100 ticks] if > 0 human individuals die when they reach this age in simulation ticks, otherwise no age ceiling,

- max-people-store: [30 energy units] if > 0 this is the upper bound on what energy humans individuals can accumulate, rest is lost to system,
- **reproduce-level-people**: [30 energy units] if a human individual's energy gets to this point it gives birth once, new-born's energy being then subtracted from it,
- **innovation-prob**: [0.009] the probability a bit in a human individual's bit-string is flipped each simulation tick for each human
- **learn-prob**: [0.1] the probability an individual looks to another (eligible) individual in the same area and (if it has higher energy than itself) copies one bit from it
- **share-tries**: [2] the number of times a human individual attempts to share any excess energy it has
- **share-efficiency**: [0.8] the proportion of energy that is transmitted during sharing (the rest is lost)
- min-share-level: [25] only energy above this value is shared if sharing occurs
- **tag-mut-sd**: [0.005] the standard deviation of the normally-distributed noise added to the tag during tag mutation
- **tol-mut-sd**: [0.005] the standard deviation of the normally-distributed noise added to the tolerance during tag mutation
- **time-between-invasions**: [100 ticks] the time after the last humans have died out that another injection of humans occurs
- **people-enter**: [1001 ticks] the tick that humans are first input into the simulation
- **num-people-enter**: [50 individuals] the number of human individuals input into the simulation at a time
- people-f-env?: [false] whether people are allowed to extract energy directly from a patch
- **coop-radius**: [1 patch] the number of neighbouring patches that sharing and learning can occur over can be just the patch (1), the patch and 4 neighbours (5), or the patch and all 8 neighbours (9).
- migration-prob-people: [0.01] the probability that a human individual will migrate

# Appendix II – Additional Results

## Sensitivity of model without human agents

Here are some additional sensitivity analysis runs.





Figure 26. Effect of Gene Size on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

Longer bit-strings enable a greater diversity to develop, however the space of possibilities is so great for sizes above 40 that this is nowhere near explored and hence does not limit the growth of complexity at these scales of space and time, (see Figure 26).



Figure 27. Effect of Environmental Diversity on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

Greater environmental diversity seems to decrease the occurrence of rich plant ecologies, (see Figure 27, right) facilitating a mixed ecology.



Figure 28. Effect of Efficiency on (left) diversity and (right) ecological type red=plant, blue=mixed, purple=single species, green=non-viable

Higher efficiencies mean that ecologies with higher trophic levels occur more often, since the higher levels can access more energy, Figure 28.

#### More Results from the Larger Random Sample of Runs with Humans

Here are some additional results from the larger random sample of runs with humans. These show the end states from 4,478 independent runs of the simulation as explained above.



Figure 29. Diversity of people (horizontal axis) and other entities (vertical axis) at the end of 4,478 independent runs, red=plant, blue=mixed, purple=single species, green=non-viable

Figure 29 shows the final diversity of human agents vs. final diversity of other entities at the end of 4,478 independent runs. Unlike the number of species/variants shown in Figure 22 there is no trade-off between human and entity diversity. Rather human diversity is quite evenly spread with peaks at maximum and minimum diversity, whilst entity diversity becomes increasingly rare at higher diversity rates.



Figure 30. Number of species/variants of people by different migration probabilities (horizontal axes), and numbers of species of other entities (vertical axes) by the end of independent 4,478 runs., red=plant, blue=mixed, purple=single species, green=non-viable

Figure 30 is a scatter graph of the sheer numbers of people and entities by different migration rates. At low, but non-zero, migration rates we see cases with relatively high numbers of species/varieties for both entities and people but for high migration rates there are fewer of these cases, with a tendency to result in very few variants of human agents or a very few species of entity. That is, at higher migration rates, the trade-off between species/variants of human agents and other entities is sharper.

## References

Bousquet, F., & Le Page, C. 2004. Multi-agent simulations and ecosystem management: a review. Ecological Modelling, 176(3-4), 313-332.

Bousquet, F., Cambier, C. et P. Morand. 1994. Distributed artificial intelligence and objectoriented modelling of a fishery. Mathematical Computer Modelling, 2018, 97-107.

Caldarelli, G., Higgs, P.G. and McKane, A., 1998. Modelling Coevolution in Multispecies Communities. Journal of Theoretical Biology, 193, 345-358.

Crutzen P. J. 2002. Geology of mankind. Nature, 415, 23. DOI:10.1038/415023a

de Aguiar, M.A.M., Baranger, M., Baptestini, E.M., Kaufman, L. and Bar-Yam, Y., 2009. Global patterns of speciation and diversity, Nature, 460, 384-387

Deffuant, Guillaume et al., 2012. Data and models for exploring sustainability of human wellbeing in global environmental change. European Physical Journal Special Topics, 214, 1, 519-545. DOI 10.1140/epjst/e2012-01704-2.

Diamond, J., 2004. Collapse: How Societies Choose to Fail or Succeed, Viking.

Drossel, B., Higgs, P.G., and Mckane, A.J., 2001. The Influence of Predator-Prey Population Dynamics on the Long-term Evolution of Food Web Structure. Journal of Theoretical Biology. 208, 91-107.

Edmonds, B. 1999. Capturing Social Embeddedness: a Constructivist Approach. Adaptive Behavior, 7, 323-348.

Edmonds, B. 2013. Multi-Patch Cooperative Specialists With Tags Can Resist Strong Cheaters. In Rekdalsbakken, W., Bye, R.T. and Zhang, H. (eds), Proceedings of the 27th European Conference on Modelling and Simulation (ECMS 2013), May 2013, Alesund, Norway. European Council for Modelling and Simulation, 900-906.

Edmonds, B. 2014. A test-bed ecological model (Version 1). *CoMSES Computational Model Library*. Retrieved from: https://www.openabm.org/model/4204

Edmonds, B. and Moss, S., 2005. From KISS to KIDS – an 'anti-simplistic' modelling approach. In P. Davidsson et al., (Eds.), Multi Agent Based Simulation 2004. Springer, Lecture Notes in Artificial Intelligence, 3415, 130–144.

Edmonds, B., 2010. Bootstrapping Knowledge About Social Phenomena Using Simulation Models. Journal of Artificial Societies and Social Simulation 13, 1, 8. http://jasss.soc.surrey.ac.uk/13/1/8.html,

Edmonds, B., 2012. Searching for "Phases" in Complex Simulation Output using Evolutionary Knowledge Discovery Techniques, (Poster) ECCS 2012, Brussels, Sept. 2012.

Edmonds, B., 2012a. Context in Social Simulation: why it can't be wished away. Computational and Mathematical Organization Theory, 18, 1, 5-21.

Edmonds, B., 2013. Complexity and Context-dependency. Foundations of Science. 18, 4, 745-755. DOI: 10.1007/s10699-012-9303-x

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling, 115, 129-148.

Hales, D. 2000. Cooperation without memory or space: Tags, groups and the prisoner's dilemma. In S. Moss & P. Davidsson, (Eds.), Multi-Agent-Based Simulation, 1979, 157-166.

Holland, J., 1993. The Effect of Labels, Tags, on Social Interactions. Working Paper 93-10-064. Santa Fe Institute. Sante Fe, New Mexico.

Hubbell SP. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton, NJ: Princeton University Press.

Kooijman, S.A.L.M. 2010. Dynamic Energy Budget theory for metabolic organisation. Cambridge University Press, Great Britain.

McKane, A. J. 2004. Evolving complex food webs. The European Physical Journal B, 38, 287–295.

Norling, E., Powell, C and Edmonds, B., 2008. Cross-Disciplinary Views on Modelling Complex Systems. In. David, N. & Sichman, J.S., Eds., Multi-Agent-Based Simulation IX, Springer, Lecture Notes in Artificial Intelligence, 5269, 183-194.

Reader, J., 1990. Man on Earth. Penguin Books.

Riolo, R.L., Cohen, M.D. & Axelrod, R., 2001. Evolution of Cooperation without Reciprocity. *Nature* 414, 441-443.

Terán, O., 2004. Understanding MABS and Social Simulation: Switching Between Languages in a Hierarchy of Levels. Journal of Artificial Societies and Social Simulation 7, 4, 5. http://jasss.soc.surrey.ac.uk/7/4/5.html

Turner, B.L. & Sabloff, J. A. 2012, Classic Period collapse of the Central Maya Lowlands: Insights about human–environment relationships for sustainability. PNAS 109(35), 13908-13914.

Wheeler, M. and Clark, A., 1999. Genic representation: reconciling content and causal complexity. British Journal for the Philosophy of Science, 50 (1), 103-135.