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ABSTRACT

Here goes the abstract

DEDICATION AND ACKNOWLEDGEMENTS

Here goes the dedication.

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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INTRODUCTION

1.1 Introduction

This project focuses on the impact of habitat destruction on communities of species. A habitat may be defined as the environment containing an organism, or collection of organisms. It has both biotic and abiotic components. Therefore habitats are constantly changing due to ongoing environmental processes. These changes may make the habitat more or less hospitable to different organisms, generating emergent effects at the species and community levels. Human activity in particular creates pronounced and significant changes in habitat. There is good evidence [?]] that anthropogenic climate change has affected living systems by changing regional habitat suitability. An example of this is the northward shift in butterfly species ranges attributed to rising temperatures [?]. Other activities such as agriculture, deforestation and urbanisation interfere directly with physical habitat components and with local flora. This alters the type of species and the community that can be supported [? ?]. Globally the scale of these man-made effects is huge. Various studies have suggested that habitat modification is the leading cause of global species extinctions [? ?]. Therefore an understanding of how ecological communities respond to changes in habitat is essential in order to mediate the destructive effects of human activity, and to create beneficial conservation, land management and restoration strategies. The subject has received much attention in the ecological literature, and this project is a continuation of that dialogue.

The destruction of habitats due to human activity has also received much attention in the media. This has done a lot to raise public awareness, and to fuel a growing number of campaign groups, charities and conservation organisations. In most cases the focus is on *single species effects*, especially on those threatened with extinction. The most notorious example of this may be the polar bear as the media face of global warming (see figure 1.1). Similarly the habitat loss



Figure 1.1: Stranded polar bears on Cross Island outside Prudhoe Bay, Alaska. The plight of the polar bear has received much attention in the media. The habitat loss it suffers from is very visible. However the focus of conservation strategies must be on the ecological communities, of which it is one member species. (Source: www.greenpeace.org.uk)

literature has largely focused on the loss of species [? ?], and has reinforced the notion of *species richness*¹ as a measure of biodiversity and ecosystem health. This is perhaps because species level effects are the most visible results of ecosystem damage, and the easiest to study empirically. However they are symptomatic of underlying system processes. At least since Darwin's marvel at the complexity of the "Tangled Bank" [?] ecologists have understood that species exist in highly interdependent communities. Therefore the ecological impacts of habitat destruction, and other human activities, must be approached from a systems perspective.

In community ecology the system of study is the ecological community - a local collection of co-existing species. The focus is on the structure, patterns and processes within the community. A key aspect of this is the pattern of *interactions between species*, which underlies many of the processes that shape the community (for more detail refer Chapter 2). Recently the habitat loss literature has begun to move away from species level effects, towards community wide effects and especially inter-specific interactions [?]. This has been facilitated by the wider availability of ecological network data, improved methods for data collection, and the ability to simulate large

¹Simply defined as the number of different species present in a community.

ecological networks and communities. Advances in ecological network theory have also provided many new metrics for community stability, biodiversity and for analysis of network structure (section 2.3). Our approach to the study of habitat loss is situated in this context.

There is now a growing consensus that ecological interactions are the key to understanding the effects of habitat loss on ecological communities [? ? ?]. In addition to the loss species, it has long been known that habitat loss also leads to the important loss of inter-specific interactions. As Janzen remarked [?] in 1974: “what escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions”. It has since been demonstrated that ecosystems experiencing habitat alteration often suffer loss of interactions *before* loss of species [? ? ?]. This can result in detectable changes in community structure, without any detectable change in species richness [?]. These structural changes have consequences for community stability, robustness and population dynamics. A significant part of the ongoing challenge is to identify meaningful measures for the structural (network) changes, and to generalise the ways in which they impact on the community. The bulk of the recent literature supports the belief of Valiente et al. [?] in “the importance of focusing on species interactions as the major biodiversity component on which the ‘health’ of ecosystems depends.”

1.1.1 Communities of single and multiple interaction types

In the habitat loss literature most studies have looked at communities with a single type of interaction. The same has been true for network ecology in general, with the bulk of the literature focused on either antagonistic or mutualistic networks. In these networks a node represents a species, and a directed link represents a certain type of interaction (for example predation). Such networks represent the interaction structure of an idealised and closed community. For example it is common to study mutualistic communities, such as plants and their pollinators, in isolation. This is represented as a bipartite network of plant and pollinator species, with mutualistic interactions between them. Both empirical and *in silico* studies have derived some apparently general results on the response of such single-interaction communities to habitat loss. We discuss some of these findings here. However in nature a single-interaction community is a subset of a larger group of species with multiple types of interaction (predation, mutualism, competition, parasitism). There has been a recent move towards studies of communities with multiple types of interaction [?], which are less simplistic models of natural systems. These hybrid communities are represented as networks with more than one type of link. We also discuss this body of work, some of which challenges previous finding based on single-interaction communities.

Perhaps most the general result, already discussed, is that habitat destruction leads to a loss of inter-specific interactions. This may be accompanied by lower interaction frequencies, changes in interaction strength, reduced connectivity, or other structural changes in the network due to rewiring. Tylianakis et al. [?] showed that empirical antagonistic communities (host-parasitoid) responded to habitat degradation with reduced evenness in interaction frequencies. This means

that certain interactions became relatively more frequent, so that energy flow through the community became concentrated along certain pathways. Also, importantly, the quantitative changes in network structure that they observed were not detectable by equivalent qualitative metrics. Neither were conventional diversity metrics, based on species abundance or richness, able to distinguish between habitats at different levels of degradation. Similarly Albrecht et al. [?] showed that insect food webs in a grassland system lost interaction diversity faster than species diversity, when subjected to habitat alteration. This suggests a biodiversity reduction in the interaction structure that is not measurable by metrics based on species abundance. Both of these examples highlight the sensitivity of results to the metrics used, when studying community response to habitat loss. Hence the large suite of metrics introduced and discussed in section 2.3.

An issue of particular interest is community stability, its response to habitat loss and its relationship to network structure. Mutualistic networks tend to have a highly nested structure and low modularity [?]. These properties are believed to improve the stability of the community [?]. It has been shown that habitat destruction can push mutualistic networks towards higher modularity, higher connectivity, and lower nestedness, thereby reducing stability [?]. Conversely antagonistic networks tend to be modular in structure, which is believed to promote stability and robustness in these communities [?]. Habitat loss has been shown to destabilise antagonistic communities by lowering modularity and increasing interaction strengths [?]. Generally the literature suggests, as expected, that habitat loss reduces community stability, irrespective of the interaction type. However the underlying changes driving this loss in stability appears to differ between mutualistic and antagonistic communities. It should also be noted here that the definition and measurement of stability is non-trivial. Lurgi et al. [5] have shown that certain stability metrics may respond differently to a changing control variable, meaning that a combined, or multi-stability approach is required.

The above examples represent attempts to understand the structural changes that occur due to habitat loss, prior to the occurrence of species extinctions. From a conservation perspective this highlights the importance of targeting inter-specific interactions and the maintenance of network structure and function, rather than focusing on species level effects [?]. Fortuna and Bascompte [?] have demonstrated that real-world networks have better persistence against habitat loss than random networks assembled using null-models. This suggests that artificially managed ecosystems may be more vulnerable to perturbations than their ‘wild-type’ equivalents, unless careful attention is paid to those properties that promote stability and robustness. In food webs there appear to be certain simple properties that mediate the impacts of habitat destruction [?]. For example omnivory is shown to increase extinction thresholds, as is a reduction in top-down control by predators. However these numerical results are for small model networks and remain to be demonstrated empirically.

Recently ecologists have realised the importance of studying ecological networks that contain multiple types of inter-specific interaction [???]. It is known that mutualistic communities have

knock on effects on food webs, and vice versa. Indeed certain species are simultaneously involved in more than one type of network or community. A powerful example of this phenomenon was demonstrated empirically by Knight et al. [?]. They showed the presence of a trophic cascade, crossing ecosystem and habitat boundaries, by which freshwater fish were able to facilitate terrestrial plant reproduction. The inclusion of such indirect and cascading effects is one of the many strengths of the network paradigm in ecology. However this study highlights the limitations of focusing on localised community subsets and single-interaction types.

A large scale study by Pocock et al. [?] was one of the first to combine networks of different types into a network of ecological networks. They used empirical networks constructed over different habitats on a farm, to construct a whole farm network. This included host-parasitoid, seed-dispersal, plant-pollinator and predator-prey networks. Using quantitative robustness analysis (section 2.3), they were able to identify keystone plant species which generated significant cascading effects across networks, and also determined the most fragile components of the meta-network. This type of integrated analysis has different implications for conservation and restoration than an approach which looks at the individual networks in isolation.

The integration of multiple interaction types has begun to shed new light on the stability of ecological communities. This is because the conventional understanding is based on studies of communities with single-interaction types. In general complex antagonistic networks with strong interactions are thought to be unstable [?]. This presents a problem for ecological theory since natural food webs, which are inherently complex, appear to be stable. The problem may lie in the fact that antagonistic networks have been studied in isolation. It has been shown theoretically that introducing mutualistic interactions into the network can be stabilising [5?]. Specifically Lurgi et al. [5] propose that increasing the proportion of mutualistic interactions at the base of a food web reduces the overall strength of species interactions. They found that this improved the stability of their model communities, according to a spatial aggregation metric (section 2.3).

Recently Sauve et al. [?] have brought into question the established wisdom on the relationship between network structure and stability. As discussed previously, the structural properties believed to promote stability differ between antagonistic and mutualistic communities. High modularity and high nestedness are thought to promote stability in antagonistic and mutualistic networks respectively. However Sauve's work suggests that, for a combined network of mutualisms and antagonisms, modularity and nestedness do not strongly affect stability. The results of Lurgi et al. also support this finding [5]. Therefore new metrics, accounting for diversity in interaction type, may be required in order to understand community structure and stability in hybrid networks².

Since hybrid networks of multiple interaction type are relatively new, there are few studies relating them to habitat loss. One study, by Evans et al. [?], uses the same empirical network of networks as [?]. They employed a robustness algorithm to determine how vulnerable the

²See suggestions in the text of [?] and talk to Alix about possibly including these in our analysis?

hybrid network is to the loss of different habitats from the farm³. Aside from this study there is a lack of empirical and theoretical results on the response of hybrid networks to habitat loss. This project aims to make a contribution towards this area. We will extend on the work of Lurgi et al. [5] to simulate multi-trophic communities with mutualistic and antagonistic interactions. By investigating the response of these communities to simulated habitat destruction we will be generating novel results and predictions which can be tested empirically in the future. To do this we will employ a range of metrics to quantify structural changes and community stability. We will focus on the regime before species are lost from the community, with an interest in the underlying changes that occur as a result of habitat destruction.

1.1.2 Spatially explicit model and metrics

Another novel aspect of this work is the spatially explicit modelling approach... And some of the spatial analysis employed...

[?] - spatially explicit analysis.

[?] mutualistic interactions decrease non-linearly. Connectance increases? Abrupt change in number of interactions, spatial skewness in number of interactions.

[?] - quantitative food web metrics did not vary between fragmented habitat patches in different landscape contexts.

[?] - interaction strengths is focus, but also spatial stability. c.f. a,b,g stability and Lurgi et al.

1.1.3 Modelling Habitat Loss

Habitat loss has been modelled in various ways..Spatial auto-correlation..how does our approach fit in with the literature..

[?] - controlled habitat destruction, large empirical project

³Interestingly they reported that two of the most important habitats, relative to their sizes, were hedgerow and wasteland.

HABITAT LOSS: MODELLING APPROACH

2.1 Agent based simulation

We study the effects of habitat loss on ecological communities using a spatially explicit agent-based model. This simulation model was first published by Lurgi et al in [5] (section 2.1.2). The landscape consists of a homogeneous 2-dimensional grid (200×200 cells) on which individuals of 60 species move around and interact subject to bio-energetic constraints. Local rules define dispersal, demographic processes and interaction behaviour of the individuals. The potential for interaction between two individuals is governed by an underlying species interaction network, which is generated using the niche model [?] (section 2.1.1.1. (GIVE A BIT MORE ABOUT NICHE HERE))

Unlike most previous *in silico* studies, the model includes both trophic and mutualistic interactions. Species belong to four trophic levels. The niche model generates a trophic interaction network. Then a fraction of the links between species in the first two trophic levels are changed to define mutualisms ($-+ \rightarrow ++$). The fraction of links switched is called the mutualistic vs. antagonistic interaction (MAI) ratio.

To simulate habitat loss, a fraction of the grid cells are made inhospitable to all species. We compare two algorithms for choosing which cells to destroy: 1) random destruction and 2) contiguous destruction. For random destruction grid cells are destroyed uniformly at random, up to the desired fraction of the total landscape. For contiguous destruction a seed cell is chosen uniformly at random, then destruction spreads radially in all directions from this point.

We simulated communities with MAI values of 0, 0.1, 0.2, ..., 1.0, with habitat loss (HL) percentages of 0, 10, 20, ..., 90. For each combination of MAI and HL values, 25 replicates were simulated with different interaction networks (same species richness, same connectance).

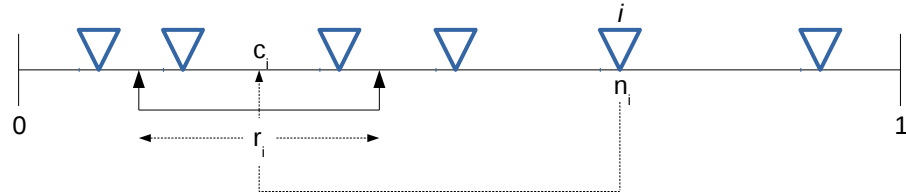


Figure 2.1: A representation of 1-dimensional *niche space* as visualised in the original publication [?], for number of species $S = 6$. The blue triangles represent the placement of species in niche space. The niche value of species i is given by n_i . The width and centre of the feeding range for species i are denoted by r_i and c_i respectively. Species i consumes all species whose niche values fall within the feeding range.

2.1.1 The interaction network

An underlying interaction network defines which direct interactions between species are allowed. This network contains two types of link: *antagonistic* (predator-prey) and *mutualistic* (plant-pollinator). To construct this network a food web, containing only antagonistic links, is generated using the niche model (section 2.1.1.1). This network consists of 60 species belonging to 4 trophic levels, with links that define the feeding relationships between them. Species in the basal trophic level represent plants and those in the trophic level above represent herbivores. To introduce mutualism a fraction of the herbivorous links are replaced by mutualistic links (section 2.1.1.2).

2.1.1.1 The niche model

We use the niche model (NM) of Williams & Martinez [?] is used to generate food webs. This simple model has been shown to produce network structures that closely resemble empirically derived food webs¹, and has become a standard tool for creation of model food webs [? ? ?]. The model has two parameters: the number of species S , and the desired connectance C . The model output is an adjacency matrix \mathbf{a} for which the element $a_{ij} = 1$ implies that species i consumes species j , and $a_{ij} = 0$ implies the absence of an interaction. Connectance is defined as the proportion of the maximum possible number of links that are realised i.e. $C = L/S^2$, where L is the number of links in the network.

Figure 2.1 illustrates the ideas of niche space, niche value n_i for a particular species i , its feeding range r_i . Niche space is the 1-dimensional range of real numbers $[0, 1]$. Each of the S

¹FIND MORE REFS HERE.

species is assigned a niche value n_i , drawn uniformly at random from the niche space. It is then assigned a feeding range with a central value c_i and a width r_i . Species i consumes all species, including itself, whose niche values fall within its feeding range.

To determine the width of the feeding range, a beta function with expectation $2C$ is used to draw a number from the range $[0, 1]$. This number is then multiplied by n_i to give the chosen value of r_i . Since $n_i \sim U(0, 1)$, we know that the expectation value $E(n_i) = 0.5$, and so $E(r_i) = C$. Therefore on average a species consumes a fraction C of the total number of species, resulting in a network with close to the desired connectance.

A beta function has two parameters: $\alpha, \beta \in \mathbb{R}^+$ [REF]. The choice of $\alpha = 1$ simplifies the probability density function to

$$f(x; 1, \beta) = \begin{cases} \beta(1-x)^{\beta-1} & \text{if } 0 < x < 1, \\ 0 & \text{otherwise.} \end{cases}$$

The cumulative distribution function is derived by:

$$\begin{aligned} P(x) &= \int_0^x \beta(1-x')^{\beta-1} dx' \\ &= 1 - (1-x)^\beta. \end{aligned}$$

Therefore, by choosing a probability value y uniformly at random from the interval $[0, 1]$, we can draw an x value from our beta distribution:

$$\begin{aligned} y &= 1 - (1-x)^\beta, \quad \text{such that} \\ x &= 1 - (1-y)^{1/\beta}. \end{aligned}$$

The expectation value of this beta distribution is given by $E(x) = \frac{1}{1+\beta}$, therefore we choose

$$\beta = \frac{1}{2C} - 1$$

to give the desired expectation of $E(x) = 2C$.

Once the width r_i has been chosen, the feeding range is placed in niche space by randomly drawing the range centre c_i from the interval $[r_i/2, n_i]$. Therefore cannibalism and looping are possible because up to half of the feeding range may contain niche values $\geq n_i$. In some cases the generated network may not be connected (i.e. contains one or more disconnected components), or two species may be trophically identical. In these cases the guilty species are deleted and replaced until the network is connected and without identical species. Also the species with the smallest niche value is given $r_i = 0$, such that there is at least one basal species (i.e. species with no prey).

INSERT NICE PICTURE OF A NETWORK!

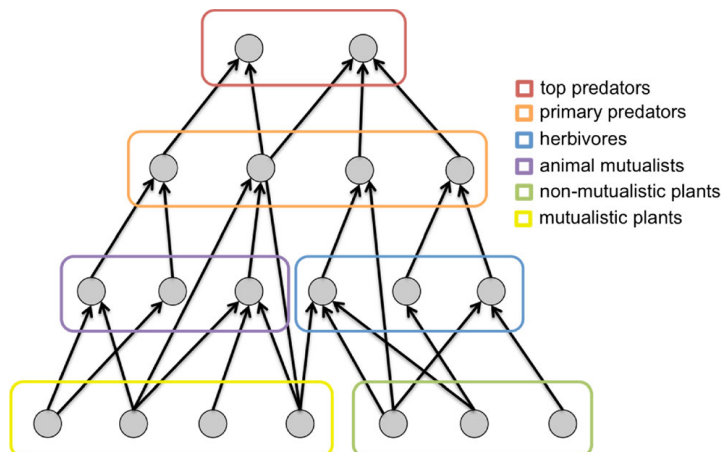


Figure 2.2: Schematic of an underlying interaction network (reproduced from [5]). Nodes correspond to species, and arrows to trophic links (antagonistic or mutualistic), from resource to consumer. The six functional groups of species are colour coded, and named in the legend. In this case there are twelve links between the first two trophic levels, six of these have been replaced by mutualistic links giving a MAI ratio of 0.5. Mutualistic plants and animal mutualists are defined by any species that has at least one mutualistic links. However both these groups of species may also have antagonistic links.

2.1.1.2 Link Replacement

Having generated a food web with only antagonistic links, we now introduce mutualism. The mutualistic interactions are trophic, as with antagonisms, since there is an energy flow from resource to consumer. For example pollinators receive nectar from flowering plants. However in a mutualistic interaction there is a benefit for both parties. In this example flowering plants are pollinated and can reproduce. In the simulation model the plants receive better dispersion abilities as a result of mutualisms (section 2.1.2.1). We impose the constraint that mutualisms can only exist between species of the first two trophic levels: plants and herbivores. Some of the antagonistic links between the first two trophic levels are replaced by mutualistic links. This changes the rules of interaction between individuals of these species in the cellular automata model (section 2.1.2.1). The fraction of these links switched is defined as the mutualistic vs. antagonistic interaction (MAI) ratio. Figure 2.2 is a schematic of a possible interaction network generated by this procedure, for a nineteen species community. In this case there are twelve links between the first two trophic levels, and six of these have been replaced by mutualistic links. The other six links remain antagonistic. Since half of the basal links have been replaced, the MAI ratio for this community is 0.5.

The result of link replacement is a hybrid network that defines two types of interaction between species. We can define two functional groups in each of the first two trophic levels. In the first trophic level *non-mutualistic plants* are basal species which do not have any mutualistic links. This group represents wind-dispersed plants which only have antagonistic interactions with

the trophic level above. *Mutualistic plants* are any basal species with at least one mutualistic link. This group are dispersed by species from the second trophic level via their mutualistic interactions and can no longer be wind dispersed. They may also be predated upon by herbivores, if they have such links. Similarly *herbivores* are members of the second trophic level which only predate on basal species, whereas *animal mutualists* may either predate or engage in mutualisms. See figure 2.2 for a visualisation of these groups.

For the simulations we generated networks with eleven different MAI ratios ($[0, 0.1, 0.2, \dots, 1.0]$). This is in accordance with the previous study [5], and allows us to look at how communities with different MAI ratios respond to habitat loss.

2.1.2 Model specification

We use the model of Lurgi, Montoya & Montoya [5] as the basis of our simulation model. It is a cellular automaton (CA) in which individuals belonging to different species move around, reproduce, die and interact. These actions are subject to bioenergetic constraint and the rules governing them are detailed in section 2.1.2.1 below. The CA landscape is a homogeneous 2D square lattice with toroidal boundaries. Each cell can contain up to two individuals: at most one animal and one plant individual. It may not contain more than one individual of either type. Types of individual are defined by its trophic position in the underlying interaction network (section 2.1.1). All basal species are plants, all other species are animals.

Distance on the lattice is defined as follows. The immediate neighbours of any given cells are the eight adjacent cells including diagonals (i.e. a Moore neighbourhood). These eight neighbours have a distance-1 from the central cell. This distance metric is used in the rules for movement and reproduction (SEE BELOW NUM?), and also in the calculation of various spatial metrics (section SECTIONNUM).

Initial conditions are defined randomly by the following setup procedure. A species is selected uniformly at random from the sixty species in the underlying network. A cell from the landscape is selected uniformly at random. If there is space in the cell, an individual belonging to the selected species is placed in the selected cell. This is repeated until the value of parameter *occupied cells* is reached.

Table 2.1 shows all the model parameters, their values and definitions. Where possible the parameters values are chosen to be biologically realistic. A discussion of values chosen for these parameters can be found in section 2.1.2.2.

2.1.2.1 Cellular-automata rules

In the following description italicised words refer to model parameters, which are defined in table 2.1. Each individual stores energy (or resource), which it expends to perform actions. If the energy of an individual drops below *min_resource* it dies and is removed from the landscape.

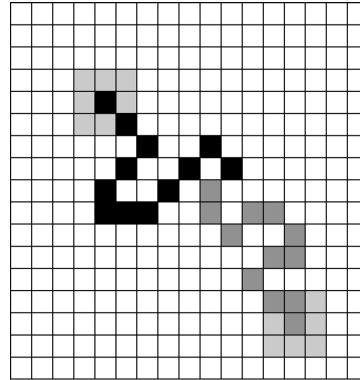


Figure 2.3: Example trajectories and neighbourhoods of two individuals.

On each iteration the basic demographic processes occur in the following order (FOR EACH SPECIES?):

1. Death
2. Movement
3. Reproduction
4. Feeding
5. Immigration

1) Death

As stated, if an individual's energy drops below *min_resource*, it is removed from the simulation.

2) Movement

For each individual, a neighbouring cell (distance 1) is selected uniformly at random. If the cell is available the individual moves there. Otherwise it remains stationary.

3) Reproduction

All species may only reproduce if their stored energy is greater than *mating_resource*. Animals reproduce sexually, plants reproduce asexually.

- **Sexual reproduction:** This occurs between two members of the same animal species if:
 - 1) There is a member of the same species in the immediate neighbourhood of the subject species; and
 - 2) there is an available cell for the offspring in the distance 4 neighbourhood of the subject individual.
 When these two conditions are met both parents give a fraction of

their stored energy (*mating_energy*) to the offspring. The offspring is placed in a cell chosen uniformly at random from the available cells within distance 4 of the subject individual.

- **Asexual reproduction:** This occurs for plants via two possible mechanisms.
 1. Wind dispersal occurs for non-mutalistic plants, on each iteration with a probability equal to *reproduction_rate*. If reproduction occurs the offspring is placed in a randomly selected available cell in the distance 4 neighbourhood. For plants, available means empty or only occupied by an animal individual. If no cells are available the plant cannot reproduce. Again a fraction of the parent plant's stored energy (*mating_energy*) is given to the offspring to the offspring.
 2. Mutualistic dispersal occurs for mutualistic plants. This action is carried out by the animal partner, and is done in the 'feeding' phase (see below), since it is also a trophic interaction. The 'seed' of the parent plant is carried by the animal partner, so it may be placed beyond the distance 4 neighbourhood.

3) Feeding

For a trophic (feeding) interaction to occur, two individuals must belong to species that are connected in the interaction network. Also the individuals must explicitly find each other in space - in the 'movement' phase one must choose the cell occupied by the other. If this happens there are three possibilities:

1. **Predation:** If neither individual belongs to a basal species a predation event occurs with probability *capture_probability*. The prey species dies and a fraction of its energy *efficiency_transfer* is given to the predator.
2. **Herbivory:** If one individual is a non-mutualistic animal and the other is a plant, they interact. A fraction of the plant's energy *herb_fraction* is lost, and a fraction (*herb_efficiency*) of this energy is given to the herbivore. Both individuals continue living. If the animal is an omnivore and additional trade-off (*omni_tradeoff*) is applied to its energy gained, since omnivores are less efficient at digesting plant matter than straight herbivores.
3. **Mutualism:** If the individuals share a mutualistic interaction they interact. A fraction of the plant's energy (*mut_fraction*) is transferred to the animal. The animal also keeps track of which plant it interacted with. If it reaches an available cell in the landscape it creates an offspring of this plant with probability *mut_efficiency*. On each iteration that an offspring is not produced, the mutualistic efficiency is reduced by a fraction *mut_cooling*.

4) Immigration

At each iteration there is a probability (*immigration*) with which each empty cell may be colonised by an individual selected at random from the original species pool.

5) Energy update

On each iteration all animal individuals' energy stores are reduced by a fraction *living_expend*, to account for metabolic losses. Also all plant individuals autotrophically increase their energy stores by a fraction *synthesis_ability*. This is the only energy input to the system.

2.1.2.2 Model Parameters

The model parameters were chosen blablabla... reference Ings et al. Which parameters are most interesting, why? Also discuss sensitivity analysis from previous publications, findings. We I conduct my own version? With regard to which parameters? (Maybe discuss this bit somewhere else).

2.1.3 Modelling habitat loss

The current project extends the above defined model of Lurgi, Montoya and Montoya [5] by implementing habitat loss algorithms. The algorithms are simple. A fraction of the cells in the landscape are made uninhabitable to all species. We denote the fraction of destroyed cells by HL. The simulations are set up and run as detailed above (section 2.1.2), after 1000 iterations one of two habitat loss algorithms is applied to the landscape. The species inhabiting the destroyed cells are deleted. Species attempting to move into destroyed cell are unable to and remain stationary. Destroyed cells are counted as unavailable for the placement of offspring. We choose the cells to destroy using one of two habitat loss algorithms: 1) Random and 2) Contiguous.

2.1.3.1 Random Habitat Loss

Cells in the landscape may contain habitats in two states: pristine or destroyed. Pristine corresponds to the cells in the original model. To destroy habitat randomly, cells are selected and destroyed uniformly at random from the set of cells containing pristine landscape. This is repeated until the desired fraction of HL is achieved.

2.1.3.2 Contiguous Habitat Loss

This algorithm results in a contiguous region of cells with destroyed habitat. A 'seed cell' is selected uniformly at random from the fully pristine landscape. The seed cell is destroyed, and destruction proceeds radially from the seed cell until the desired fraction of HL is achieved. This process follows the same toroidal boundary conditions as the CA.

| Parameter name | Value | Description |
|--------------------|-------|--|
| OCCUPIED_CELLS | 0.4 | Fraction of the grid initially occupied by individuals randomly placed on it. |
| MAX_RESOURCE | 20 | Maximum amount of resource an individual may possess at any given time. |
| MIN_RESOURCE | 3 | Death threshold: minimum amount of resource at individual may possess. Any individual possessing less than this amount at any given iteration will die (see text). |
| LIVING_EXPEND | 0.01 | Fraction of resource an individual spends in living every iteration of the model. Metabolic rate. |
| MATING_RESOURCE | 0.5 | Fraction of MAX_RESOURCE that is required for an individual to be able to reproduce. |
| MATING_ENERGY | 0.2 | Fraction of resource given to the offspring by the parent during reproduction. Each parent gives the same fraction. The total amount depends on how much resource the parent possesses at the time of reproduction. |
| IMMIGRATION | 0.005 | Probability that a new individual will appear in a cell of the grid each iteration. The species this individual belongs to is randomly chosen from the original species pool. |
| SYNTHESIS_ABILITY | 0.1 | Fraction of resource that is autotrophically created by each individual from the basal species every iteration. This is the only energy input to the system. |
| HERB_FRACTION | 0.7 | Fraction of resource lost to herbivores by individuals belonging to a basal species during a trophic event, i.e. a species in the first trophic level feeding on a species in the basal level. |
| OMNI_TRADEOFF | 0.4 | Fraction of resource that omnivores are effectively able to gather when feeding on a species from the basal level (a plant). |
| MUT_FRACTION | 0.25 | Fraction of resource of a primary producer (basal species individual) that a mutualistic partner obtains when an interaction of this type occurs. |
| CAPTURE_PROB | 0.4 | Probability that a predator individual embark upon a trophic relationship with one of its prey individuals when it encounters it. |
| EFFICIENCY_TRANS F | 0.2 | Fraction of the resource the prey that is assimilated by the predator in a carnivorous interaction, i.e. trophic interaction not involving individuals from the basal species. |
| HERB_EFFICIENCY | 0.8 | Fraction of the resource of the prey assimilated by the herbivore in an herbivorous interaction. |
| MUT_EFFICIENCY | 0.8 | Efficiency of an individual mutualist when dispersing a plant partner. In other words, the probability with which a mutualistic individual will facilitate the creation of a new individual of the last species of plant it visited when it is positioned on an empty cell immediately after it interacted with a mutualistic plant partner. |
| MUT_COOLING | 0.9 | Cooling factor for the mutualistic efficiency of plant dispersers (mutualists). This is the fraction of mutualistic efficiency that remains after each iteration. |
| REPROD_RATE | 0.01 | Reproduction rate of non-mutualistic plant species. Probability with which an individual belonging to a plant species that does not possess mutualistic partners for dispersal will create an offspring in any given iteration of the simulation run. |

Table 2.1: The parameters of the model and what they mean.

2.1.4 Implementation

The code for the simulation model was originally written by Miguel Lurgi for research leading to the publication [5]. He and Daniel Montoya were responsible for the bulk of the model development, testing and parameter selection - a considerable task. My task was to take this legacy code and work with it to generate results that would allow us to study the effects of habitat loss.

The model is implemented in *Python*, with several switches that ensure portability between different versions of python. The programme makes extensive use of *numpy* and *networkx*, amongst other *Python* libraries. The original code was well written to allow for the easy implementation of new mechanisms. The intention was always to extend the model for further study. For example there is a parameter for *habitat type*, whereby the landscape would be heterogeneous with certain habitats best suited for different species. (In the current implementation this is not used and the landscape is homogeneous.) There was also a prototype algorithm for contiguous habitat loss.

Working with the legacy code I implemented the random habitat loss algorithm, and tested both the contiguous and random algorithms to ensure they were performing as desired. I also added methods to an already extensive library for saving simulation outputs, with a view to conducting more analysis on the spatial state of the system². I then ran numerous simulations without habitat loss (HL= 0) to ensure that the model reproduced the results presented in [5].

Simulation ensembles were run on Blue Crystal Phase 3 (BC3), Bristol's computer cluster. Compatibility issues arose because only *networkx* version 1.9 is available on this system, which has significant differences in the return

My contribution to the model was the implementation of the random habitat loss algorithm, and running all the simulations on Bristol's computer cluster Blue Crystal. The former was trivial but key to this project. The latter involved a considerable amount of debugging and scripting and testing. I also made

I conducted post-simulation analyses in the statistical package *R*, and in *Python*. Analyses in *R* used adapted legacy code from the previous project. Analysis and plotting methods implemented in *Python* were written by myself.

Write here about code, my contributions, Blue Crystal. Repeats runs, result format, run times etc.

2.2 Dynamics of the model

Display and discuss several example full runs. Also with varied parameters?

Well mixed approximation?

²IMPORTANT: don't write about this if you are not going to do the analysis properly.

2.2.1 Transience

Discuss and analyse transience. How long is it? Are there general relationships? Perhaps use simplified modelling (ODEs) to try and predict the length of transience.

2.2.2 Long term distribution

Is the final dynamics (after transience) steady state? What can we say about this?

2.2.3 Diffusion behaviour

How is species movement/dispersion affected by habitat loss? Can we derive a diffusion coefficient?

2.3 Ecological metrics and analysis methods

Introduce, define and discuss each metric.

Stability - Jacobian, dynamic stability, multi-stability, CoV, reproductive stability.

Robustness - secondary extinctions, cascading effects [?]. Re-wiring algorithms?

2.3.1 Biodiversity metrics

Richness, Simpsons, Shannon Entropy.

2.3.2 Stability metrics

Coefficient of Variation, May Stability

2.3.3 Network metrics

GenSd, VulSd, Gq, Vq, MTP, H2', Connectance, Nestedness, Compartmentalisation

2.3.4 Spatial metrics

Moran's I, Geary's C. Spatial autocorrelation. Centroids.

2.3.5 Interaction strength metrics

IS1, IS2, IS3 [?].

HABITAT LOSS WITH HIGH IMMIGRATION

3.1 Response of ecological metrics

For both habitat loss scenarios there is no loss of species richness up to 90% habitat loss. However significant changes are observed in metrics relating to community composition, network properties and stability. In general the qualitative response of these metrics is not governed by MAI ratio i.e. the direction of the trends are the same across MAI ratios, although the extent of the response may vary.

Although habitat destruction does not lead to extinctions, it does reduce the total biomass of the communities. This is measured by the total number of individuals of all species remaining at the end of a simulation, which we average across replicate communities. Figure 3.1 shows that, although mutualistic communities contain more biomass, the loss of biomass due to habitat destruction is ubiquitous. This is not surprising.

How community stability is affected by loss of habitat is of particular interest. Temporal stability is measured by the coefficient of variation (CV) of the total biomass of the system. (This metric is calculated over a number of iterations after the transient dynamics.) A higher CV indicates lower stability, because there are greater fluctuations in the dynamics. We observe that temporal stability is affected differently by the two habitat loss scenarios. As shown in figure 3.2, random destruction increases temporal stability, whereas contiguous destruction decreases it. What is driving this different response in the dynamics?

From figure 3.3 it is clear that the response in temporal stability is closely correlated with interaction strengths, as measured by the metric IS3. Random habitat destruction is characterised by a decrease in total interaction strength, whereas contiguous destruction results in a dramatic increase. It is reasonable to assume that these changes in IS3 are causing the different responses

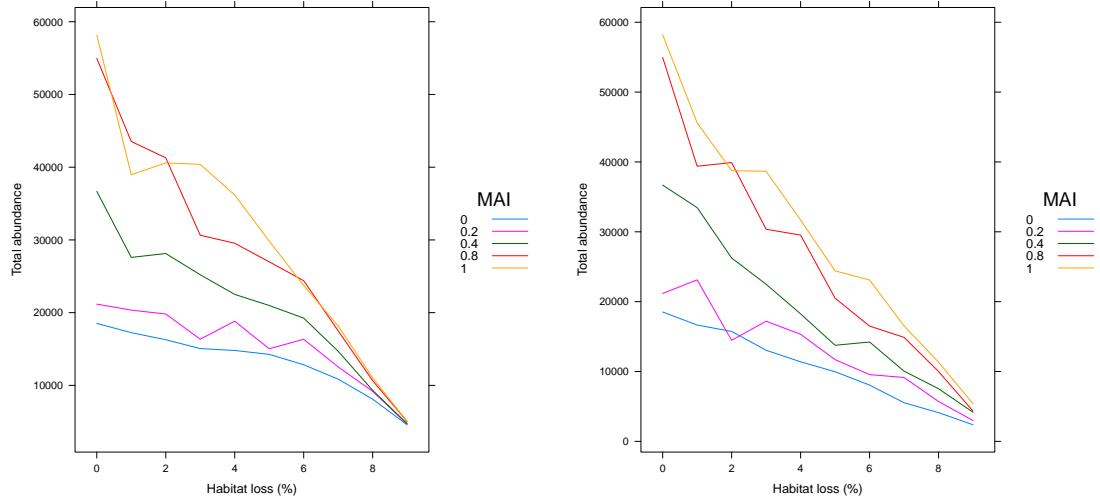


Figure 3.1: **Mean total number of individuals** across replicate communities decreases with habitat loss, for all MAI ratios. Left: random destruction. Right: contiguous destruction.

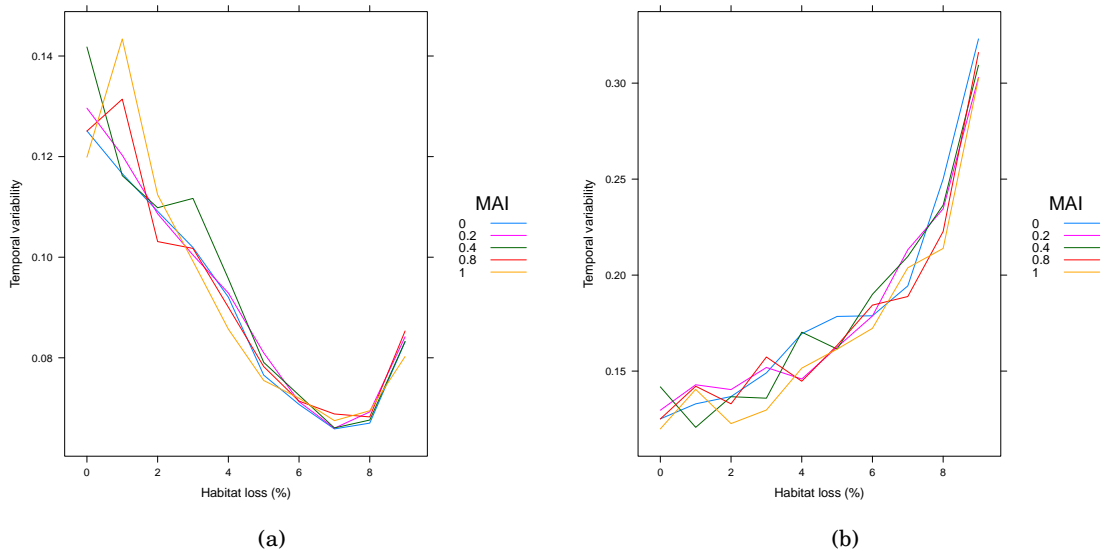


Figure 3.2: **Mean CV in total biomass** across replicate communities against habitat loss for selected MAI ratios. Left: random destruction leads to an increase in temporal stability, as indicated by a decrease in CV. Right: contiguous destruction dramatically reduces temporal stability.

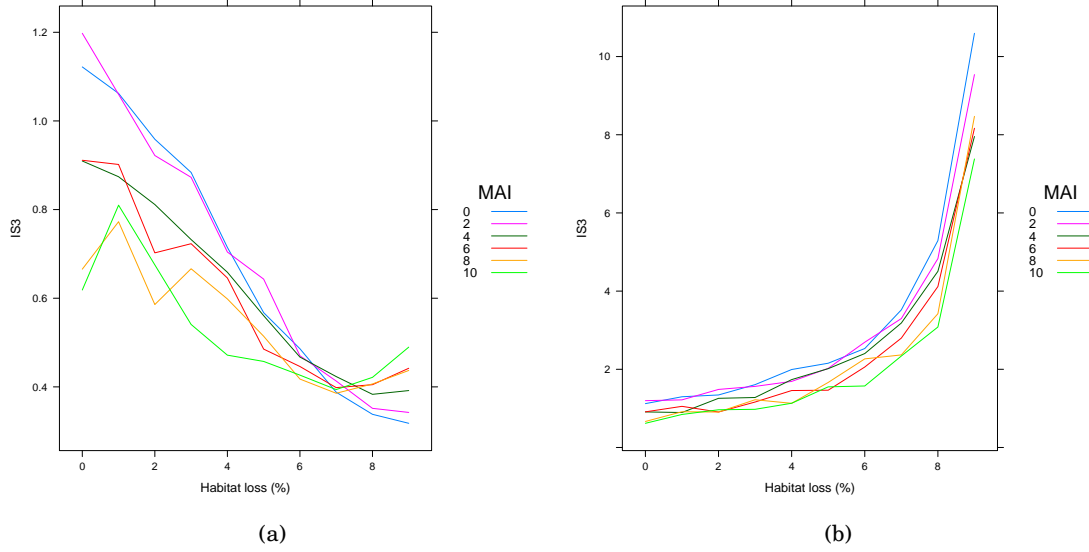


Figure 3.3: Interaction strengths: The sum of the elements of the interaction matrix, averaged over replicate communities, for selected MAI ratios. Left: random destruction reduces total interaction strength. Right: contiguous destruction dramatically increases total interaction strength.

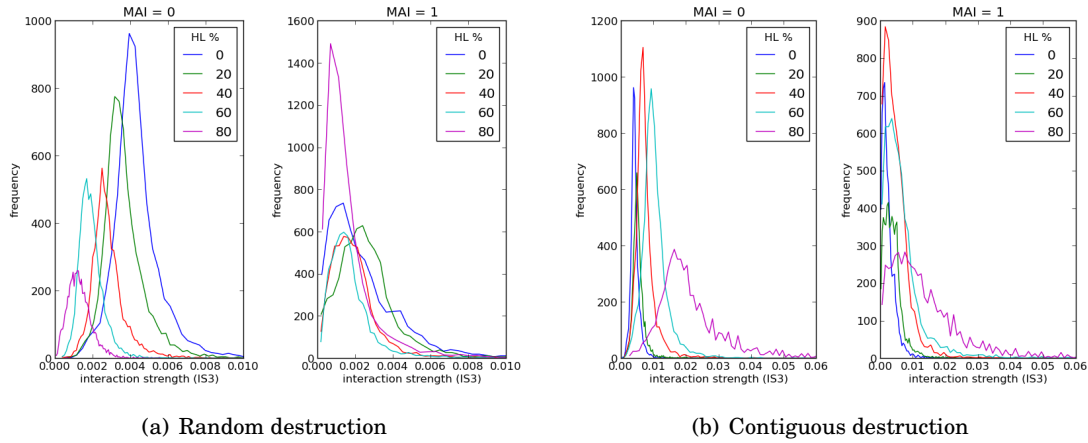


Figure 3.4: IS3 distributions: The interaction strength distribution shifts leftwards for random habitat loss, and rightwards for contiguous loss. The extent of this shift is mediated by MAI ratio - it is most visible for MAI= 0, and least visible for MAI= 1.

in temporal stability. This is supported by the literature, where it is well documented that strong trophic interactions destabilise population dynamics [REFERENCES]. It is not so obvious what affect on dynamics should be expected from an increase in the strength of mutualistic interactions, which are included in this metric. However, figures 3.2 and 3.3 suggest that this is also destabilising.

The trends in total interaction strength are due to underlying shifts in the distribution (figure 3.4). This is made visible by a shift in the modal peak to lower or higher interaction strengths, for random or contiguous loss respectively. The extent of this shift is mediated by MAI ratio, with greater shifts for lower levels of mutualism.

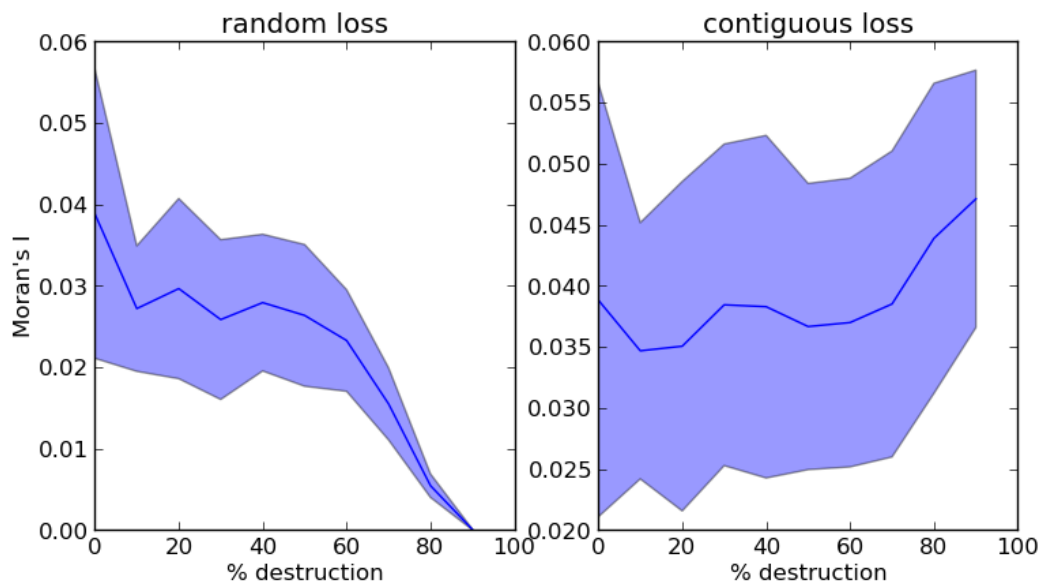


Figure 3.5: **Spatial autocorrelation:** Moran's I is calculated for all species distributions and averaged over the community. These plots show the results averaged over all replicates and over all MAI ratios. Solid lines indicate the mean value, and shaded areas indicate ± 1 standard deviation. This metric suggests that species distributions, on average, become less aggregated in space due to random destruction. Whereas they appear to become more spatially aggregated as a result of contiguous destruction.

What is causing the different responses of IS3 to the different habitat loss scenarios? Spatial aggregation of species distributions is quantified using Moran's I [REFERENCE]. According to this metric, species distributions become less aggregated in space as a result of random destruction (figure 3.5). Whereas they appear to become more aggregated in space under contiguous destruction. If species are more aggregated in space, it may be easier to find an interaction partner. This would benefit predators (and mutualists), potentially leading to stronger de-stabilising trophic interactions. The mean frequency of interactions (figure 3.6) shows some evidence for this effect. On average there are fewer interactions in communities suffering random habitat destruction, than those with contiguous destruction. However the difference is small, suggesting another mechanism is required to explain the strong responses of IS3 and temporal stability.

It is likely that other changes in network properties and community composition can explain the changes in IS3. The elements of the interaction matrix, used to calculate IS3 are given by [? ?]:

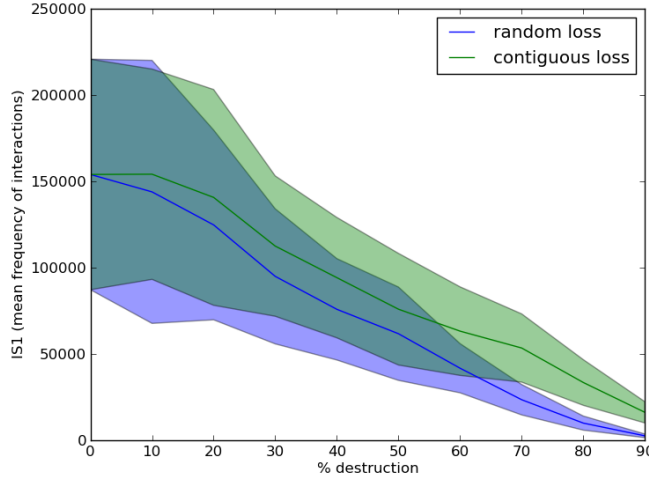


Figure 3.6: **Interaction frequencies:** The metric for interaction strength IS1 averaged over all replicates and all MAI values. This metric is the sum of the elements of the interaction frequency matrix i.e. the total number of interaction occurring within a given period of time. Solid lines indicate the mean value, and shaded areas indicate ± 1 standard deviation. For contiguous destruction interactions are slightly more frequent, on average, than for random destruction.

$$(3.1) \quad \alpha_{ij} = \frac{b_{ij}}{N_i N_j},$$

where α_{ij} is the effect of species j on species i ; b_{ij} is the biomass flow from i to j (here measured by the frequency of the interaction, equivalent to IS1) and N_i, N_j are the number of individuals belonging to species i and j respectively. Therefore the elements of the interaction matrix are dependent on the relative abundances of the interacting species, as well as the frequency of the interaction. A more detailed analysis of community composition will let us explain to observed trends.

3.2 More preliminary results

By averaging results over MAI ratios we are able to effectively obtain more replicate communities. When doing this certain metrics appear to display trends in response to habitat loss that are not clearly visible without this averaging. We perhaps need to justify this approach, and to fit statistical models to quantify the significance of the trends in certain metrics.

3.3 Further development and work to do

3.3.1 Work to do

- Write introduction
- Write up ecological metrics
- Amend figure captions
- Plot example networks
- Plot dynamics
- Analyse dynamics (transience, steady-state)
- Fix conflict in trophic level results

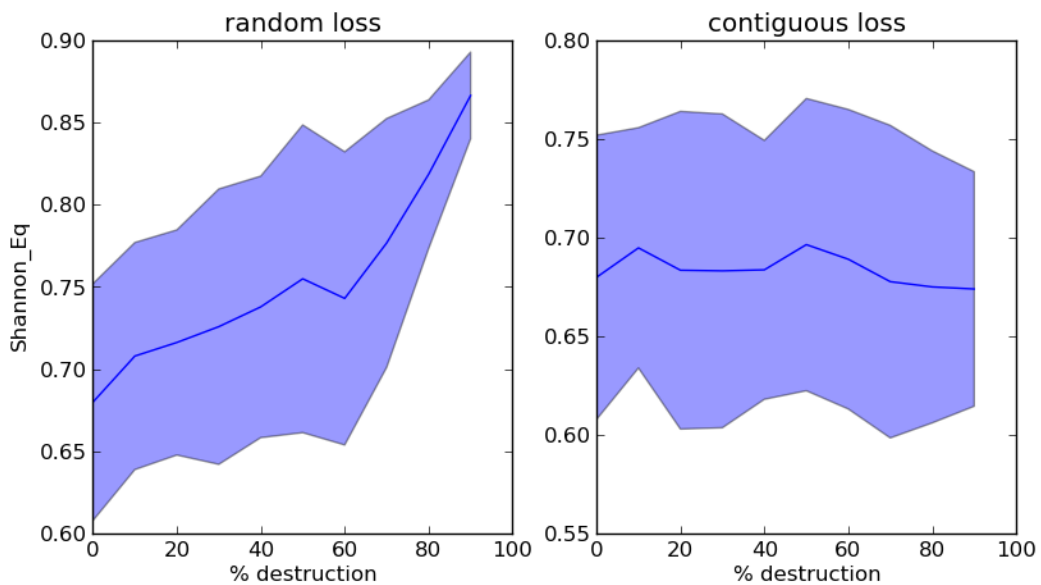


Figure 3.7: **Shannon evenness:** average over MAI ratios and replicate communities. Under random habitat destruction communities on average become more even. Under contiguous destruction there is no change.

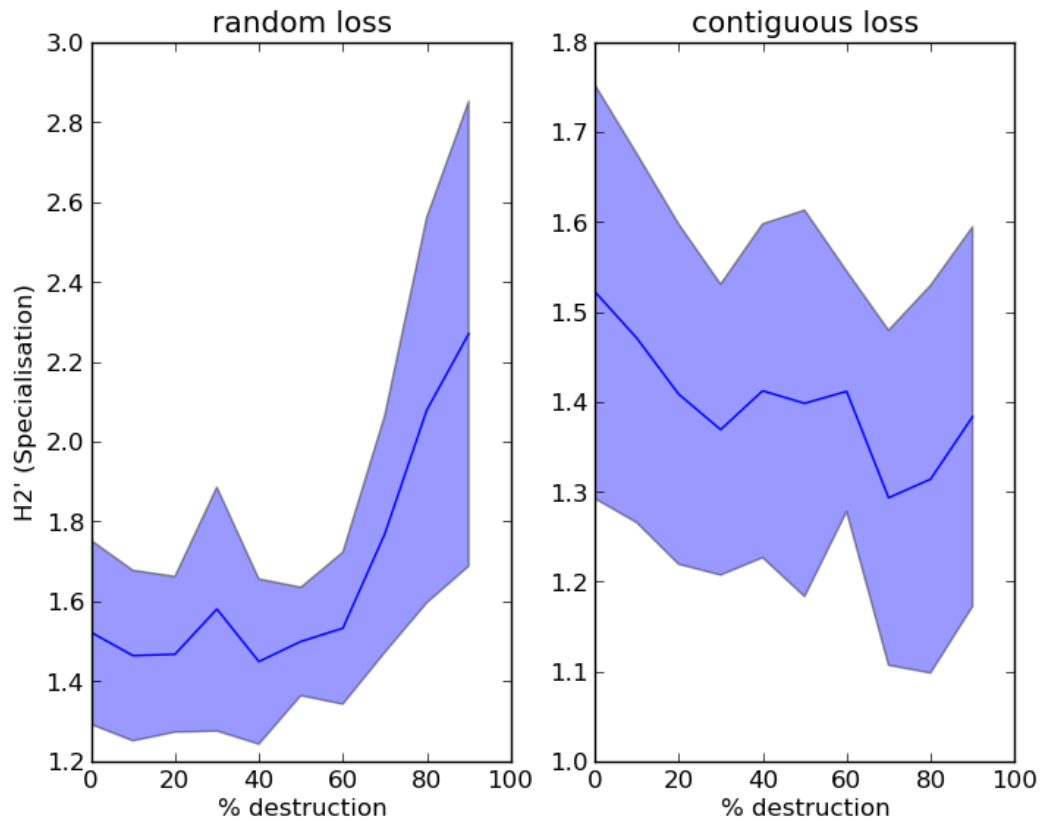


Figure 3.8: **Specialisation:** $H2'$ is a metric that quantifies the degree of specialisation of interactions in the mutualistic sub-network. Mutualists appear to become less specialised under random destruction, and more specialised under contiguous. (This appears to disagree with previous plots of $H2$, but I can't see why - the numbers used are taken from output_network.csv, column titled $H2$.)

- Analyse ecological metrics by trophic level (basal, intermediate, top)
- Understanding IS3 response: plot $IS1/N^2$, look at individual runs
- Compare movement of species to diffusion coefficient in porous medium
- Plot RADS with species coloured according to trophic level.

3.3.2 Further development

- Run simulations with lower immigration
- Well mixed approximation. Simplified model for analysis

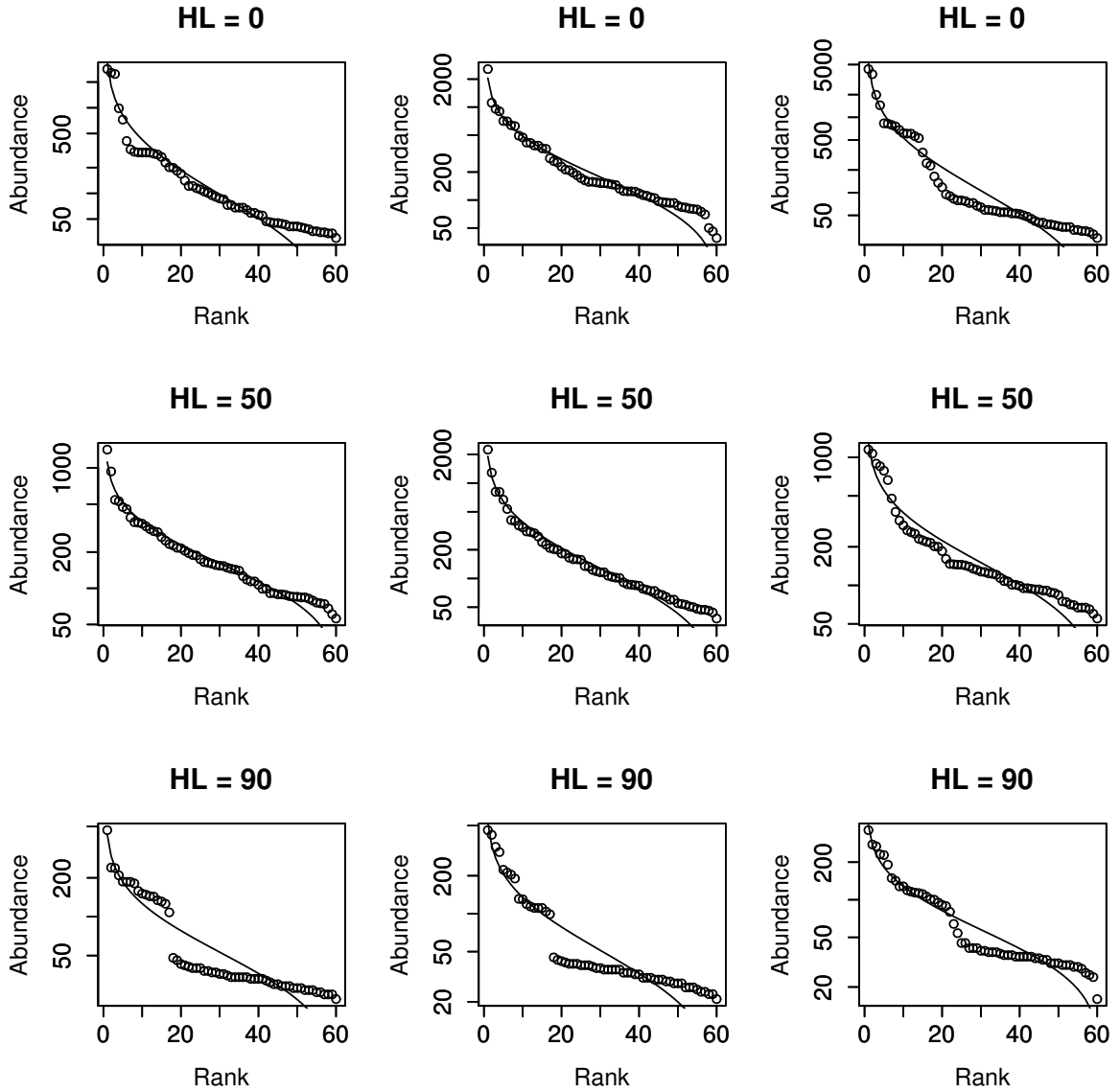


Figure 3.9: **RADs for Random habitat loss:** Rank abundance distributions for MAI= 0, three replicate communities shown for selected levels of habitat loss (0,50,90). In the case of random destruction we expect the communities to become more even on average, based on Shannon_Eq metric, (figure 3.7)

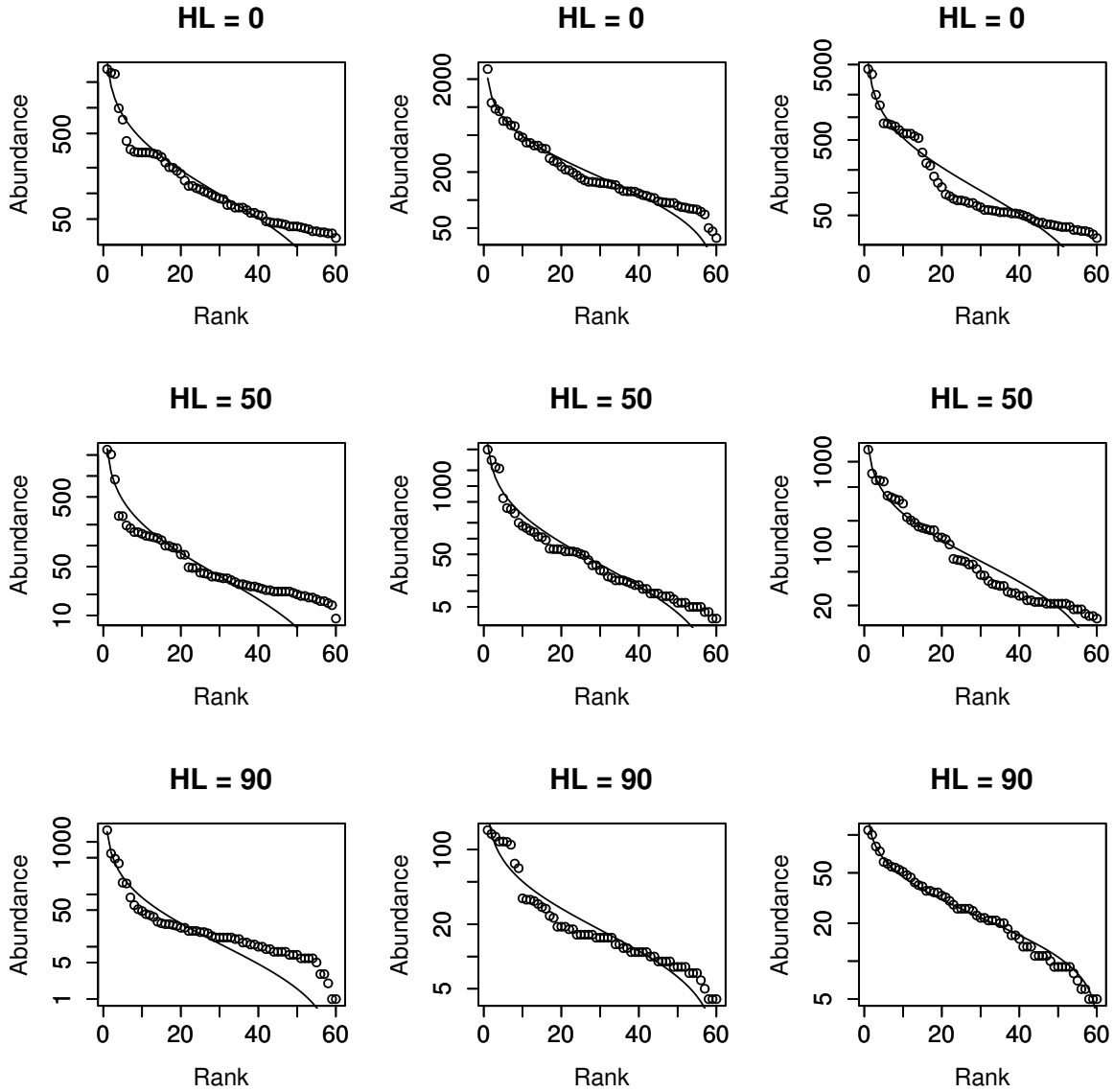


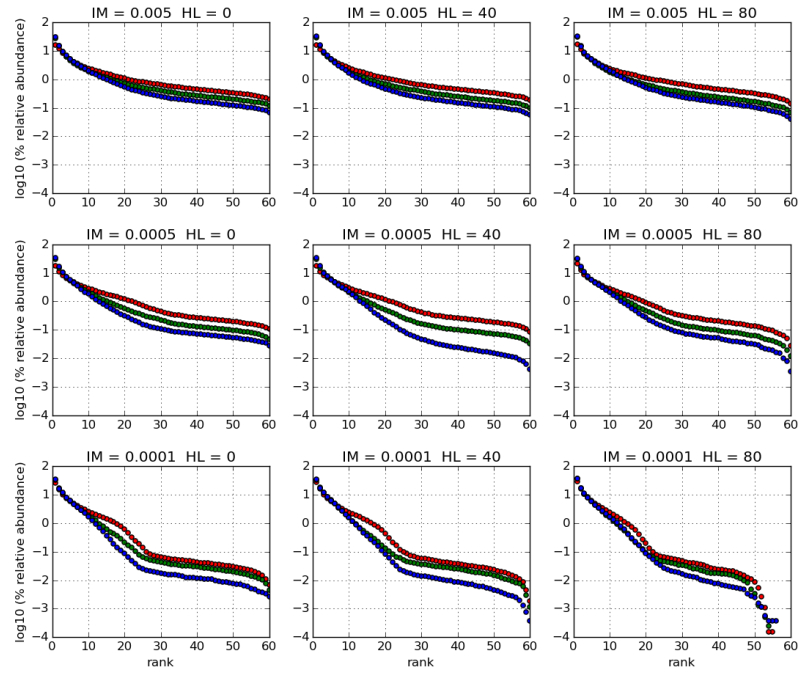
Figure 3.10: **RADs for Contiguous habitat loss:** Rank abundance distributions for MAI= 0, three replicate communities shown for selected levels of habitat loss (0,50,90). In the case of contiguous destruction we expect no trend in evenness on average, based on Shannon_Eq metric, (figure 3.7)

- Can we calculate robustness from network, and test this against what extinctions we get?
(With lower immigration)

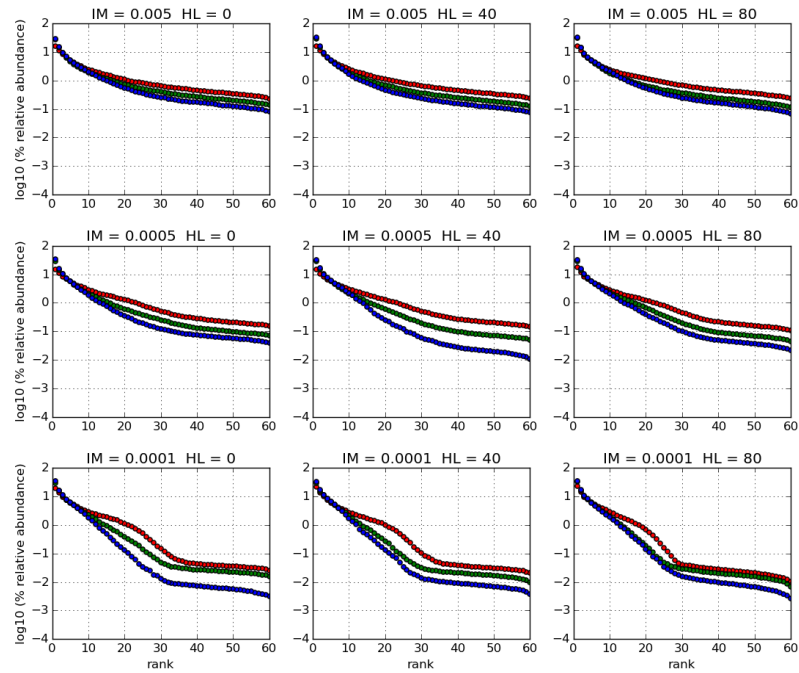
VARYING IMMIGRATION RATE

4.1 RADS with averaging

Here we show the difference between rank abundance distributions calculated using two different samplings from the simulations..



(a) From snapshot of final simulation state



(b) Abundances averaged over final 1000 iterations

Figure 4.1: **Average rank abundance distributions** over one hundred simulation runs, for nine different pair values of immigration rate and habitat destruction. Each distribution is calculated using the mean relative abundance of the ranked species. The different colours correspond to different MAI ratios: red = 0.0; green = 0.5; blue = 1.0.

4.2 New results: without vegetarian predators

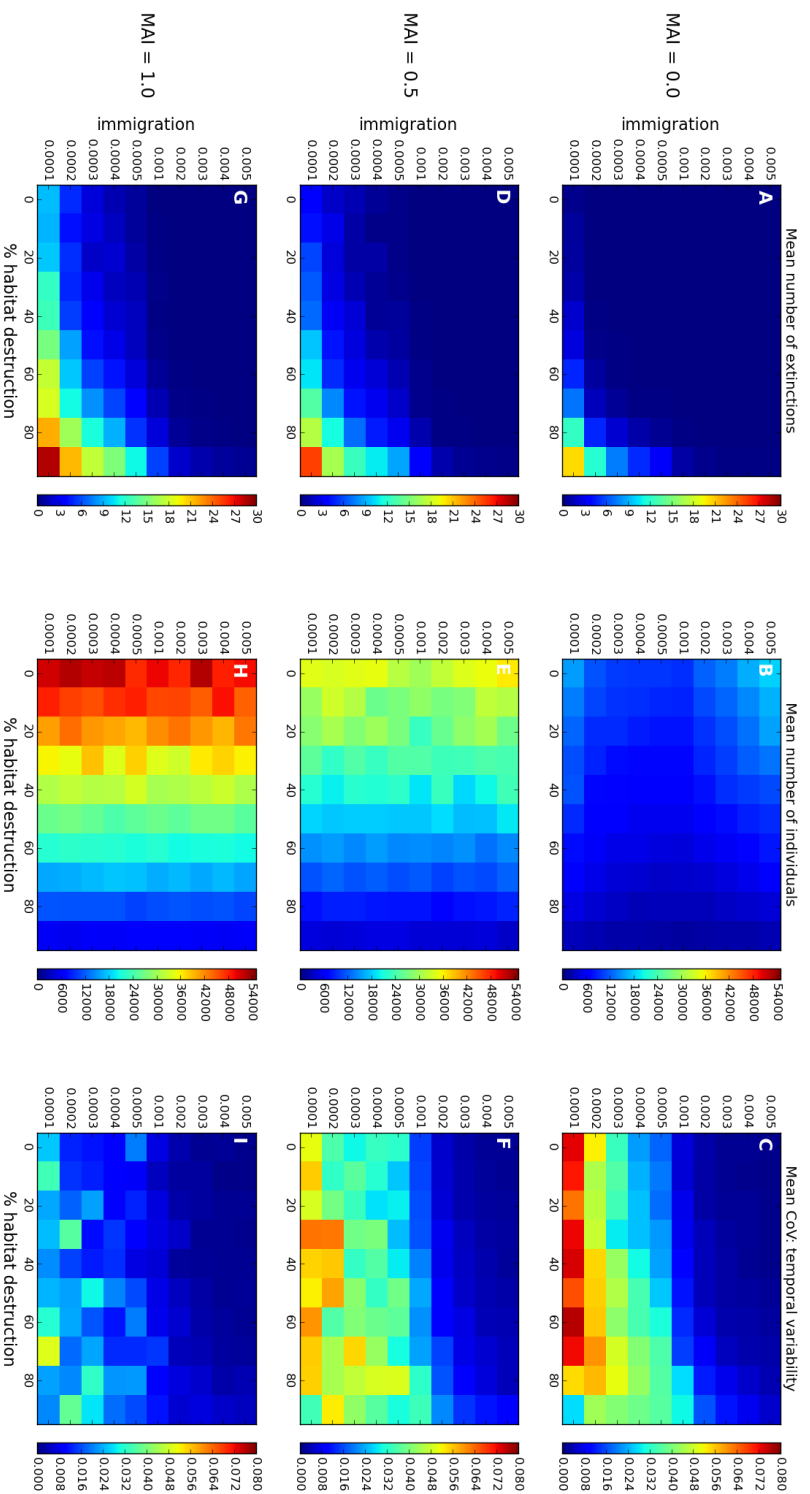
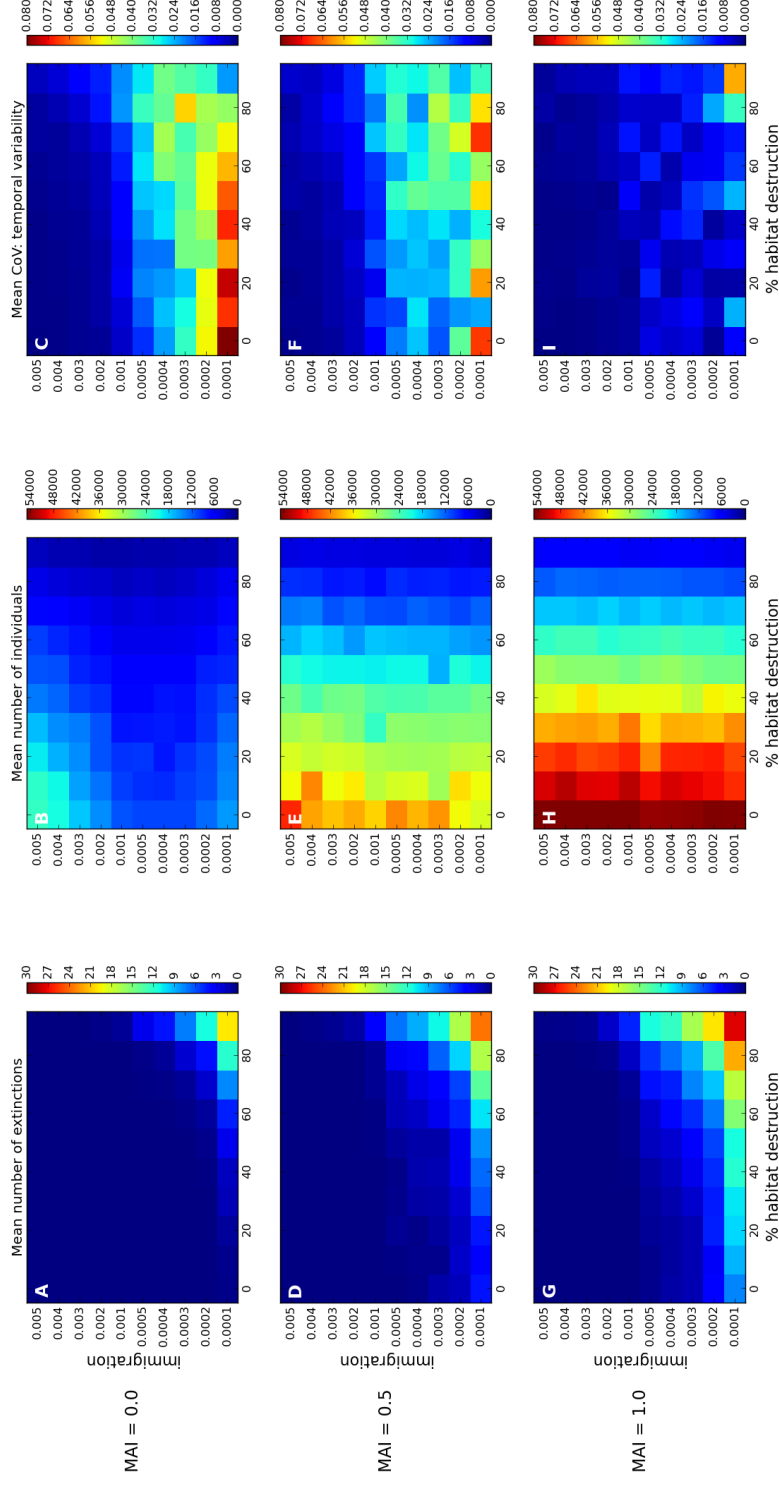


Figure 4.2: VEGETARIAN PREDATORS. Summary heat maps: Each heat map shows the value of a certain response metric across a 2-dimensional slice of parameter space. The parameters varied are immigration rate IR (y-axis) and percentage habitat destruction HL (x-axis). Each row of plots corresponds to a different MAI ratio as labelled. To construct the heatmaps one hundred repeat simulations were run for each combination of parameter values, with each simulation using a different underlying network. The mean value of the response metrics is taken over the hundred repeats. Therefore each pixel shows an estimate of the expectation value of the metric at those parameter values. The left column shows the expected number of species that are extinct at the end of a simulation; the central column shows the expected biomass (total number of individuals) at the end of a simulation; and the right column shows the expected temporal variability (coefficient of variation of total biomass) of the dynamics during the final thousand iterations of a simulation. The latter is used as a proxy for stability (see text).



STATIONARITY

TODO: not forget this useful link :) jasss.soc.surrey.ac.uk/15/2/7.html !!

TODO: how do metrics vary with measurement length/through time...

5.1 Motivation

We look here at stationarity because it was seen in previous chapter that in certain circumstances the population dynamics become highly variable, as measured by the temporal variability metric.

Ecological relevance... There has been a strong tradition of understanding ecosystems as existing at or near some stochastic equilibrium or steady state [2] (issue of short time scale fluctuations and thermodynamics systems). This is motivated partly by observation of constancy in ecological communities through time [REFS] and also by theoretical considerations - for examples various stability metrics require the assumption of a stable equilibrium.. stability people ?? and section ??.

There is also the concern that high variability affects the results we present... previously results were collected.. but averaged over replicates... here we look for stationarity.. if stationary.. we also look at how results differ depending on how they are measured for a highly variable simulation... OUTLINE WHAT IS TO FOLLOW:

- Thermodynamic equilibrium is... therefore can talk about extrinsic state variables..
- Different concepts of equilibrium in ecology - IBT suggest that island communities exist in a dynamic equilibrium between immigration and local extinctions.. [9].

- Steady-state can mean different things in different contexts. In general we define it as a condition under which certain properties of the system can be defined which are unchanging in time. For example..a chaotic attractor can be considered a steady-state
- Whether or not real we consider..
- Chaotic attractor could be steady-state..

In the previous work ([5] and section ??) the results presenetd were mainly taken as a final value at the end of the simulation. This is true for the Diversity and Abundance metrics, taken from outputecosystem. This is also true of mutualistic subnetwork - which is only taken at the final iteration (over period of 200 iterations). And Network properties are all caculated from the final 200 iterations of the simultion i.e 4800 to 5000. Here we investigate this, the assumptions behind it and the potential affect on results. This investigation is in part inspired by the result that the CoV in the total biomass increases as the IR is dreceased, bringing into question the assumptions behind taking ‘snapshot results’.

5.2 Second-order stationarity

We introduce here three tests for second-order (or ‘weak’) stationarity in time series. As discussed above the stationarity of our simulation output is primarily of interest for the pratical reasons of obtaining reliable results. However it is also of interest for various reasons relating to ecological theory. Second-order stationarity may be defined as the time invariance of the first and second moments of the time series data. Specifically this means that [?]:

$$(5.1) \quad \mathbf{E}(x(t)) = m(t) = m(t + \tau) \tau \in \mathbf{R},$$

$$(5.2) \quad \mathbf{E}((\bar{x} - x(t))(\bar{x} - x(t + \tau))) = f(\tau) \tau \in \mathbf{R}, [CHECKTHIS]$$

for a process $x(t), t \in \mathbf{Z}^+$. If these conditions are then met we may say that each value of x is drawn from the same probability distribution, and that this distribution is constant in time. From now on we will refer to this as *stationary*. If the conditions are not met, then we cannot say that there is a constant underlying distribution. We then call the time series *non-stationary*. The non-stationarity may be due to a trend in the data or a change in the parameters of the data generator, for example.

In our case the data generator is the IBM model and there are several possible causes of non-stationarity. It may be that there is no steady-state equilibrium¹ in the model. For example the number of individuals may undergo a random-walk. From previous analysis this situation seems unlikely (we have observed what appear to be deterministic population cycles), but it has

¹Not exactly sure what to call this - stable distribution...??

not been explicitly tested for. Another possibility is that there is a steady-state equilibrium, but that there is a long transience and the equilibrium is not reached during the time frame of our simulations. A reasonable hypothesis is that the dynamics contains a deterministic and a stochastic component. Deterministic component must be stable..to explain lack of extinctions...Noise can induce oscillations about stable equilibrium [REF]. Or the oscillations may be deterministic in nature, suggesting a high dimensional attractor. Although this could be considered a steady-state, as discussed, it does not necessarily appear stationary. This would depend on the magnitude of the oscillations. This raises an important point about equilibria and stationarity, and may motivate further types of test...

5.2.1 Tests for stationarity

We compare three different tests of stationarity: the Kwiatkowski-Phillips-Schmidt-Shin (KPSS) [4]; the Augmented Dickey-Fuller (ADF) [8]; and the Priestley-Subba Rao (PSR) [6] tests. All three are implemented in the programming language *R* [7] - the former two in the package *tseries*, and the latter in the package *fractal*.

The ADF test has null hypothesis that the series is non-stationary. The test models the data as an auto-regressive process (see discussion below), and the null hypothesis is that this process has a *unit root*. The test produces a statistic that is negative. The greater the magnitude of the test statistic the more evidence there is to reject the null hypothesis in favour of stationarity.

The KPSS test complements the ADF test in that the null hypothesis is stationarity. The data is modelled as the sum of a random-walk and an error component, and tests the hypothesis that the variance of the random walk is zero. The test statistic is always positive, and the greater its magnitude the more evidence there is to reject the null hypothesis in favour of non-stationarity.

The null hypothesis of the PSR test is also that the series is stationary. The test is based on the idea that non-stationary processes have power spectra that change over time [6]. These are called *evolutionary spectra*. The test, as implemented in *R*, returns several statistics. We quote the ‘p-value for T’ which can be thought of as the confidence that the estimated spectral density functions are constant in time.

The first two tests (ADF and KPSS) makes assumptions about the process that generated the data. For example, in the case of the ADF test, it is assumed that the data can be modelled as an autoregressive process. Grazzini [?] refers to such tests as *parametric* and points out that their simple assumptions about the data generator process may be too restrictive (REPHRASE) for time series generated by complex systems models, such as our IBM. With this in mind we proceed with these tests because they are part of the standard set of tools currently used for time series analysis. Interestingly the PSR test and another, test proposed by Nason [?] and based on wavelets analysis of the time varying power spectrum, do not require such parametric assumptions...wavelets..waveletss..

5.2.2 Characterising the tests

To test the performance of the stationarity tests (section 5.2.1) we use three example time series, which we refer to as HI, RW and NS. The first, HI, is taken from a single IBM simulation run with high immigration rate (IR= 0.001), zero mutualism (MAI= 0.0) and otherwise default parameters (table ??). The series represents the total number of individuals of all species at each iteration (below we investigate other metrics). The simulation was run for 50,000 iterations, compared with the 5000 used in previous chapters, to ensure that any non-stationarity is not due to insufficient run-time. The first 1000 iterations were discarded, since these contain clearly transient dynamics (see figure 5.3), leaving a time series of 49,000 points. A high immigration rate was chosen because it reduces the temporal variability of the dynamics, as was discussed in chapter 4. Therefore the HI series is more likely to be stationary than the output of a simulation with lower IR.

The series RW and NS are chosen as a negative and a positive control respectively. Both have the same length as HI. RW is a non-stationary series generated by a one-dimensional *random-walk*, defined as:

$$(5.3) \quad x(t) = \sum_{i=1}^t Z_i,$$

where Z_i are independent random variables that may take values of either -10 or $+10$, both with probability half. An ensemble of these random walks was generated and a single instance was chosen with mean and variance closest to the HI series. (RW has a mean and standard deviation of 15525.2 and 1549.8 respectively, compared to 15915.8 and 1545.6 for HI.) For comparison, NS is a stationary series generated by drawing each value independently from a normal distribution with mean and variance equal to that of HI. The three series are plotted in figure 5.1.

| | A.D.F. | | P.S.R. | | K.P.S.S. | |
|----|----------|---------|--------|--------------|----------|---------|
| | stat | p-value | stat | p-value | stat | p-value |
| HI | -15.401 | <0.01 | - | 0.0004782808 | 0.5395 | 0.03277 |
| RW | -4.0386 | <0.01 | - | 0.9929773 | 18.7453 | <0.01 |
| NS | -37.5348 | <0.01 | - | 0.811097 | 0.0466 | >0.1 |

Table 5.1: Results of applying the three stationarity tests to the example time series shown in figure 5.1. P-values that indicate evidence for stationarity at 95% are highlighted in green. The test statistics are also given for the ADF and KPSS tests.

Initially we apply the three tests to the complete time series (49,000 points). The results are shown in table 5.2.2. The ADF finds significant evidence that all three series are stationary, at 99% confidence. The test statistic indicates that there is most evidence for NS to be stationary, followed by HI, then RW. We may be suspicious of this since we know that RW is generated by

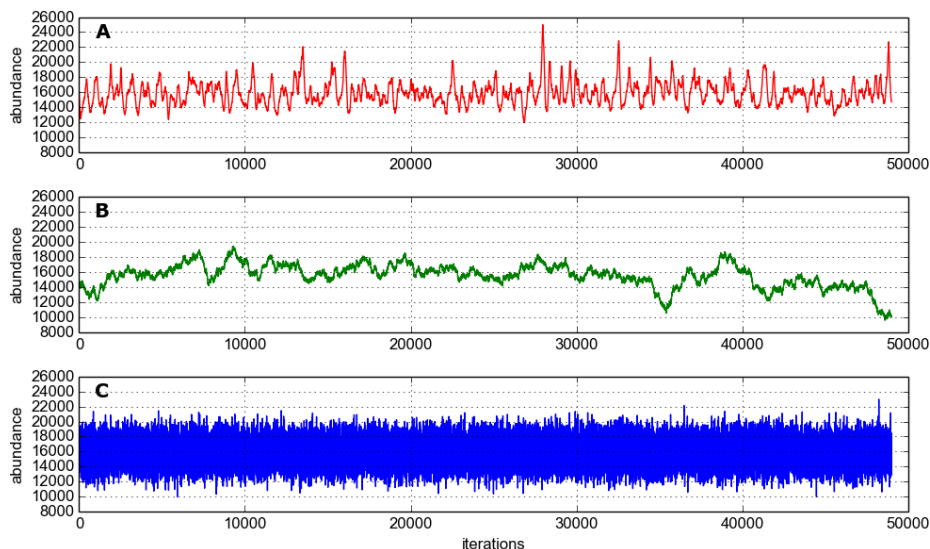


Figure 5.1: The three time series used to characterise the performance of the stationarity tests. The initial 1000 points removed such that all are 49,000 points long. (A) **HI**: total abundance dynamics of an IBM simulation with high immigration rate; (B) **RW**: a random walk without drift, as described in the text; and (C) **NS**: a series generated by independent sampling from a normal distribution.

a non-stationary process. However this is a special case of a random walk, chosen from several thousand to closely match the the first two moments of HI. Therefore it may not be unreasonable that it can pass as stationary. The KPSS test ranks the series in the same order, based on the magnitude of the test statistic. According to this test NS is clearly stationary (accept H_0), and RW is clearly non-stationary (reject H_0 at 99% confidence²), whilst HI is borderline. For HI we would accept the null-hypothesis of stationarity at 95% confidence, but reject it at 99%.

The PSR test provides strange results. It concludes that RW and NS are both stationary, whilst HI is non-stationary with a high degree of confidence ($p\text{-value} < 0.001$). In fact, according to the PSR test, RW is more likely to be stationary than NS. This result contradicts what we know about the series, so we do not use this test in the analysis that follows. However the apparently erroneous result may contain interesting information about the HI series and the process that generated it. The test attempts to detect a time-varying power spectrum, as a signature of non-stationarity. This signature may be characteristic of adaptive dynamical systems, or systems exhibiting some kind of aperiodic dynamics. In general wavelets have proven a useful tool to study signals with time-dependent frequency spectra, and have found application in the analysis of non-stationary ecological time series [? ?]. However a preliminary investigation using the *R* package *biwavelet* did not appear fruitful and is not pursued further in this thesis³.

²This may not be surprising - or RW not a good test case - since the test models the data as a random-walk!

³Although we may well refer back to this if we do discover chaos in the IBM!

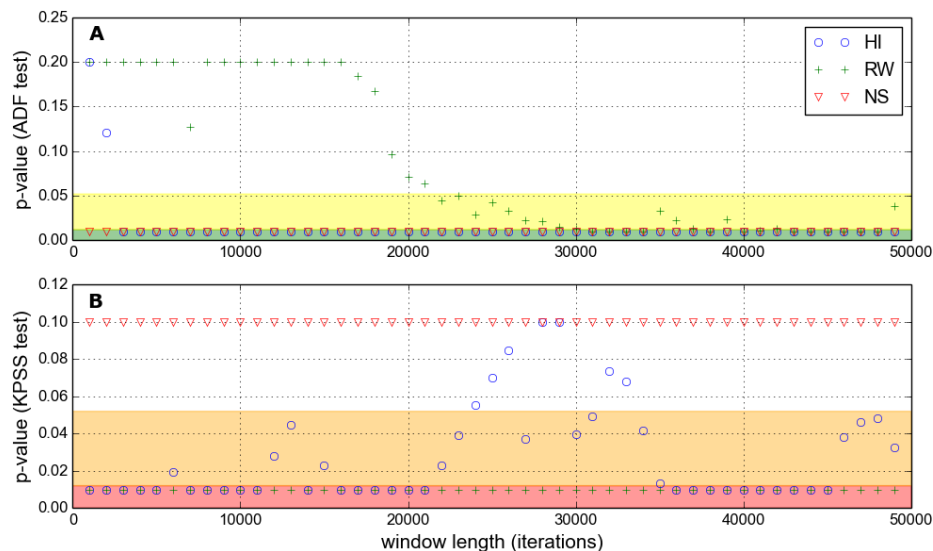


Figure 5.2: Two tests for stationarity applied to samples of varying size (window length). Samples are taken from the three time series (HI,RW,NS) shown in figure 5.1. All three time series contain 49,000 points. Sample windows begin at the first point and increase in length from 1000 to 49,000 points. (A) ADF test, with p-values capped at 0.20. 95th and 99th percentile in yellow and green respectively, indicating significant evidence for stationarity. (B) KPSS test, with p-values capped at 0.01. 95th and 99th percentile in orange and red respectively, indicating significant evidence for non-stationarity.

Having discarded the PSR test, the ADF and KPSS are applied to the three series (HI,RW,NS), with varying sample sizes. Samples of increasing length (1000 to 49,000) are drawn from the series, beginning at the first time point, and the tests are applied to the sample. As we saw in table 5.2.2, the two tests again to perform differently. The KPSS test correctly identifies the RW and NS series as non-stationary and stationary respectively, for all sample sizes. This is shown in panel B of figure 5.2. The ADF test (panel A figure 5.2) correctly identifies the NS series as stationary for all sample sizes. For short sample sizes it also identifies the RW series as non-stationary. However, for sample sizes much above 20,000 the ADF test finds significant evidence that the RW series is stationary, at 95%. This is an interesting result. Although RW is generated by a non-stationary process, it appears to fool the ADF test by staying stationary enough over a long enough time scale.

There is mixed evidence for the stationarity of the HI series, as shown in figure 5.2. The ADF test, for all sample sizes above 2000, finds significant evidence that the HI series is stationary. Whereas the KPSS test, on the whole, gives significant evidence that the HI series is non-stationary. (There are only seven cases where there is insufficient evidence to reject the null hypothesis that the HI series is stationary, and these occur at sample sizes between 24,000 and 34,000.) It appears that the KPSS test is a stricter test of stationarity, and is less sensitive to the size of the sample. It may be that the sensitivity of the ADF to sample length is useful.

It is possible that the method of sampling from the time series affects the results of the stationarity tests. For example sampling near the beginning of an IBM simulation run may be more likely to give the non-stationary series because of transient dynamics. Alternatively a non-stationary data generator may produce sections of time series that appear stationary purely by chance. This sensitivity to sampling is investigated by reversing the time series and repeating the above analysis. For HI, RW and NS we see no qualitative change in the results. We also scan sampling windows of fixed length along the series to look for time dependence in the test results. The time at which samples are taken appears to make little difference, and there is no systematic change in the results (FIGURE? MENTION REMOVAL OF TRANSIENCE AND LOW IR CASE.).

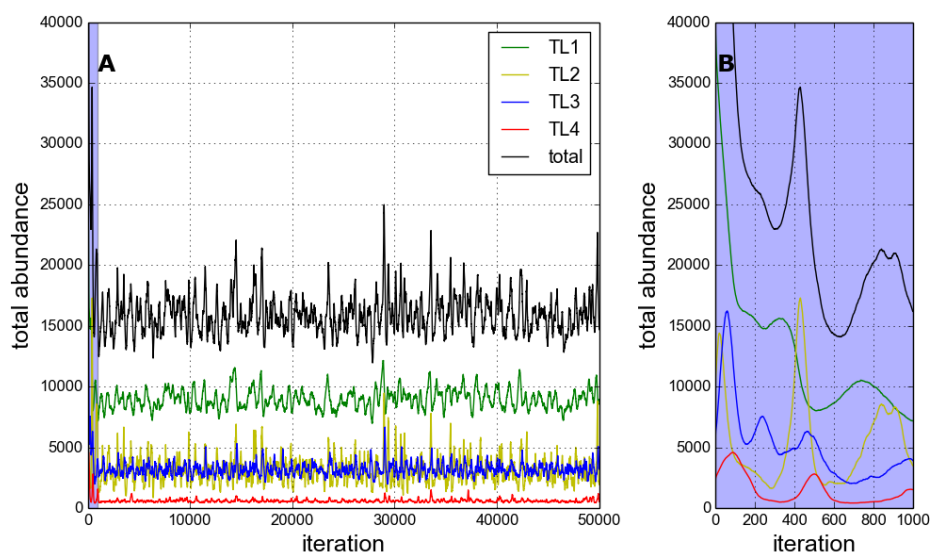


Figure 5.3: Dynamics for the HI simulation, broken down by trophic level ($TL1 - 4$). Abundance is measured by the number of individuals. (A) The whole simulation run of 50,000 iterations. (B) Enlargement of first 1000 iterations, showing transience.

HI simulation. There are metrics other than the total number of individuals which we can test for stationarity. Most time series methods are applicable to one-dimensional data. However our abundance data is 60-dimensional, since we have 60 species by default. Simply summing over species (l1-norm) is not necessarily the most informative metric to use. One possible issue is that the phase differences between species oscillations that we would expect due to trophic interactions (see chapter ?? may mean that temporal variability is cancelled out when aggregating abundances in this way. This raise the question: what aspect of our simulated communities do we want to be stationary? (From a practical perspective - to obtain reliable results.) Many of the ecological metrics that we used in previous chapters depend on the relative abundances of species or trophic levels. It may be the case that the total number of individuals is stationary, but

that the trophic or species level dynamics cause changes in community composition over time. Therefore we now look at how the stationarity tests perform at these two resolutions.

The dynamics of the HI simulation are aggregated by trophic levels to create four new time series TL1 – 4. These *trophic dynamics* are plotted in figure 5.3. The initial period of transience is expanded in panel B, and as previously this part of the time series (first 1000 iterations) is removed. (It is worth noting that at lower immigration rates we cannot be certain that the obviously transient dynamics is contained within the first 1000 iterations - we will look at the in more detail later.) The ADF and KPSS tests are applied to the four trophic series separately and the results are shown in figure 5.4. All trophic levels are stationary according to the ADF test for samples sizes greater than 4000. TL1 appears to be least stationary according to ADF, requiring a sample size of 4000 before the null hypothesis is rejected at 95%. According to the KPSS test TL1 is non-stationary for all sample sizes, whilst TL2 and 3 are stationary for samples sizes above 9000 and 2000 respectively. KPSS gives mixed results for TL4, with no clear dependence on sample size. It is hard to reconcile these results with an observation of the dynamics in figure 5.3, indicating the usefulness of the statistical tests...

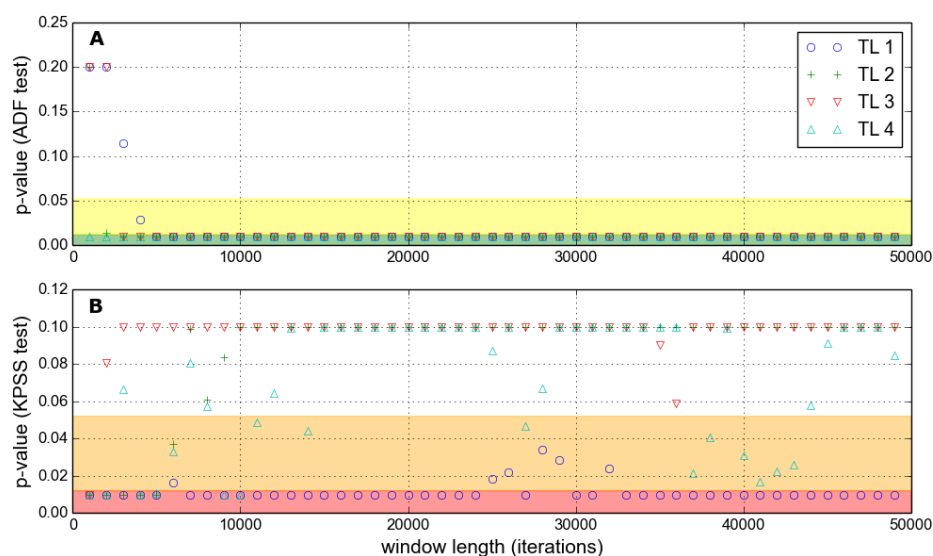


Figure 5.4: Similar to figure 5.2, but here the tests are applied separately to each trophic level of the HI simulation. The four time series (TL1 – 4) represent the total number of individuals belonging to each trophic level at every iteration.

The dynamics of every species in each trophic level are plotted in figure 5.5. It is clear here that the community is dominated by a few abundant species, mainly in the lower trophic levels, with a large number of relatively scarce species. It also appears from this figure that the more abundant species exhibit large amplitude oscillations in their dynamics⁴. This leads us to

⁴Interesting question: is this true across the board, and are their oscillations only large in amplitude because their mean is greater - what is the distribution of CoVs..later in chapter?

hypothesise that the most abundant species may be non-stationary, whereas the least abundant species may be stationary. We test this hypothesis but applying the ADF and KPSS tests to the three most abundant (on average) and three least abundant species in the HI simulation.

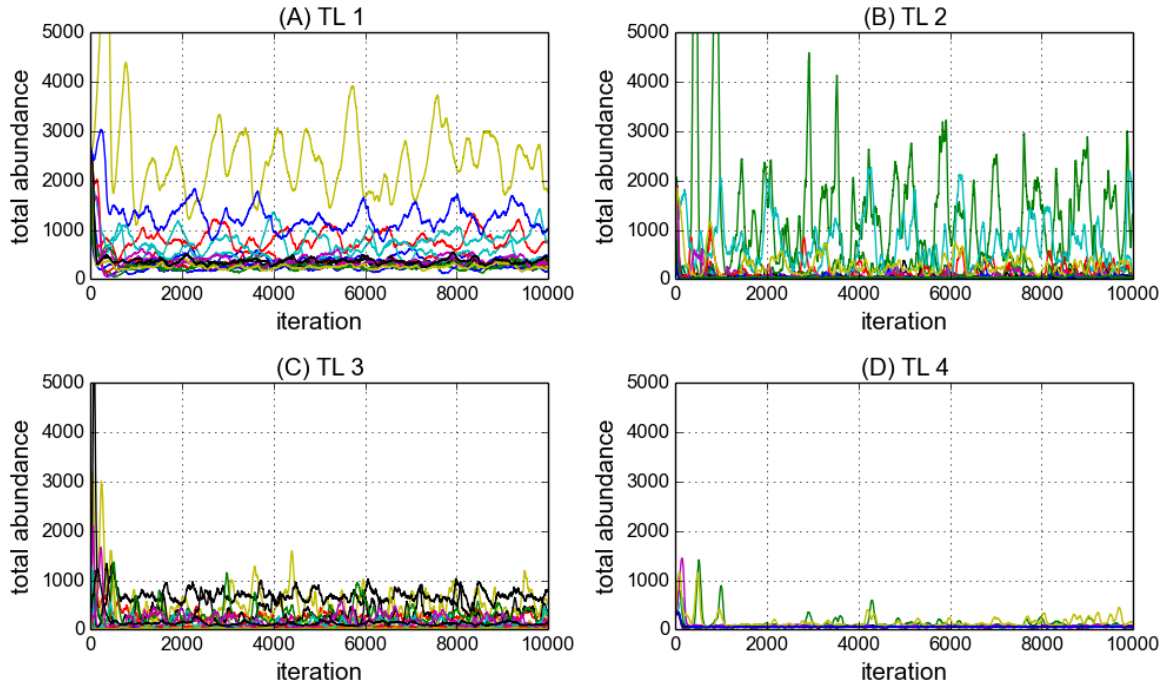
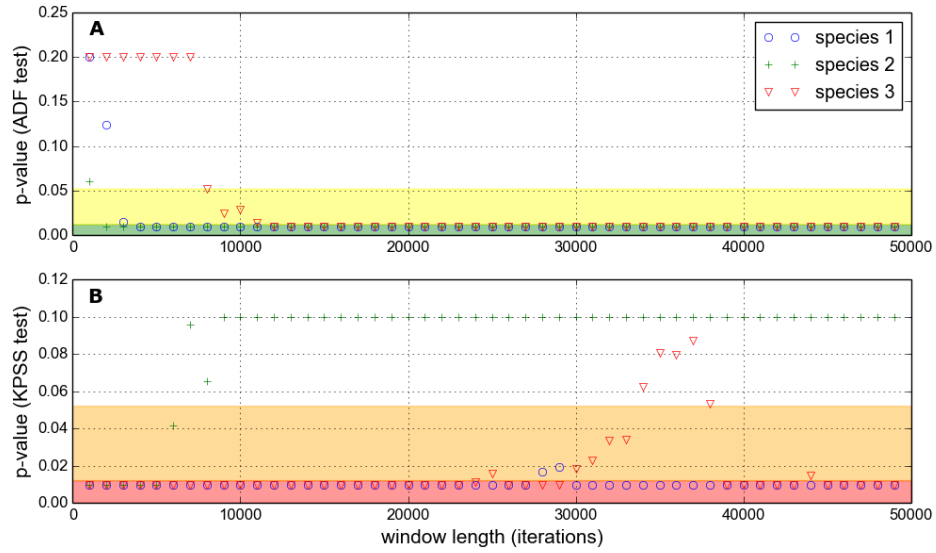


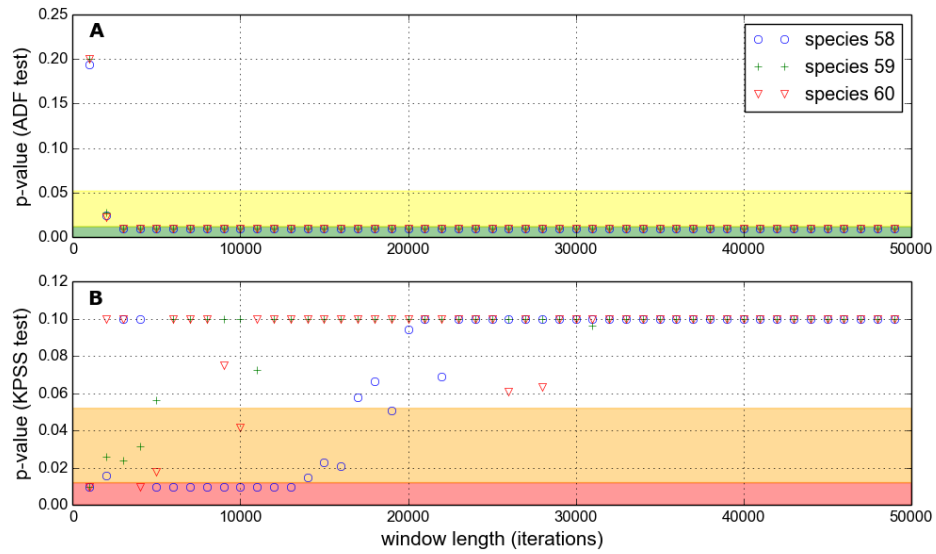
Figure 5.5: Dynamics of every species in the first 10,000 iterations of the HI simulation, broken down by trophic level. Panels (A)-(D) show all the species belonging to each trophic level (TL1 – 4).

We see from figure 5.6 that all six species are stationary according to ADF, given sufficiently large sample size. However the sample size for all three abundant species to be stationary is greater ($\sim 10,000$ points) than for the least abundant species. This suggests that the most abundant species are indeed ‘less stationary’ than the least abundant species. The KPSS test supports this conclusion. KPSS finds all the least abundant species are stationary above sample sizes of $\sim 18,000$, whereas two of the most abundant species are non-stationary for almost all sample sizes. (WHICH SPECIES CORRESPOND TO FIGURE 5.5??).

In general we conclude that the choice of which metric to use....what do they tell us..what to watch out for...



(a) Three most abundant species



(b) Three least abundant species

Figure 5.6: Similar to figure 5.2, but here the tests are applied separately to individual species from the HI simulation. (A) The abundance time series of three species with highest average abundances. (B) The three species with lowest average abundance.

5.3 Ensemble simulations and NM1

The above tests are now applied to ensembles of simulations runs....We ran ensembles with HI and LI and also 50 repeats with the same network....(copy/remove this repeated text from previous section...) We run 100 repeats of long 50,000 iteration simulations, for the base case of zero HL and no mutualism. This is done for a high level of IR (0.001) and a low level of IR (0.0001). We will refer to these two cases here as high immigration (HI) and low immigration (LI) respectively.

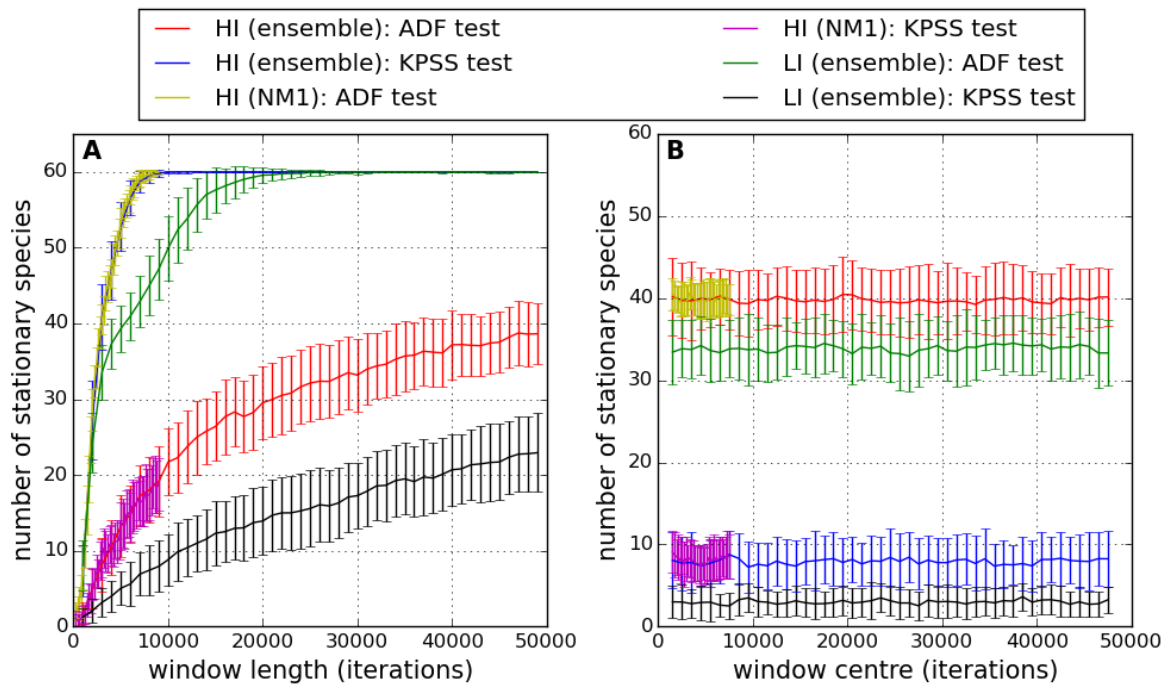


Figure 5.7: The number of stationary species according to the two stationarity tests (ADF and KPSS), averaged over three different ensembles of simulations: HI(ensemble); HI(NM1) and LI(ensemble) as described in the text. The first two are high immigration runs, whilst the latter is low immigration. Solid lines indicate the mean results for the ensemble, and error bars indicate ± 1 standard deviation from the mean. (A) Each species abundance time series is sampled with a window of increasing length, as in figure 5.6. (B) Each species series is sampled with a window of length $wl=3000$, which is scanned along the series as in figure ???. For both tests results are interpreted at 95% confidence interval.

Which of these figures goes first??

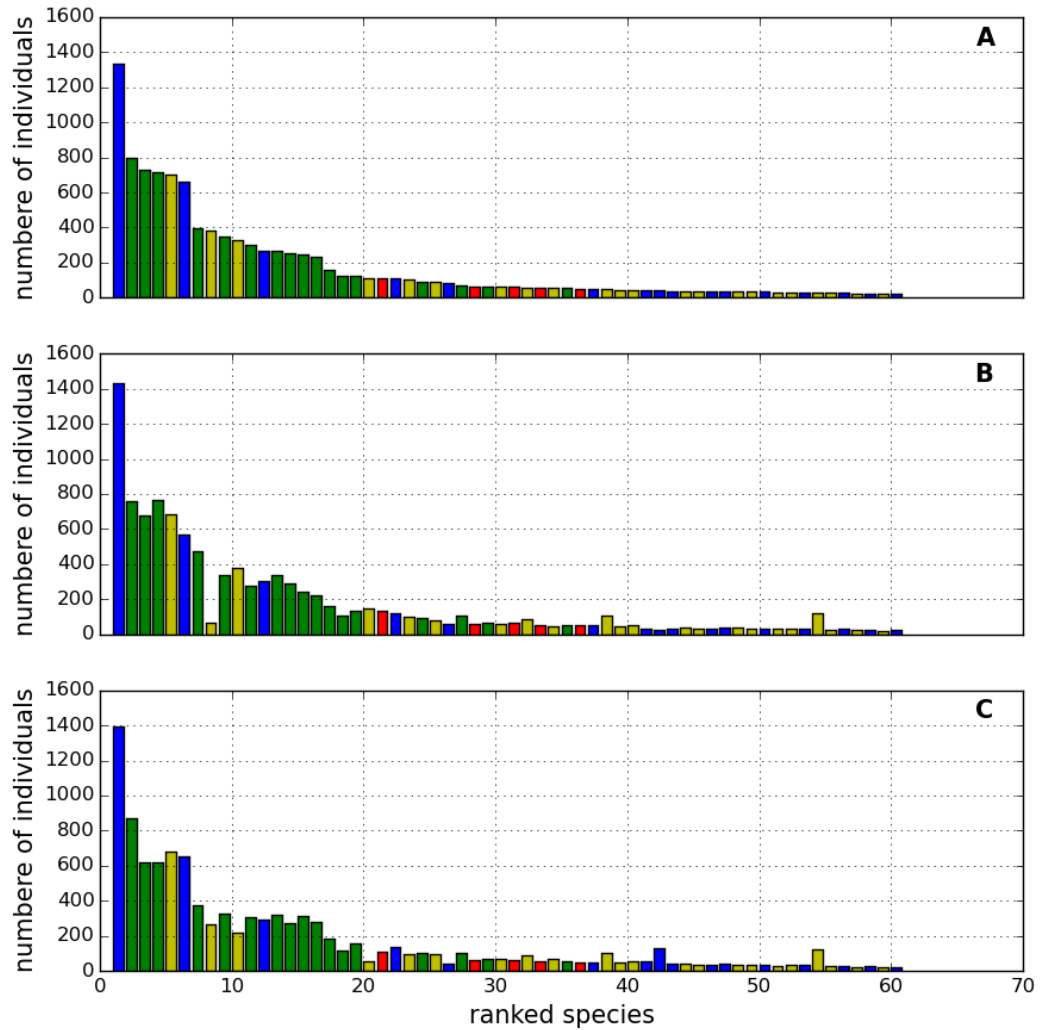


Figure 5.8: Rank abundance spectra (RAS) for three simulations run using the interaction network NM1 (see text). Species abundances are measured by taking the mean abundance over the final 1000 iterations of the simulation. The species are ranked according to their abundances in the first simulation (panel (A)). This ordering is retained in panels (B) and (C), which represent different simulations. Colouring of species by trophic level is consistent with previous figures.

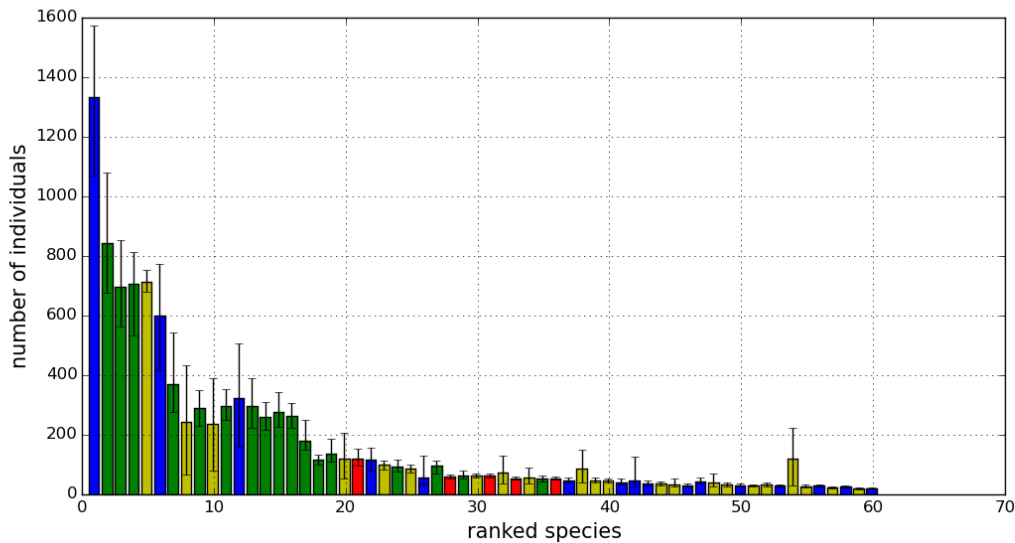


Figure 5.9: The average rank abundance spectrum (RAS) for the ensemble of 50 simulations run using interaction network NM1 (see text). Species abundances measured as in figure 5.8, and ranked as in panel (A) of that figure. The main bars indicate mean abundance values, whilst the error bars indicate the minimum and maximum abundances over the ensemble.

5.4 Chaotic dynamics?

Although in many cases a statistical steady-state appears to be reached, there are complex dynamics and fluctuations within that state (see section ??). Here we look at if these are due to noise or deterministic dynamics. We follow work presented by Saul in his PhD thesis [3]. We also draw inspiration from the demonstration that plankton communities may undergo chaotic dynamics - [1], and their focus on the Lyapunov exponent.

5.5 Discussion

This behaviour may or may not be seen in real communities - chaotic dynamics have been demonstrated in plankton, how about terrestrial ecosystems? However we come back again to limitations - snapshot measurements are taken - with replicate in time. Average over these? Check for differences between them - what is the actual procedure? Can we comment here?

Computationally we should perhaps compare the approaches of taking snapshots and averaging over many iterations...DISCUSS WITH ALAN.

Other question - does it reach the same steady-ish state every time? Is it always the same species that dominate/just bubble along.

PERSISTENCE IN CLOSED COMMUNITIES

TODO: These results also have trophic links between bottom and top levels. Need to re-run these simulations? TODO: Come back to this chapter having done work on stability... e.g. Are the persistent communities stationary? TODO: Look at Thilo's reference on constructing stable GLM topologies (distinct pairs approach..)

TODO: Are the 'good net' persistent net works here stationary?? TODO: Find smaller stationary networks (4-10 species, and fit GLV!!) [w or w/o immigration] TODO: Finish All chapters on the IBM!!

6.1 Motivation

At the beginning of chapter 4 we saw that species persistence is low in communities without immigration (figure ??). We defined the term *community collapse* as the extinction of all non-basal species from the landscape. With a zero immigration rate (IR) antagonistic communities collapsed in all simulations, whilst mutualistic communities ($MAI = 0.5, 1.0$) sometimes show persistence of a few species in higher trophic levels. It appears that our model struggles to produce stable and persistent communities without immigration. This may also be the case in the real-world. It certainly appears that immigration plays an important role in shaping natural communities [REFS]. In the previous chapter we saw that the IR can alter the structure of simulated communities and affect how they respond to habitat loss. In this chapter we fix the IR at zero, and explore other factors contributing to the stability of simulated communities. In particular we ask whether it is possible to obtain stable and persistent communities without immigration. We begin with a discussion (section 6.2) on the concept of stability and why it is

important in ecology. We then explore how certain model parameters¹ impact on persistence (Section 6.3), and ask what role is played by the structure of the interaction network (section ??).

6.2 Stability in ecology

Stability as a fundamental property of ecological community? - but we do not know how they manage to be stable - our mathematical representations do not always suggest that they are stable - examples. Also do not even really know in which ways they are stable, and to what extent they are - there are clearly points of instability - mass extinctions, community collapse...

Stability is an important concept in ecology. However there is no single coherent definition that ecologists use. In the work up to this point stability has been a key consideration - we have defined, and used in our analysis, a number of different metrics relating to it. In what follows we explicitly compare the different stability concepts used in ecology. Before going into the details we note the key point that real-world ecosystems generally appear to be stable, in some sense. A lack of stability may suggest wildly varying population dynamics, extreme responses to extrinsic disturbances, or the extinction of species, depending on your definition of stability. Although there are examples of these phenomena in nature (e.g. spring bloom in plankton abundances, desertification, mass extinction events), luckily they are the exception not the norm. Therefore stability has become a key property of ecological communities (and meta-communities) that we must try to understand.

To include here:

- Influence of dynamical systems (population modelling) - Lyapunov stability. Steady-state/Equilibrium assumption vs Plasticity, adaptivity.
- Limitations with what can be measured in the field. Other metrics used instead:
- Resilience, Robustness, Persistence, Temporal variability.
- Spatial stability metrics (alpha,beta,gamma). Issue of scale. [?]
- Immigration as an important mechanism behind stability/persistence - see previous chapter
- Competitive exclusion
- Network structure as a contributing factor to stability (large body of literature, also hybrid-networks)
- Biodiversity thought to be good for stability - insurance hypothesis [ref], others?
- Functional stability - see iee paper. Is this a widespread concept?

¹We could include more parameters in this analysis e.g. synthesis ability

Argue that the metric/concept of stability used depends on the context/questions you are asking. Here we choose to focus mainly on persistence and on species extinctions. Specifically we try to overcome the problem that most non-plant species go extinct with there is no immigration.

Resilience

Robustness

6.2.1 Dynamical systems and stability

The mathematics of dynamical systems has made a major contribution to the field of ecology, and the paradigm of an ecological community as a complex dynamical system remains prevalent amongst theoretical ecologists. As discussed in section ??, there are some theoretical ecologists who question the use of the concept. In this context stability has a rigorous meaning that relates to the dynamics of the mathematical system. This stability concept is often referred to as dynamical stability or asymptotic stability, and is derived from the eigenvalues of the linearised system close to equilibrium. Conceptually it tells us if the system will return to the equilibrium if perturbed a small way. Related concepts tell us...[?]]

[?] - complexity versus stability debate. Random matrix theory. Important misinterpretation of his equation..

[?] - the ensemble of possible networks scales combinatorially with number of species. Variation in interaction strengths is shown to destabilise large networks. For a 50 species network probability of stability is $\sim 10^{-3}$ with connectance 0.1. This suggests that our sample size for repeat simulations is very small indeed. (Does it explain why dynamics without immigration is unstable?)

6.2.2 Network structure and stability

The popularity of the network perspective in community ecology makes it natural to ask what effect the interaction structure has on stability. This question represents a large body of literature. As we saw, the dynamical systems approach makes explicit the relationship between network structure and stability (section ??). This is not so easy with natural communities and empirical data..for various reasons..lack of information, do not have knowledge of underlying dynamics, unclear if there is an underlying dynamic model with fixed stability [REFs]. Therefore some community properties must be understood in terms of plasticity...

As discussed in section ??, the bulk of network ecology has focussed on networks of single interaction types. The same is true when it comes to stability. The general consensus has been that the properties conferring stability on antagonistic and mutualistic networks differs. This is discussed in the introduction.

[?] simulated 7200 mutualistic and trophic networks, with varying diversity, connectance, nestedness, and modularity. During simulations species become extinct, which changes the initial network structure, and therefore changes these metrics also. Results confirmed by looking at empirical networks. Attributed to perhaps indirect effects: apparent competition and apparent facilitation.

[?] later shows that these findings do not hold when combining interaction types into a single network.

[?] and [5] ...

[?] - experimental manipulation of strong and weak interactors.

6.2.3 Spatial stability

alpha beta gamma stability metrics?? ref??

6.3 Model parameters versus persistence

We first attempt to improve the persistence of our simulated communities by varying certain model parameters. The parameter space of the model is large (see table ??), therefore we do not attempt to explore all of it. Previous work by Lurgi et al. [5] in developing the model has ensured the realism of the bio-energetic parameters (where possible they are derived from literature - more on this). Therefore we restrict our exploration to the region of the default parameters. It may be that there exists somewhere a region of stable coexistence of all species for zero IR. If there does, we will not find it. However we may attempt to improve persistence and assess the impact of varying sensibly chosen model parameters.

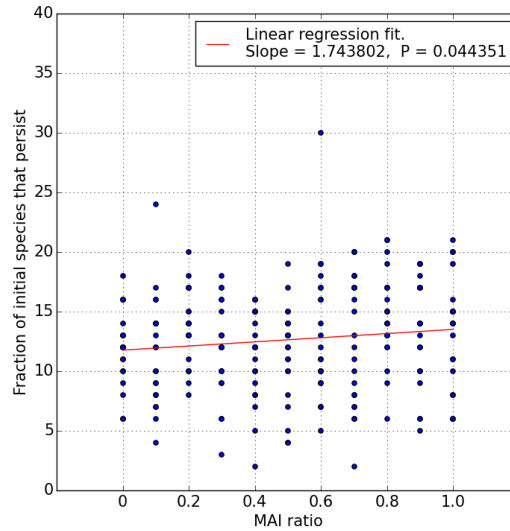


Figure 6.1: Species persistence is plotted for 22 repeat simulations at each MAI ratio. Persistence is measured as the fraction of the initial 60 species that have not gone extinct by the end of a simulation (5000 iterations). Each blue dot gives the number of persistent species for a single simulation. The red line shows a linear regression fit with slope and p-value given in the inset.

6.3.1 Mutualistic to antagonistic interaction (MAI) ratio

A key theme throughout this thesis, and one of the main novel aspects of this research, is the inclusion of mutualistic interactions into simulated trophic dynamics. In some cases we have seen that these mutualistic interactions play a stabilising role in the community (in contrast to May’s classic ‘orgy of mutual benefaction’). Therefore it seems natural to ask what role the MAI ratio plays in the persistence of communities at zero IR.

Figure 6.1 shows that there is an increase in overall species persistence with MAI ratio. Although the trend is statistically significant it is small, with an expected increase of about twelve

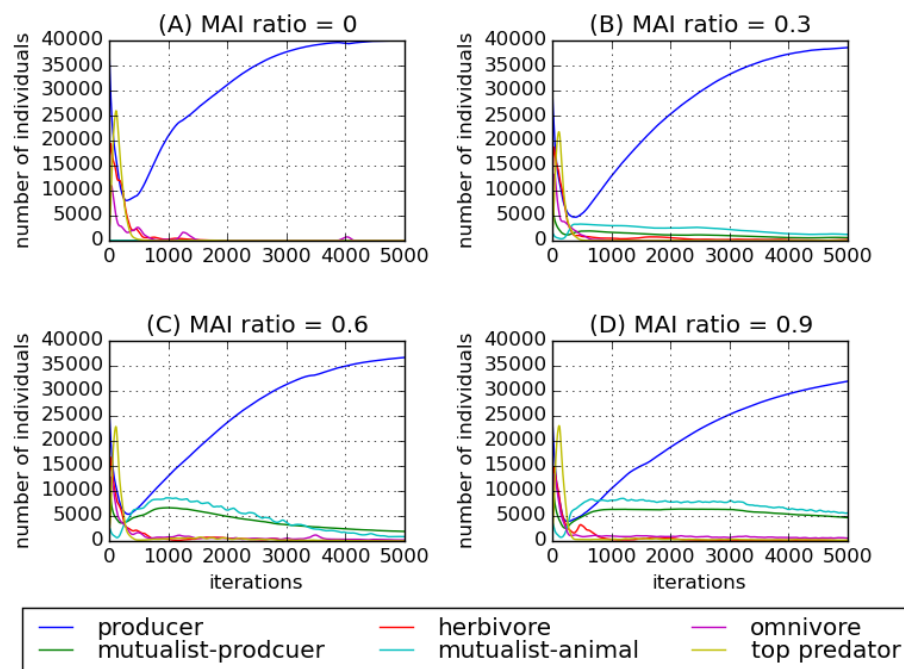


Figure 6.2: Mean dynamics by functional group for four different MAI ratios. The coloured lines represent the abundance dynamics of the different functional groups, as indicated in the legend. Abundance at each simulation iteration is measured by the total number of individuals belonging to all species of a given functional group.

to fourteen species over the whole range of MAI ratios. For antagonistic communities ($MAI = 0.0$) we know to expect community collapse. This is observed in figure 6.2, which shows the expected abundance dynamics of each functional group (FG). In panel A we see that the abundance of producers rises to fill the whole landscape ($200 \times 200 = 40,000$), whilst the abundance of all other FGs is at or near zero. From the other panels (B-D) we see that increasing the MAI ratio particularly benefits the mutualistic species (both producers and animals) as expected, and appears to also confer some benefit to members of the other FGs. Ecologically this makes sense - if mutualism strongly benefits mutualistic species, it will also benefit those species that feed on them. (It also appears that increasing the MAI ratio increases the time taken to reach steady state - the abundance of producers in panel D is clearly still rising.)

As we have seen previously (sections ??, ??) the MAI ratio affects community composition as measured by the relative abundances of the FGs. Figure 6.4 shows us that the relative abundance of non-mutualist producers falls sharply as the relative abundance of mutualist species, both plants and animals, increases. It appears that the mutualist-producers outcompete the non-mutualists, thanks to the benefit gained by a plant in switching to mutualism (section ??). Interestingly this also benefits the mutualist-animals, but not the herbivores, which show no

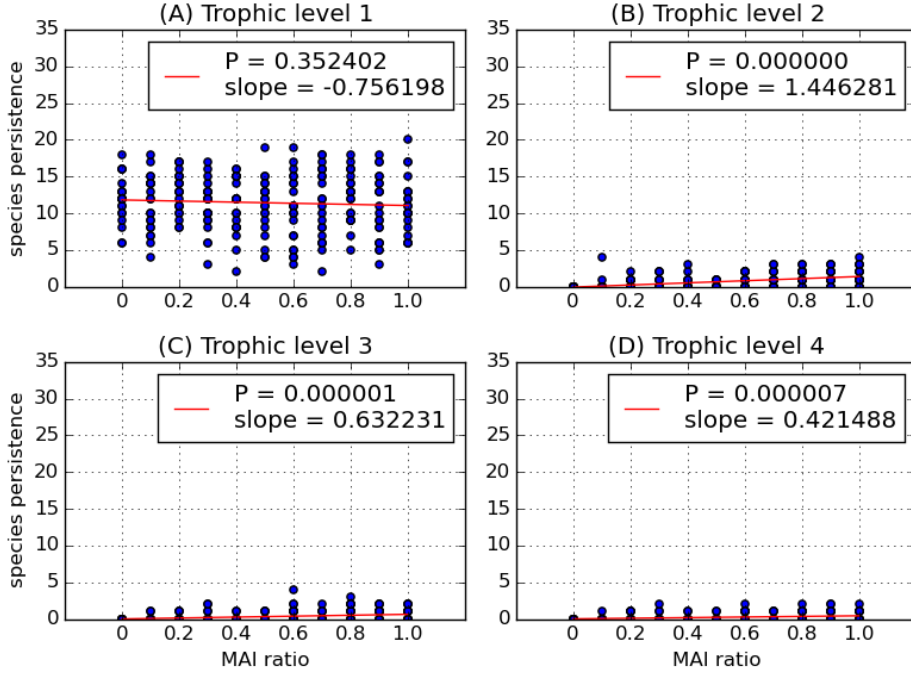


Figure 6.3: Species persistence by trophic level over a range of MAI ratios. Each blue dot corresponds to the number of remaining species from that trophic level at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. The red lines show linear regression fits, with slopes and p-values given in the insets.

significant increase in relative abundance².

Despite the changes in the distribution of abundances, there is little change in the species richness of each trophic level. Figure 6.3 shows that the overall increase in species persistence is due to an increase in the species richness from zero to about one or two, in trophic levels two, three and four (panels B,C,D). We may have expected a greater increase in persistence, especially in the second trophic level, where the expected absolute and relative abundance increases considerably. The fact that less than two species are expected in this trophic level at $MAI = 1.0$ suggests that either competition or stochastic effects are important³ here.

²perhaps there is competition between these two FGs? Would have thought that those herbivores which feed on mutualistic plants would benefit from their increased availability? - only in absolute numbers, some suggestion of this in panel D of figure 6.4. Why do they then die out?

³Since cannot recover from extinctions.

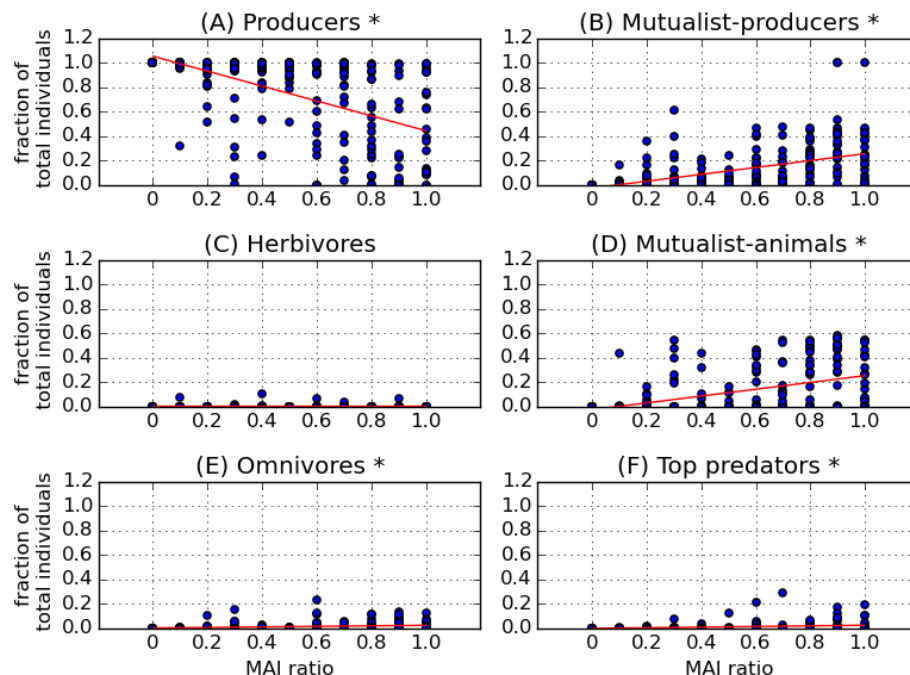


Figure 6.4: Relative abundance (RA) by functional group for a range of MAI ratios. RA is measured as the fraction of the total individuals that belong to a given functional group. Each blue dot corresponds to the RA at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. Red lines show linear regression fits. Panels marked with an asterisk * (A,B,D,E,F) have fits with p -value < 0.0001 .

6.3.2 Reproduction rate (RR)

The problem of low persistence in high trophic levels remains. Mutualism has some small effect, but even at $MAI = 1.0$ we expect only one or two species on average in the non-basal trophic level. The initial transience in the abundance dynamics (figure 6.2) is characterised by a sharp decline in plant abundance (mutualist and non-mutualist), which reaches a minimum and then rises again. It was hypothesised that this overconsumption and therefore limited availability of plant individuals, causes many of the extinctions. Indeed in these simulations $\sim 85\%$ of the extinctions occur during the first 500 iterations. Therefore we look at the possibility of improving persistence by increasing the reproduction rate (RR). This parameter defines that rate at which non-mutualist producers reproduce (via the wind-dispersal mechanism, see chapter ??). Therefore this increasing this mechanism should improve the availability of plant biomass in the system, with potentially cascading effects. The RR parameter does not affect mutualist-producers, which only reproduce via their interactions with mutualist-animals and not via wind-dispersal.

Simulation results are presented for $MAI = 0.0$ and $MAI = 0.5$. The main results are as follows:

- Increasing RR increases overall species persistence (figure 6.5). The effect is greater for antagonistic communities.
- The sharp decline in plant abundance during the transience is reduced (figures 6.10, 6.11). As we reasoned, this does results in increased absolute abundances of all FGs at both MAI ratios. This is visible in these figures.⁴
- The relative abundances by FG indicate that top-predators do very well out of the increase in RR (figures 6.8, 6.8). This is due to the flaw in the niche model already discussed.
- As before the increased abundance by FG does not necessarily translate into increased species richness (figures 6.6, 6.7). Again there is a weak trend - increasing the RR by a factor of twenty, results in one or two more species on average in the higher trophic levels. In the mutualistic communities ($MAI = 0.5$) increasing the reproduction rate is bad for persistence in the second trophic level.
- We choose a higher reproduction rate for the further simulations in this chapter because overall it improves persistence in all FGs. It is not unrealistic to improve the reproductive ability of plants. Importantly it does affect the trade-off between mutualism/non-mutualism for plants.

⁴Look at when extinctions occur? Plot cumulative extinctions against time?

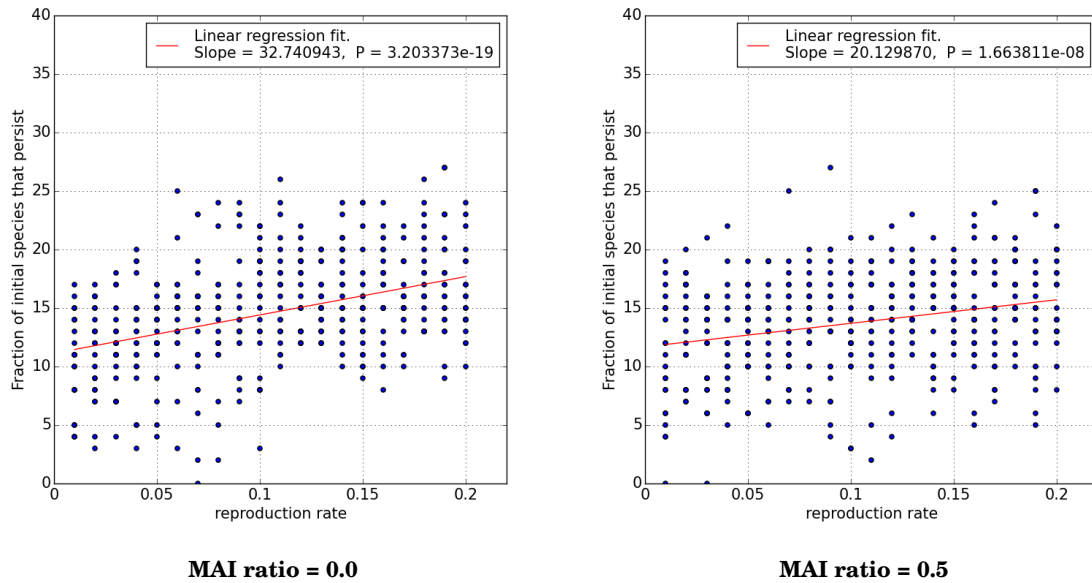


Figure 6.5: Species persistence against reproduction rate (RR), with 22 repeat simulations at each RR. Persistence is measured as the fraction of the initial 60 species that have not gone extinct by the end of a simulation (5000 iterations). Each blue dot gives the number of persistent species for a single simulation. The red line shows a linear regression fit with slope and p-value given in the inset.

6.3.3 Landscape size

Another hypothesis was that spatial competition was causing the community collapse. Simulations run to test persistence response to both the size of the landscape. This was done for MAI = 0.0 and 0.5, with 25 repeat networks at each landscape size. Increasing the size of the landscape should reduce the effect of spatial competition and therefore increase persistence.

The total abundance increases by around 100 fold, as the width of the landscape is increased from 100 to 1000. For MAI=0.0 it goes from 10586 to 1015475 individuals on average. Figures 6.12 and 6.13 summarise the results for antagonistic and mutualistic communities respectively. In both cases there is an overall increase in species persistence with landscape size, driven by small increases in the species richness of all trophic levels. However the effect is small and it does not appear that it would resolve the species persistence problem for a landscape of a size we could realistically simulate. Therefore further simulations use the same landscape size of 200.

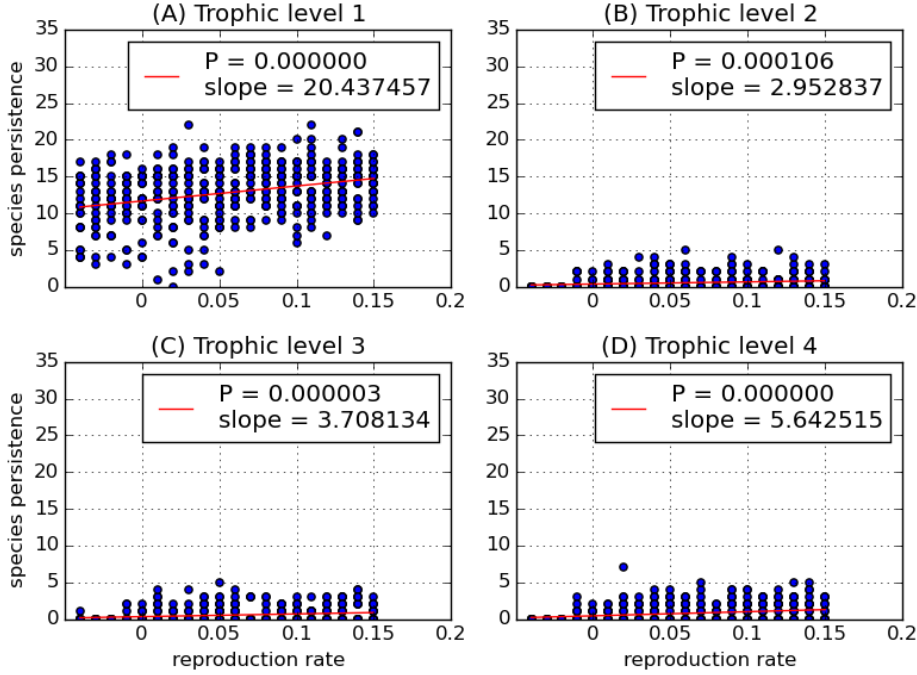


Figure 6.6: **MAI = 0.0**. Species persistence by trophic level over a range of reproduction rates. Each blue dot corresponds to the number of remaining species from that trophic level at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. The red lines show linear regression fits, with slopes and p-values given in the insets.

6.3.4 Number of initial species

All previous simulations have been run with an interaction network and initial species pool consisting of 60 species. We consider the possibility that beginning the simulation with a larger network may result in a greater number of persistent species. (In fact increasing the number of possible interaction networks and therefore making it less likely to find a stable one?).

With more than around 70 species it became impossible to use the network generation procedure (discuss why). Therefore we used the pure niche model, and implemented an algorithm to re-wire niche model networks such that the original trophic constraints could be met. We refer to the pure niche model networks and the re-wired networks as *niche* and *rewired* respectively.

The number of initial species does not appear to effect the total abundance⁵ There is an increase in overall persistence, in the case of the rewired networks. As shown in figures 6.14 and 6.15 this increase is almost entirely due to plants. Therefore this does not overcome the problem that very few species persist at higher trophic level. We are still include to propose that this is

⁵Need to plot this? Could include some plots in an appendix.

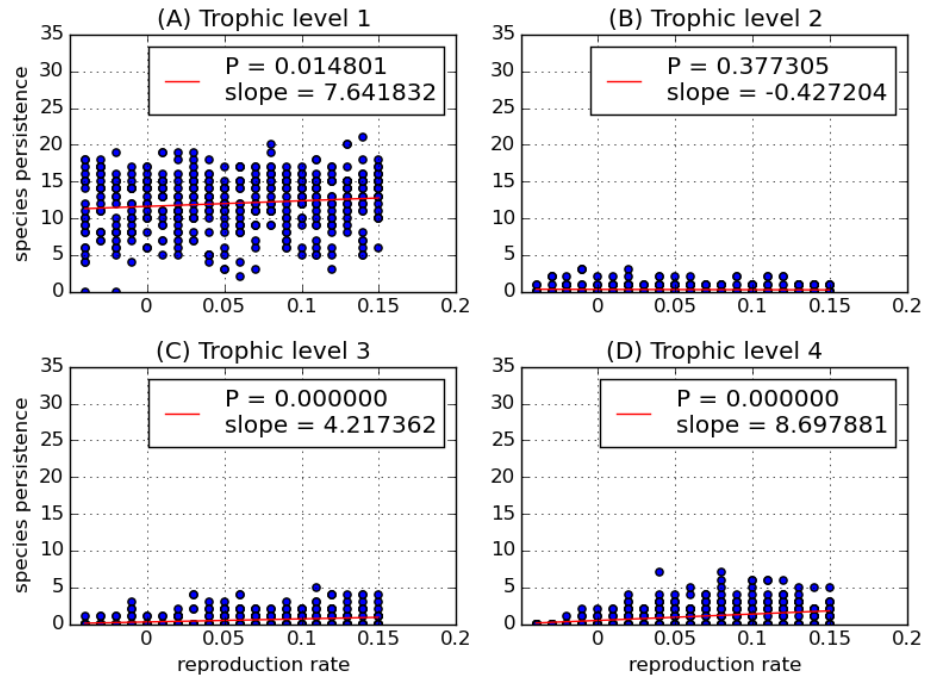


Figure 6.7: **MAI = 0.5**. Species persistence by trophic level over a range of reproduction rates. Each blue dot corresponds to the number of remaining species from that trophic level at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. The red lines show linear regression fits, with slopes and p-values given in the insets.

due to competition, combined with stochastic extinctions during transience.

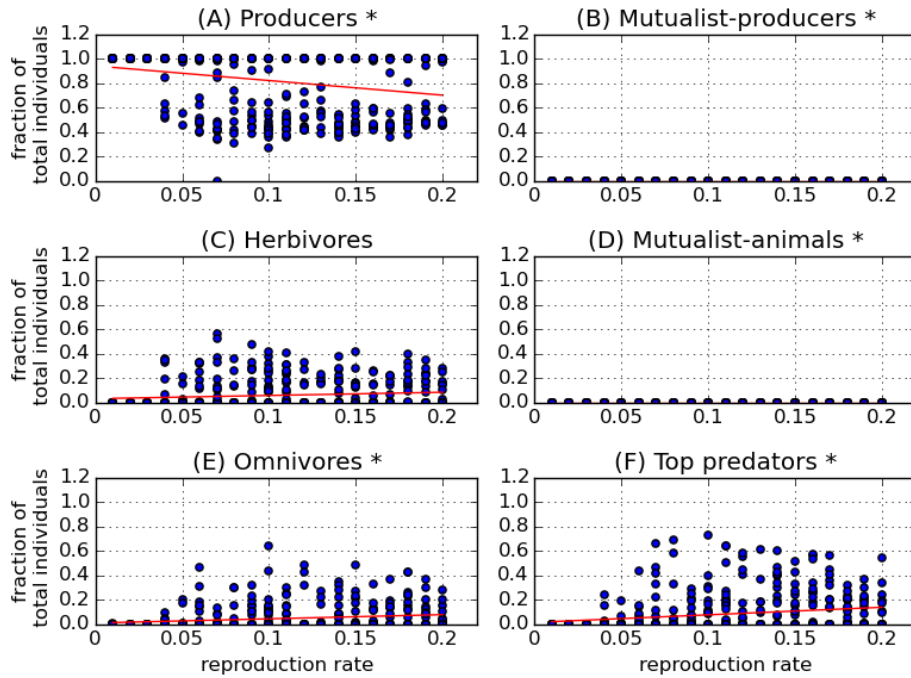


Figure 6.8: **MAI = 0.0**. Relative abundance (RA) by functional group for a range of reproduction rates. RA is measured as the fraction of the total individuals that belong to a given functional group. Each blue dot corresponds to the RA at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. Red lines show linear regression fits. Panels marked with an asterix * (A,B,D,E,F) have fits with p-value < 0.0001.

6.4 Why are some communities more stable than others?

Despite extensive investigation of model parameters persistence at zero IR is remains poor. However in the results presented above one thing stands out - there considerable variation in the results between simulations.

- Is this variation due to noise, or inherent differences between each simulation? (Below we show that it is inherent by repeating simulations with the same network.)
- Therefore the difference must be due to interaction network. Accepted in the field that network structure affects stability (see section 6.2). Is this true in the real world?
- We choose one 'good' and one 'bad' network each with 120 species. Chosen by looking at the 25 repeats and picking the one with the highest/lowest number of species in all trophic levels. We show that this difference between the two networks is repeatable - that there is evidence for a systematic difference between how many species persist and therefore one is better than the other (see figure 6.17).

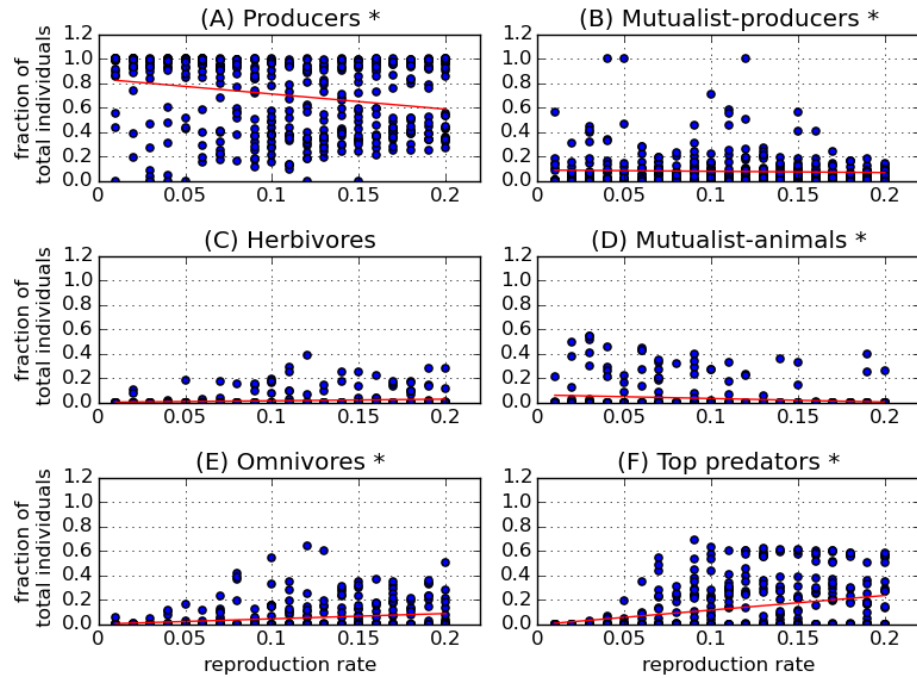


Figure 6.9: **MAI = 0.5**. Relative abundance (RA) by functional group for a range of reproduction rates. RA is measured as the fraction of the total individuals that belong to a given functional group. Each blue dot corresponds to the RA at the end of a single simulation. There are 22 repeat simulations at each MAI ratio, each using a different interaction network. Red lines show linear regression fits. Panels marked with an asterisk * (A,B,D,E,F) have fits with p-value < 0.0001.

We need to extend this analysis and crucially work out **where this chapter is going!**. ToDo:

- Re-do this analysis for 30 species (easier to visualise than 120)
- Look at individual species. Do they go extinct in the same order?
- Look at network metrics that have been associated with stability. E.g. are modular networks more stable?

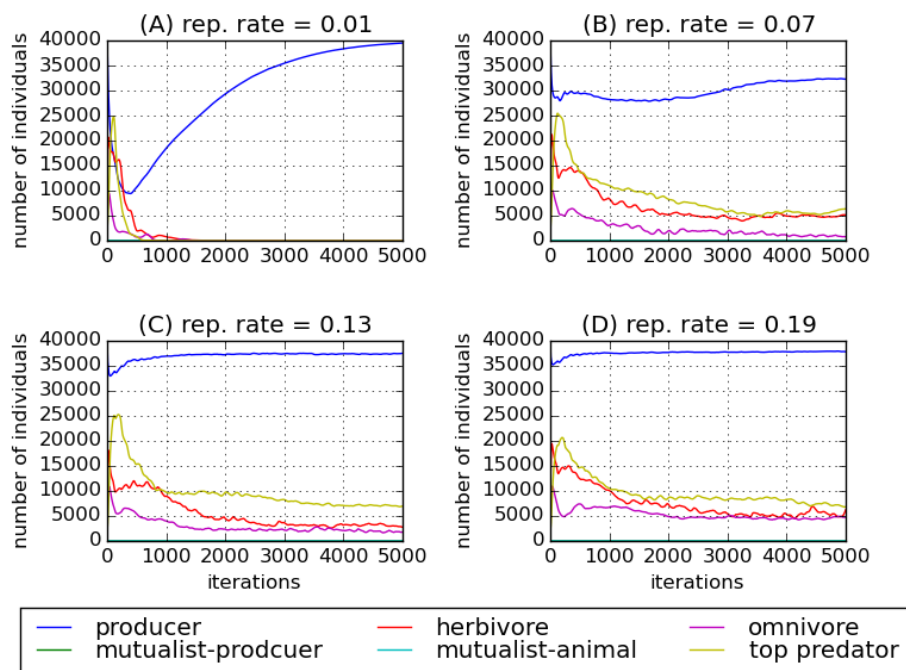


Figure 6.10: **MAI = 0.0**. Mean dynamics by functional group for four different reproduction rates. The coloured lines represent the abundance dynamics of the different functional groups, as indicated in the legend. Abundance at each simulation iteration is measured by the total number of individuals belonging to all species of a given functional group.

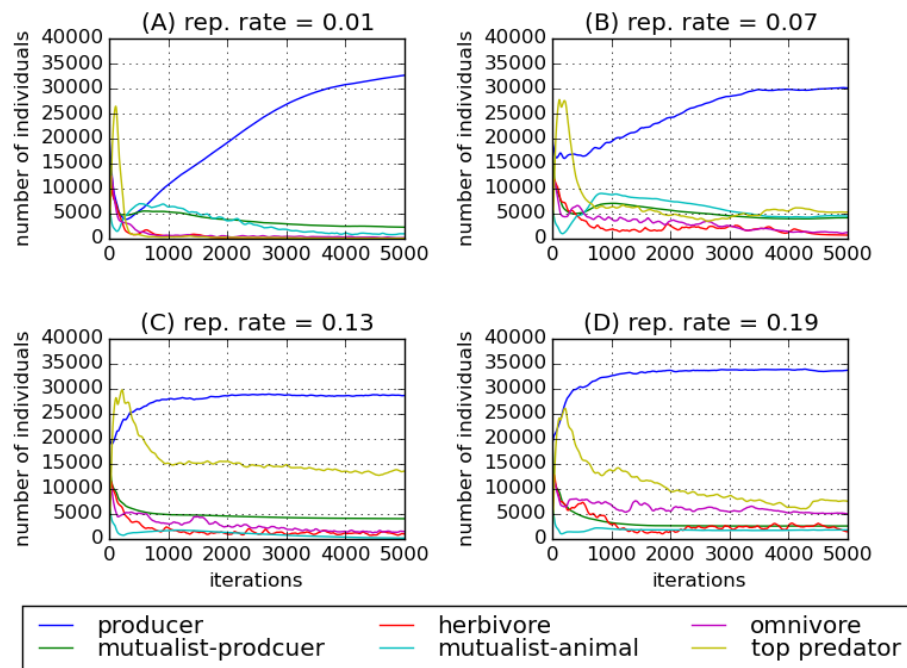


Figure 6.11: **MAI = 0.5**. Mean dynamics by functional group for four different reproduction rates. The coloured lines represent the abundance dynamics of the different functional groups, as indicated in the legend. Abundance at each simulation iteration is measured by the total number of individuals belonging to all species of a given functional group.

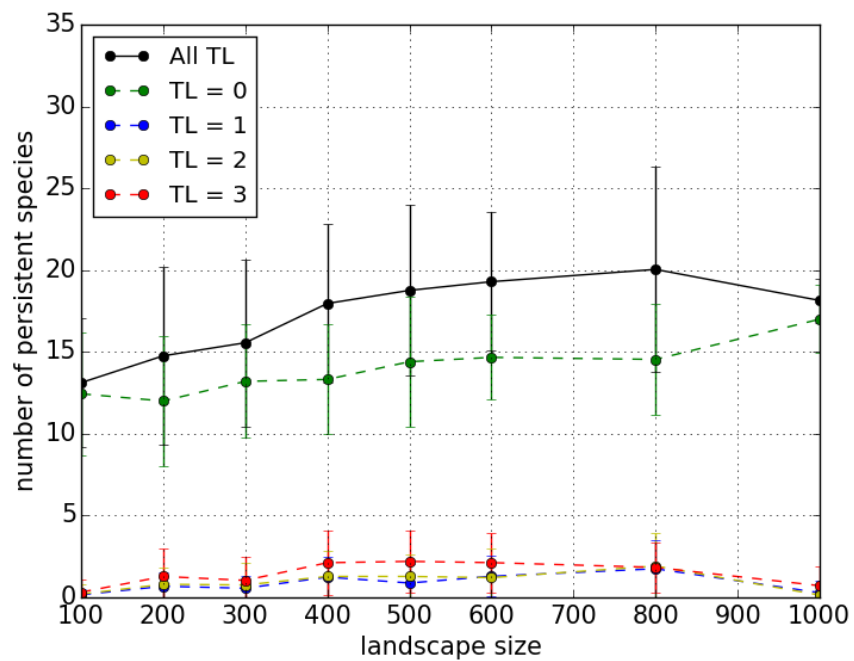


Figure 6.12: **MAI = 0.0**. Landscape size against species persistence, total and broken down by trophic level. The points show the mean value over 25 replicates and the error bars show \pm one standard deviation.

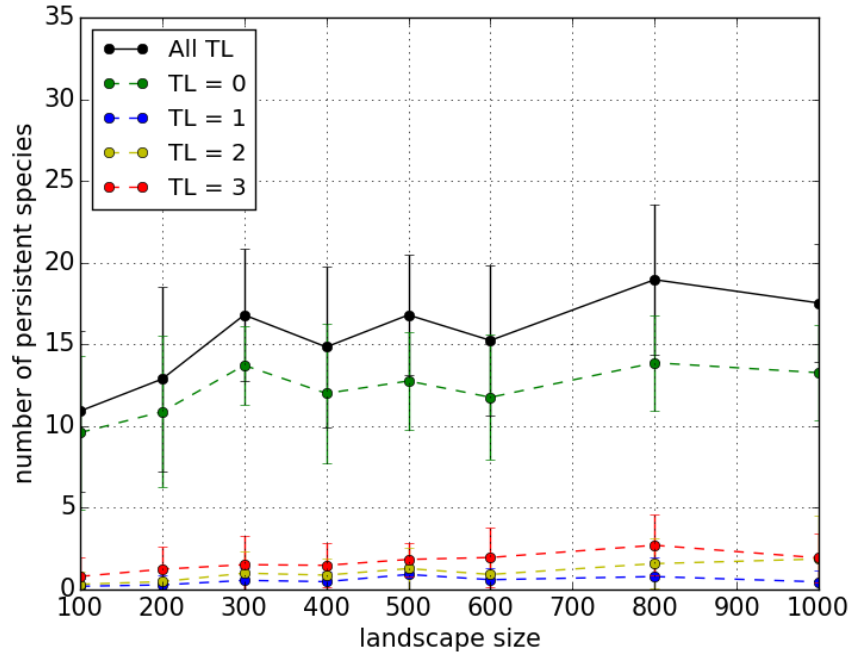


Figure 6.13: **MAI = 0.5**. Landscape size against species persistence, total and broken down by trophic level. The points show the mean value over 25 replciates and the error bars show \pm one standard deviation.

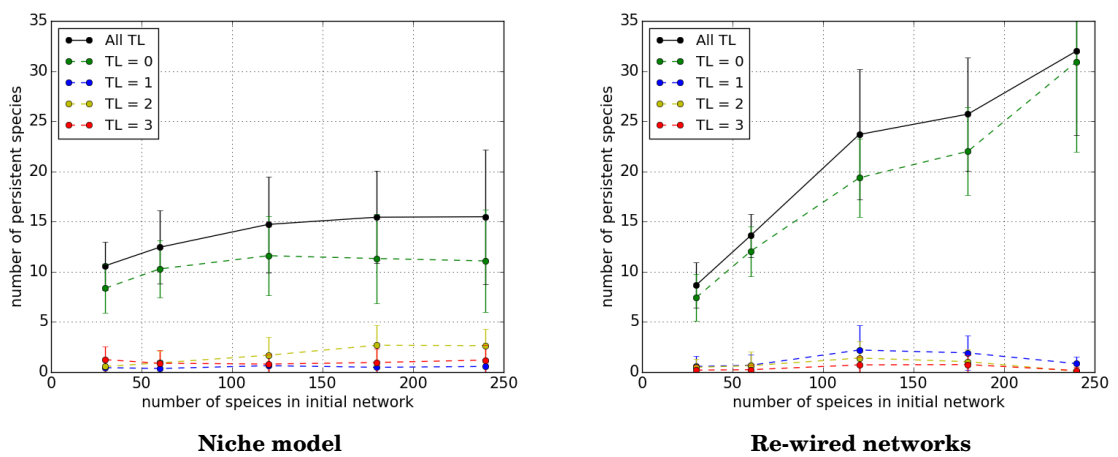


Figure 6.14: **MAI = 0.0**. Number of initial species against species persistence, total and broken down by trophic level. The points show the mean value over 25 replciates and the error bars show \pm one standard deviation.

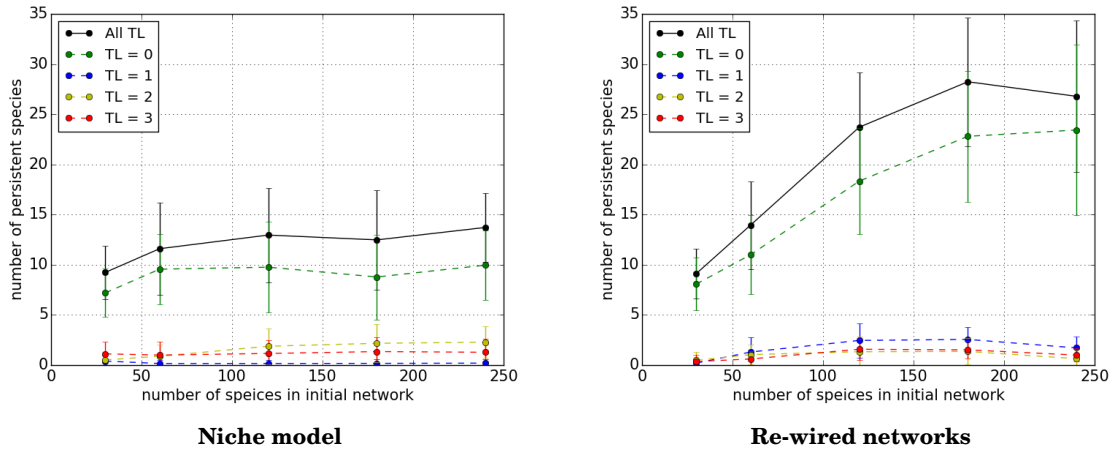
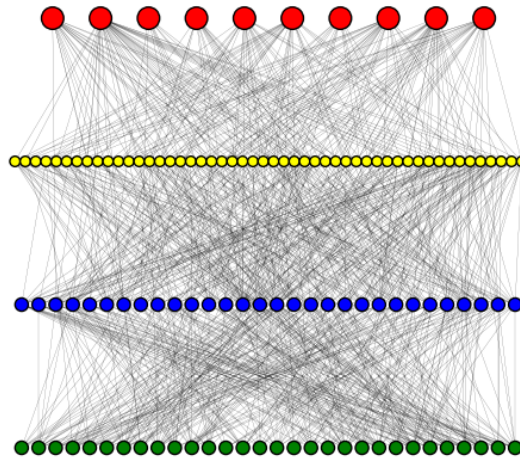


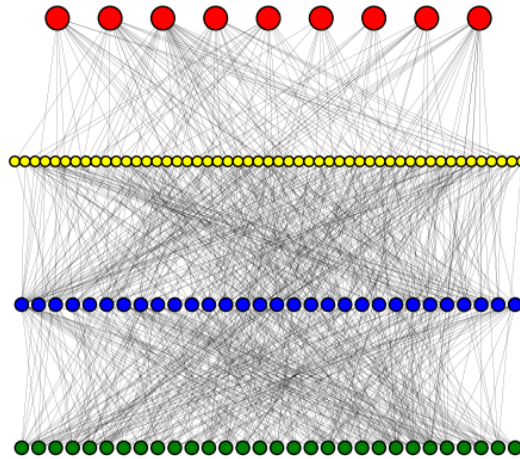
Figure 6.15: **MAI = 0.5**. Number of initial species against species persistence, total and broken down by trophic level. The points show the mean value over 25 replicates and the error bars show \pm one standard deviation.

Example 'bad' network (ID=59). Re-wired from niche model.



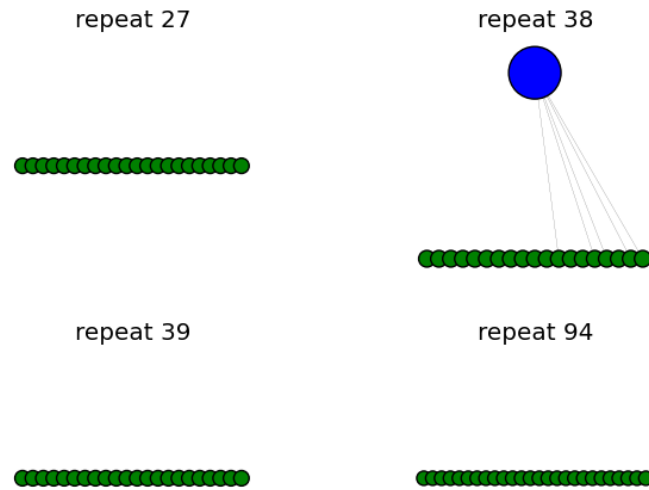
Bad network

Example 'good' network (ID=52). Re-wired from niche model.

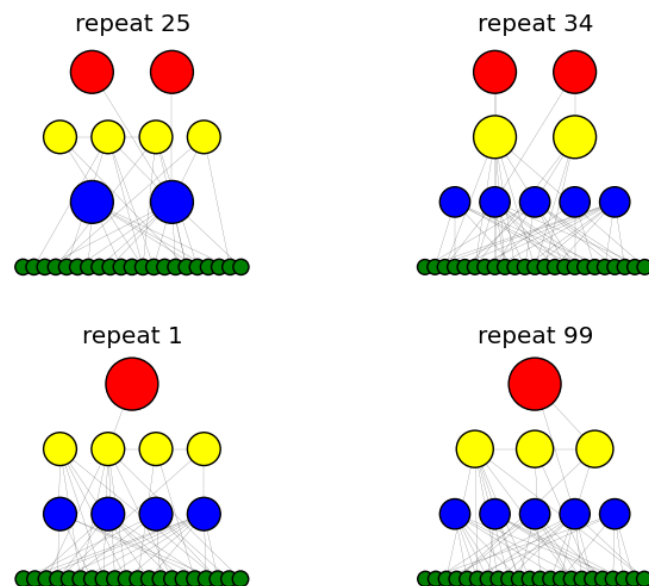


Good network

Figure 6.16: Two 120 species interaction network. One produces better persistence than the other, although in both cases most species go extinct.



Bad network



Good network

Figure 6.17: Examples of the networks of species that remain at the end of a simulation.

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