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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 [27] 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 [26]. 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 [4, 19]. 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 [9, 35]. 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 [9, 34], 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" [5] 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 [36]. 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 [13, 14, 22]. 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 [15] 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 [1, 12, 36]. This can result in detectable changes in community structure, without any detectable change in species richness [35]. 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. [36] 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 [17], 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. [35] 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. [1] 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 [2]. These properties are believed to improve the stability of the community [33]. It has been shown that habitat destruction can push mutualistic networks towards higher modularity, higher connectivity, and lower nestedness, thereby reducing stability [14, 31]. Conversely antagonistic networks tend to be modular in structure, which is believed to promote stability and robustness in these communities [33]. Habitat loss has been shown to destabilise antagonistic communities by lowering modularity and increasing interaction strengths [14]. 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. [20] 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 [22]. Fortuna and Bascompte [11] 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 [21]. 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 [10, 17, 23]. 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. [18]. 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. [28] 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 [25]. 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 [20, 24]. Specifically Lurgi et al. [20] 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. [29] 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 [20]. 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. [7], uses the same empirical network of networks as [28]. They employed a robustness algorithm to determine how vulnerable the

²See suggestions in the text of [29] 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. [20] 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...

[30] - spatially explicit analysis.

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

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

[25] - 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..

[8] - 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 [20] (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 [37] (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).

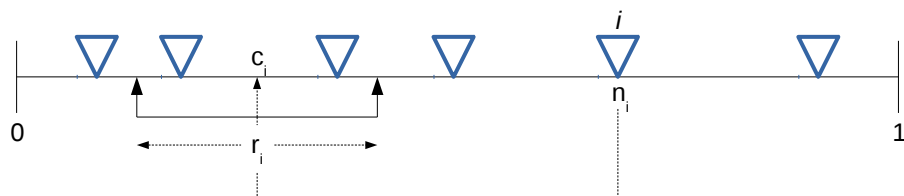


Figure 2.1: A representation of 1-dimensional *niche space* as visualised in the original publication [37], for number of species $S = 6$. The blue triangles represent the placement of species in niche space. The niche value of species i is given by n_i . The width and centre of the feeding range for 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 [37] 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 [6, 32, 37]. 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!

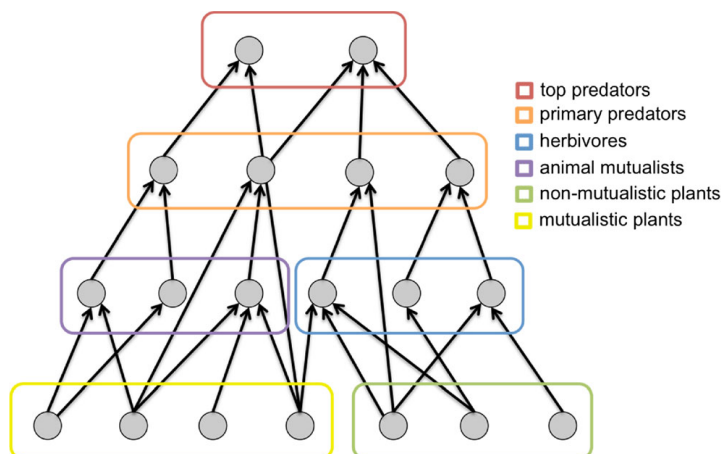


Figure 2.2: Schematic of an underlying interaction network (reproduced from [20]). Nodes correspond to species, and arrows to trophic links (antagonistic or mutualistic), from resource to consumer. The six functional groups of species are colour coded, and named in the legend. In this case there are 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 [20], 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 [20] 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.

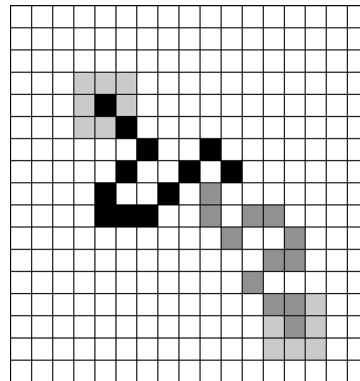


Figure 2.3: Example trajectories and neighbourhoods of two individuals.

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 individuals energy drops below *min_resource*, it is removed form the simulation.

2) Movement

For each individual, a neighbouring cell (distance 1) is selected uniformly at random. If the cell is avaible 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 memebbers 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 neihgbourhood 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 [20] 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 [20]. 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 [20].

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 [7]. 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 [3].

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

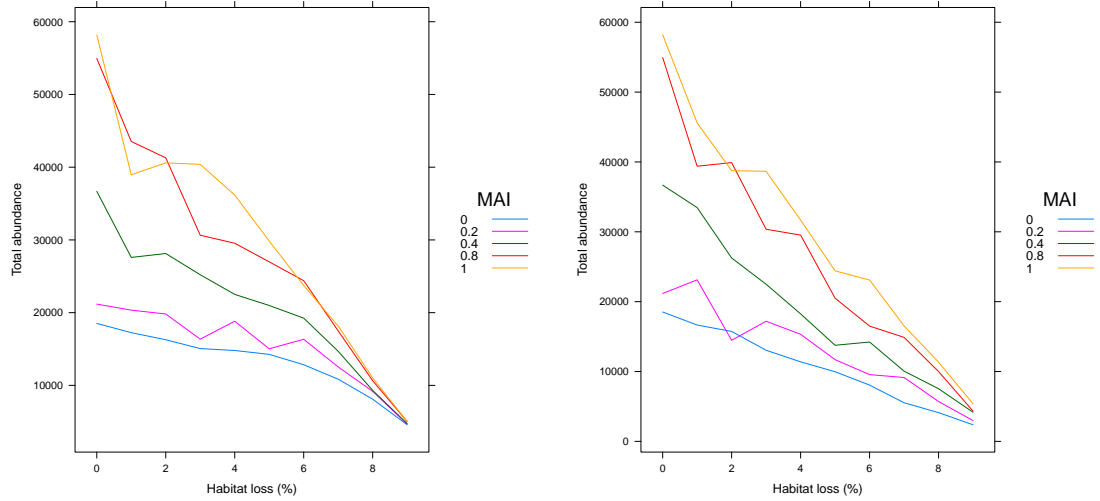


Figure 3.1: **Mean total number of individuals** across replicate communities decreases with habitat loss, for all MAI ratios. Left: random destruction. Right: contiguous destruction.

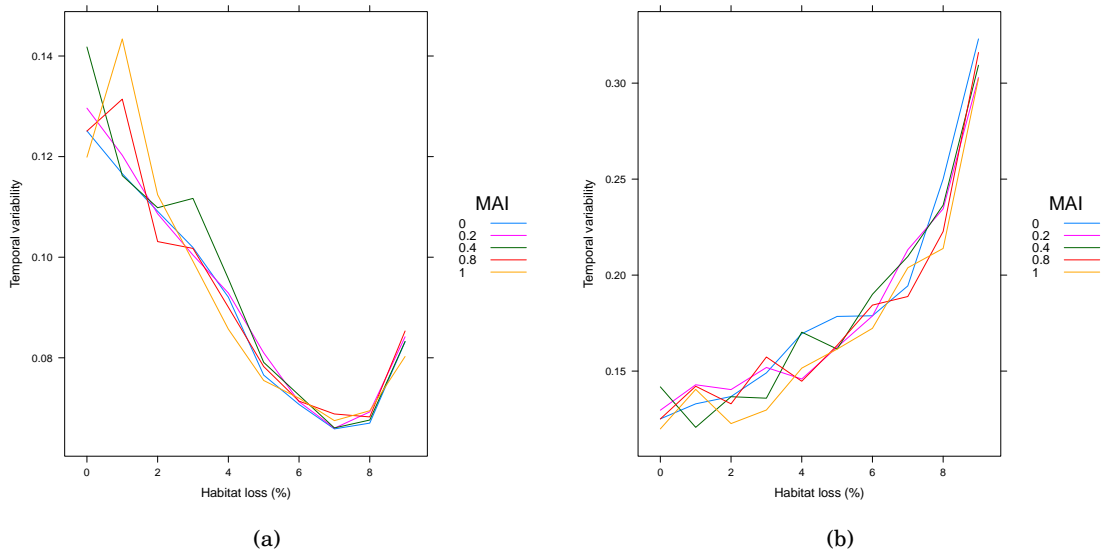


Figure 3.2: **Mean CV in total biomass** across replicate communities against habitat loss for selected MAI ratios. Left: random destruction leads to an increase in temporal stability, as indicated by a decrease in CV. Right: contiguous destruction dramatically reduces temporal stability.

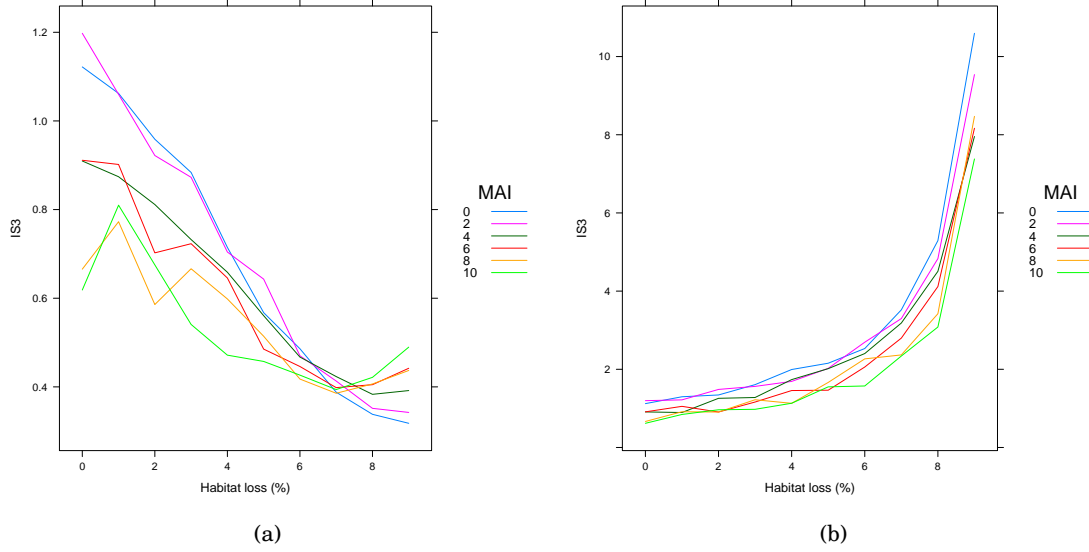


Figure 3.3: Interaction strengths: The sum of the elements of the interaction matrix, averaged over replicate communities, for selected MAI ratios. Left: random destruction reduces total interaction strength. Right: contiguous destruction dramatically increases total interaction strength.

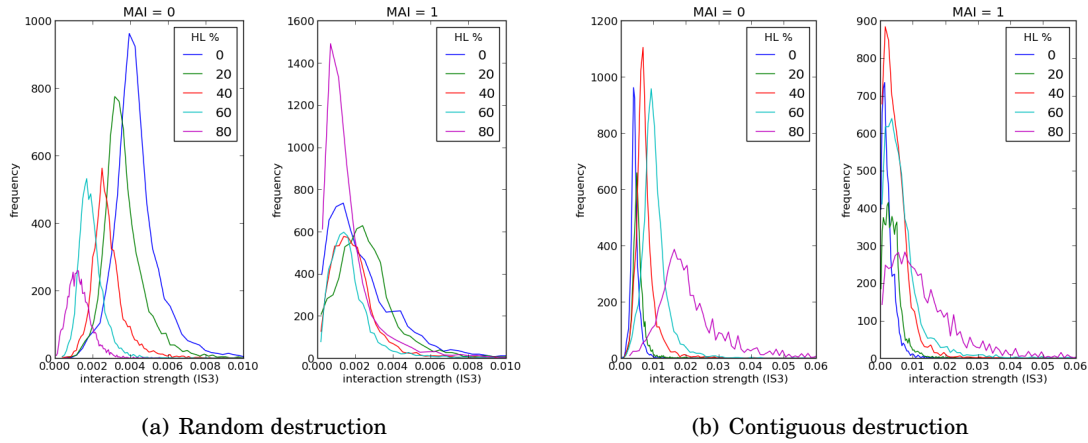


Figure 3.4: IS3 distributions: The interaction strength distribution shifts leftwards for random habitat loss, and rightwards for contiguous loss. The extent of this shift is mediated by MAI ratio - it is most visible for MAI= 0, and least visible for MAI= 1.

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.

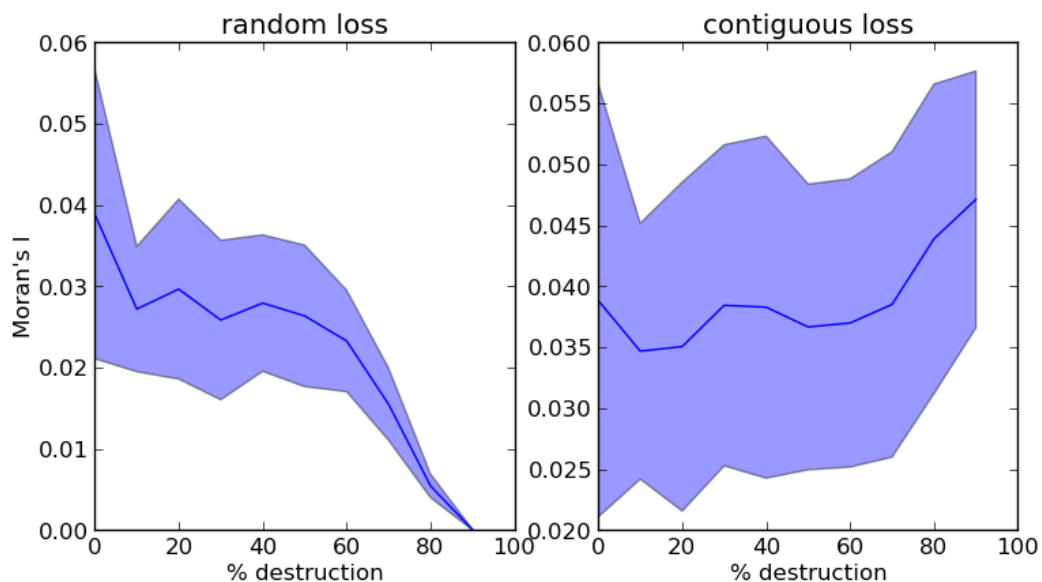


Figure 3.5: **Spatial autocorrelation:** Moran's I is calculated for all species distributions and averaged over the community. These plots show the results averaged over all replicates and over all MAI ratios. Solid lines indicate the mean value, and shaded areas indicate ± 1 standard deviation. This 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 [3, 38]:

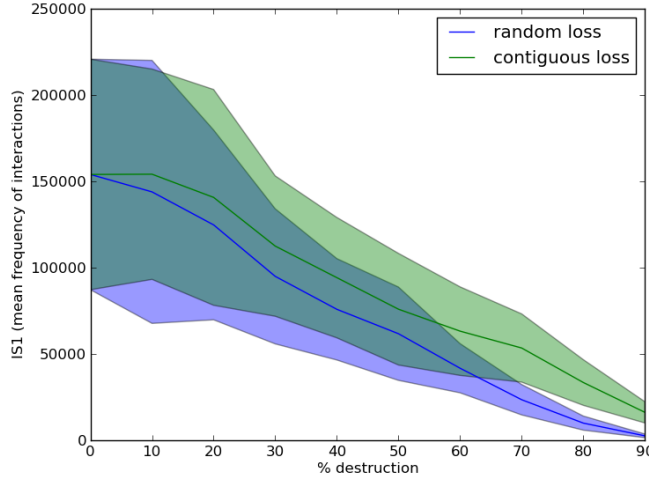


Figure 3.6: **Interaction frequencies:** The metric for interaction strength IS1 averaged over all replicates and all MAI values. This metric is the sum of the elements of the interaction frequency matrix i.e. the total number of interaction occurring within a given period of time. Solid lines indicate 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

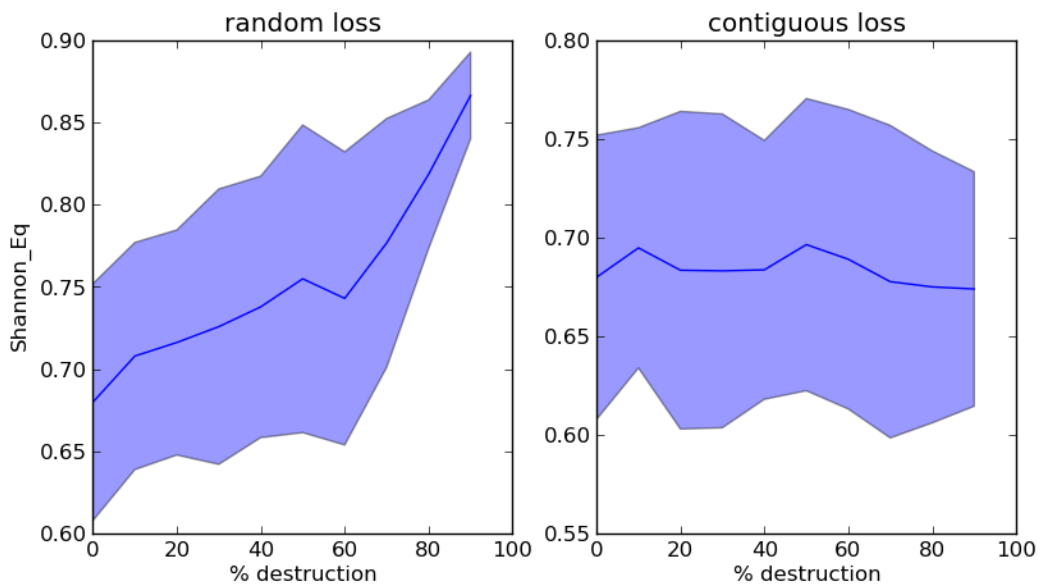


Figure 3.7: **Shannon evenness:** average over MAI ratios and replicate communities. Under random habitat destruction communities on average become more even. Under contiguous destruction there is no change.

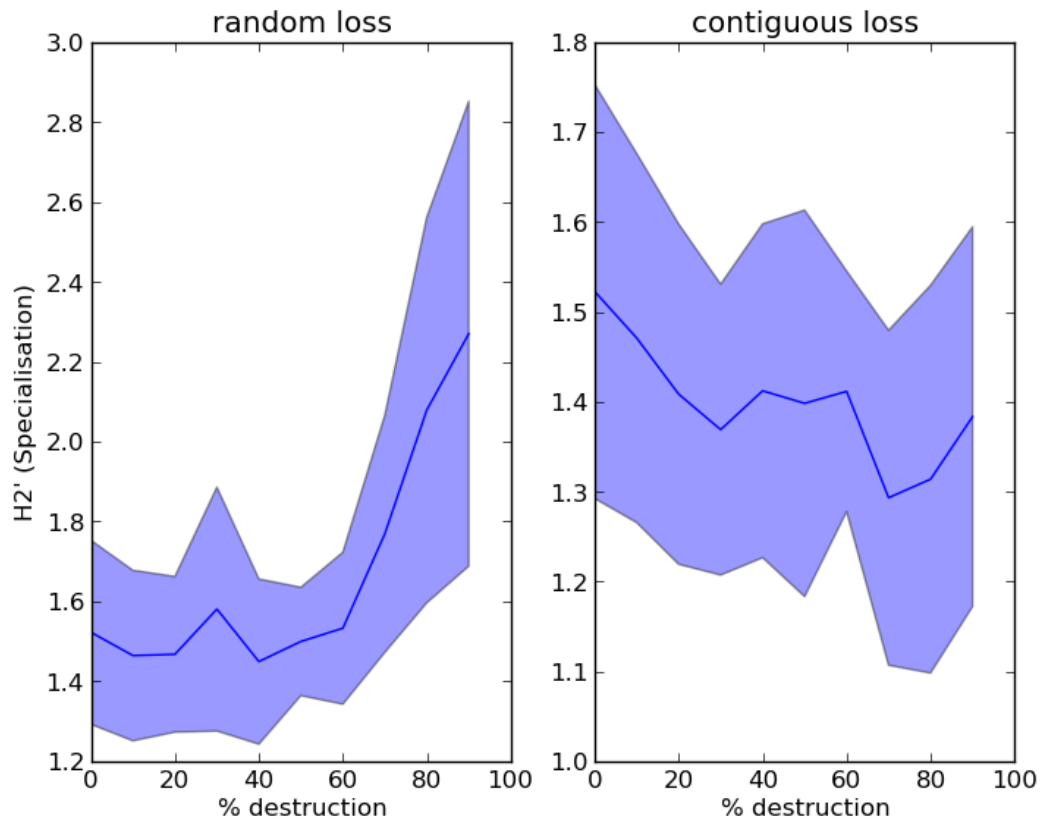


Figure 3.8: **Specialisation:** $H2'$ is a metric that quantifies the degree of specialisation of interactions in the mutualistic sub-network. Mutualists appear to become less specialised under random destruction, and more specialised under contiguous. (This appears to disagree with previous plots of $H2$, 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

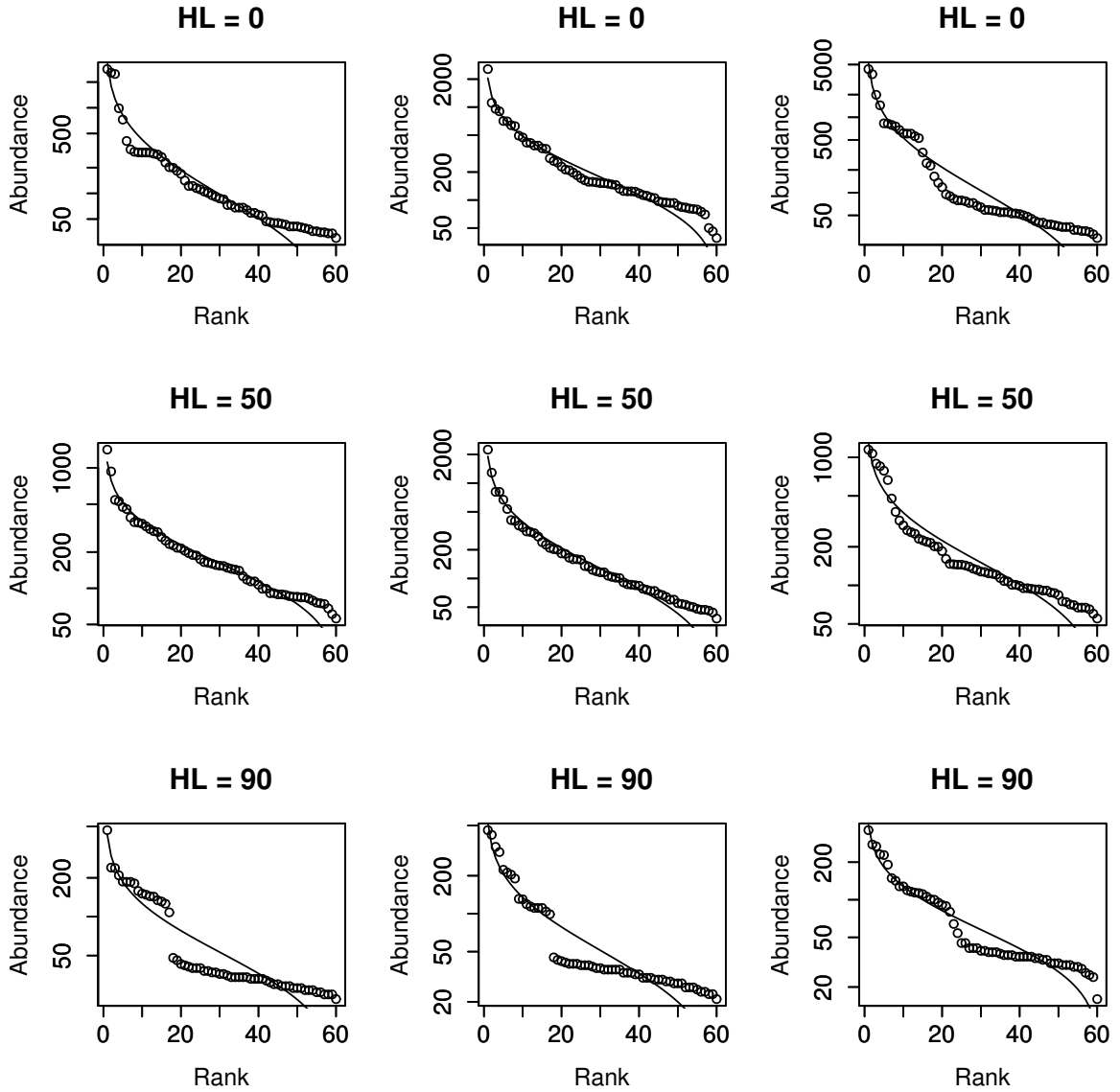


Figure 3.9: **RADs for Random habitat loss:** Rank abundance distributions for MAI=0, three replicate communities shown for selected levels of habitat loss (0,50,90). In the case of random destruction we expect the communities to become more even on average, based on Shannon_Eq metric, (figure 3.7)

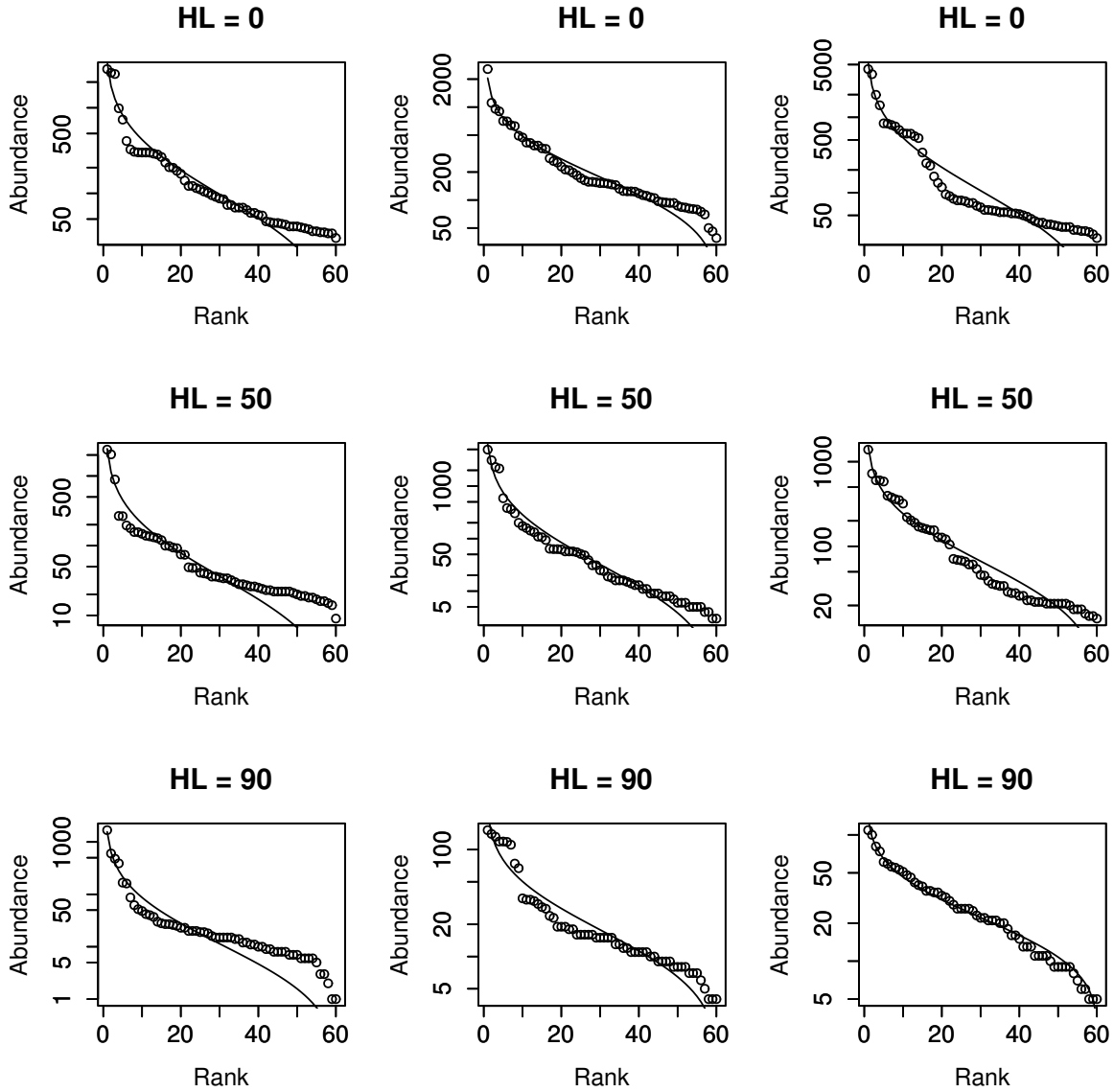


Figure 3.10: **RADs for Contiguous habitat loss:** Rank abundance distributions for MAI= 0, three replicate communities shown for selected levels of habitat loss (0,50,90). In the case of contiguous destruction we expect no trend in evenness on average, based on Shannon_Eq metric, (figure 3.7)

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

VARYING IMMIGRATION RATE

4.1 Assumptions of what has gone before

- Discussion of what we will now refer to as "default parameter values"
- Conclusion that there is something unrealistic about the immigration mechanism (rate too high)

4.2 Literature review for immigration

Possibly include here a summary of recent work on immigration, including IBT and meta-community theory. (Alternative is that this goes in introductory chapter.)

4.3 Simulations without immigration

One conclusion from chapter ?? is that the immigration mechanism is unrealistically high. As discussed, for the purposes of our investigation, it was informative to explore community responses to habitat loss that are not driven by changes in species richness. Therefore a high rate of immigration was desirable to prevent community collapse. However the result that no extinctions are observed even at 90% habitat destruction is suspect. This is clearly representative of a special case in which the habitat is locally very close to total destruction but the community is sustained by strong immigration from, presumably less impacted, surrounding habitats. We now consider other scenarios by changing the immigration rate parameter. At the other extreme we have communities with zero immigration. This represents a closed system. Although this does not exist in nature, certain systems may come close. For example an island community that is a

sufficiently distant from other land (see discussion on Island biogeography) will have very low immigration. Systems that are effectively closed may also be artificially achieved in controlled situations e.g. laboratory mesocosm, zoo/managed landscape.

We present here results which demonstrate that with zero immigration community collapse is inevitable, with the current model parameters. It is observed that all non-plant species go extinct, even for pristine landscapes with zero habitat destruction. (show a figure which demonstrates this conclusively). This result is explored further in chapter ?? where we look at the possibility of creating stable communities without immigration. For now we accept the general result that, under the default conditions, zero immigration results in community collapse. We are then interested in the regime between these two extreme of zero immigration, where we see many extinctions even at $HL = 0$, and high immigration where we see no extinctions even at $HL = 90$. Is there some immigration value for which the community is stable at low levels of habitat destruction, but where collapse occurs at higher levels of destruction?

4.4 Exploration of parameter space: habitat loss and immigration

Here we explore how immigration mediates the effects of habitat loss, for three different MAI values. A two dimensional slice of parameter space was explored as follows. Simulations were run for a range of different immigration values, and different levels of habitat destruction. One hundred repeat simulations were conducted at each pair value, using different network topologies generated with the niche model. All other parameters were held constant at default values (section ??).

Results of these simulations can be concisely represented as heat maps over the region of parameter space explored. Figure 4.1 shows the average response of three summary metrics to changes in immigration and habitat destruction. As was discussed in section ??, no species extinctions are expected for sufficiently high levels of immigration. This is because the immigration mechanism provides a significant recovery effect. It allows species that have gone locally extinct (from the simulation landscape) to recover by occupying empty cells. Therefore, for immigration values close to those used in the original simulations (chapter ??), the average number of species that have gone extinct at the end of a simulation is close to zero¹. This is true for all MAI ratios as shown by the left column of heat maps in figure 4.1. Reducing the immigration value weakens the recovery effect and therefore

¹Since it is possible for a species to go extinct and to subsequently recover it may be sensible to use another definition of 'extinct'.

4.5 Further investigation of these trends - RADS, dynamics

4.6 Habitat loss with low immigration

Figure 4.1: **Summary heat maps:** describe them.

5.1 Persistence without immigration?

5.2 Why are some networks more stable than others?

Chapter on ecosystem stability, with focus on this model? (Stability is implicitly involved in all the work up to this point, so does not constitute a separate chapter?)

Or chapter on inferring species interaction strengths from time series.

APPENDIX



APPENDIX A

Begins an appendix

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