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1.1 Motivation

An ecosystem is a subset of the *biosphere* - the entirety of the living systems on this planet. Ecosystems are a fundamental concern for humanity because the multitude of services they provide support human civilisation [11]. Additionally living systems are closely coupled, in a two way relationship, to the abiotic systems of the planet. Lovelock, and other proponents of the *Gaia theory* [82], suggest that these biotic and abiotic components together form a single homoeostatic system which maintains conditions that are harmonious to life. Regardless of the validity of this theory, it has become increasingly clear that human activity is currently changing these global (biotitc and abiotic) systems. It is well established that the recent increase in global temperatures is anthropogenic []. Furthermore is has been conservatively estimated that the rate of species extinctions during the last century ~~has~~ was between 8 and 100 times the background extinction rate [25]. This elevated extinction rate is undeniably related to human activities, with land-use-change and loss of habitat cited as the primary causes [40, 104]. Therefore studies into the detailed effects of habitat loss, and into the development of ecological theory in general, are urgently required in order to mitigate the effects of this *biodiversity crisis*. Together such studies represent a body of knowledge with important implications for conservation, restoration and ecological stewardship.

The breadth and scale of human impact on ecological systems is in itself sufficient motivation for this thesis. Much work has been done already in this area but, as we shall see, many questions remain open. In particular the dynamics and structure of *hybrid-ecological communities* - collections of species that interact in diverse ways - are relatively unstudied []. Furthermore, the response of such communities to habitat loss has not been considered. In general, several recent studies have highlighted the importance of subtle and underlying changes to the structure

of ecosystems that result from habitat loss, and which precede species extinctions []. As we shall see the field is moving beyond a focus on species extinctions, towards an understanding of these underlying structural changes. In this thesis we conduct a number of experiments, using computer simulations, that aim to contribute to this understanding. Particular attention is paid to the role of species interactions in generating observable patterns, and in mediating the effects of habitat loss. *In silico* investigations such as this are a useful tool in the development of ecological theory. However their scope and interpretation must not be misunderstood (see section 1.4). In the current chapter we present an overview of the literature that is relevant to the investigation, but before departing on that journey it is necessary to explain the context of the project as a whole.

This work is funded by the Bristol Centre for Complexity Sciences (BCCS). Therefore the content of the thesis falls under that generously sized umbrella term - *complexity science* - which may leave some readers perplexed. They would not be to blame, especially given that the project motivation just provided rests on real-world *ecological* concerns. Ladyman, Lammbert and Weisner review the various definitions of a complex system [78]. They attempt to synthesise a concrete definition of this concept, which they argue has previously been rather loosely and carelessly applied. The authors arrive at the following tentative definition of physical complexity:

> "A complex system is an ensemble of many elements which are interacting in a disordered way, resulting in robust organisation and memory."

They assert that this definition contains conditions necessary, but perhaps not sufficient for complexity, and propose an alternative *data driven* definition under which a complex system is one that generates data with a high measure of Statistical Complexity [27]. Indeed to define a complex system is no easy task. Depending on who you ask there may be further necessary conditions such as *emergence*, *hierarchical organisation*, *de-centralised control* and even anti-reductionist properties such as *top-down causation*. If a definition may be reached then complexity science can be easily understood as the study of such systems. However, given the lack of a concrete definition of complex systems, many of my contemporaries prefer a more *pragmatic approach* to the question - what is complexity science? A fair summary of the consensus view is that complexity science represents a broad set of mathematical and computational tools which find application in increasingly diverse areas of the natural and social sciences. This expansion is driven by the ever increasing availability of data; advances in high performance computing; and the development of the tools themselves. For some the tools used, and the fields of study in which they find use, are too disjoint to call complexity science a unified field. It is my view that this pragmatic approach is not dissimilar to the *instrumentalist*, or "shut-up-and-calculate", interpretation of quantum mechanics[105], which finds popular support in the face of the difficult and unresolved philosophical questions posed by that theory. Further discussion on the nature of complexity is not relevant to this thesis, other than to say that if a general definition of a complex system were arrived at, then its criteria may be met by the concept of the *ecological community*.

1.2 Community ecology

In fact the assertion that an ecological community represents a complex system is not beyond question. We consider the issue here, and in doing so we introduce the field of *community ecology*. The field itself is well developed, with a vast body of literature, such that a comprehensive overview is beyond the scope of this thesis. Numerous references throughout this section may provide the reader with further insight into the key areas of interest.

An ecological community may be broadly defined as a collection of species that coexist in time and space. The study of these collections, *community ecology*, attempts to understand their structure, dynamics and function. A key tenet in the field is that coexisting species interact with one another. This multitude of interactions gives rise to a *tangled web* of inter-dependence between species, that ecologists have been aware of at least since the time of Charles Darwin [29] (see quote in front matter), and probably long before. The interactions occur locally between individual members of species (e.g. two rabbits mate, one rabbit is eaten by a fox) in a manner that is arguably *disordered*. On a larger scale robust patterns of organisation exist, in particular the biodiversity patterns of species richness and abundances [112, 122]. Therefore it is tempting to conclude that the ecological community fits the definition of physical complexity quoted in the previous section. However the issue is not so easily resolved.

Perhaps the key question is whether large scale community patterns do in fact result from low level mechanics, such as the interactions between individuals. This question has been an ongoing source of debate. Numerous studies have demonstrated that empirically observed biodiversity patterns are consistent with *random* models of community assembly []. In particular *neutral theories of biodiversity* [] assert that the species in a community are functionally identical, or at least that any difference between species is *neutral* with regards to their fitness. The fact that such neutral models are able to predict aggregate community patterns appears to reduce the complexity the system. As stated by Purves et al. [112], in a truly neutral community all species may be replaced by a single species without loss of community function. In such a case all biodiversity patterns are meaningless artefacts of randomness. However empirical observations tell us that species are not functionally identical, instead they display differential traits. Pruves et al. give the example of carbon uptake and storage in a forest. Trees have different life cycles (growth and decay rates especially), and therefore they display functionally different temporal profiles of carbon sequestration. As such, altering the species composition of the tree community, will alter the *function* of the community (at least in terms of carbon storage). Therefore even proponents of *neutral* theories cannot claim that they explain it all. In general neutrality provides useful *null models* against which to test the relative importance of other factors, such as species interactions, in shaping communities.

In general the consensus view is that species interactions do play a role in community assembly. Strong support for the influence of species interactions on community structure comes in the form of empirically observed *trophic cascades* [75, 116]. A trophic interaction is one in which

energy is transferred between the interacting partners. Food-webs and food-chains represent collections of species interacting in such a way. The connectivity in these systems means that an action which influences one species may have knock-on effects on the other species. Consider a simple three species food chain, in which grass is eaten by rabbits, which in turn are eaten by foxes. Grass represents the *basal trophic level* and is the sole source of all energy is this system, being the only *auto-trophic* species. If all grass is removed from the system the species in higher trophic levels go extinct: both the rabbits, and indirectly the foxes, will starve. This is a *bottom up* trophic cascade. Alternatively an action may be taken which benefits the fox population. An increased numbers of foxes is likely to have *top-down* cascading effects. For example, more foxes means fewer rabbits, which in turn means more grass. Clearly there is a dynamic element to any such changes, as we shall see throughout this thesis.

The reintroduction of wolves into Yellowstone National Park is perhaps the most famous example of a real-world trophic cascade. The grey wolf (*Canis lupus*) was reintroduced to Yellowstone in 1995. Analysis by Ripple and Beschta [116] suggests that the abundance of mature aspen and cottonwood trees increased during the following 15 years, and attributed this increase to a reduction in elk numbers due to predation by wolves. They also noted an increase in beaver and bison numbers, which they speculate resulted from reduced competition for resources with the elk. However the changes observed displayed spatial pattern. Specifically they recorded differences in the response to wolf reintroduction between the southern and northern regions of the park, and between highland and riparian (riverside) areas. Subsequent research [86] supports the existence of a trophic cascade in Yellowstone, but highlights the importance of other factors, such as landscape heterogeneity and environmental conditions, in determining its effect. From this we conclude that species interactions can indeed play an important role in ecology, but that their effects cannot be fully understood in isolation[1].

Another powerful example of a trophic cascade was published by Knight et al. [75]. In their study it was shown that the presence of fish in pond communities can indirectly facilitate plant reproduction in neighbouring terrestrial communities. The pathway of influence is depicted in figure 1.1. Fish feed on dragonfly larvae in ponds, reducing the number of adult dragonflies which predate on pollinators. The presence of fish was shown to measurably benefit nearby plants by increasing pollination rates. This example again highlights the importance of species interactions, but carries with it a warning to the community ecologist. The definition of a community as an object of study (given at the beginning of this section) requires a delineation according to spatial scale or habitat type. From [75] it is clear that such a delineation can prove problematic because communities may influence one another. The pathways of influence are not confined to species with complex life histories, such as the dragonfly. More simply communities may influence one another via dispersal and immigration: the movement of individuals throughout space.

It is necessary to be aware of the limitations faced when focusing on a *local* community. Ricklefs

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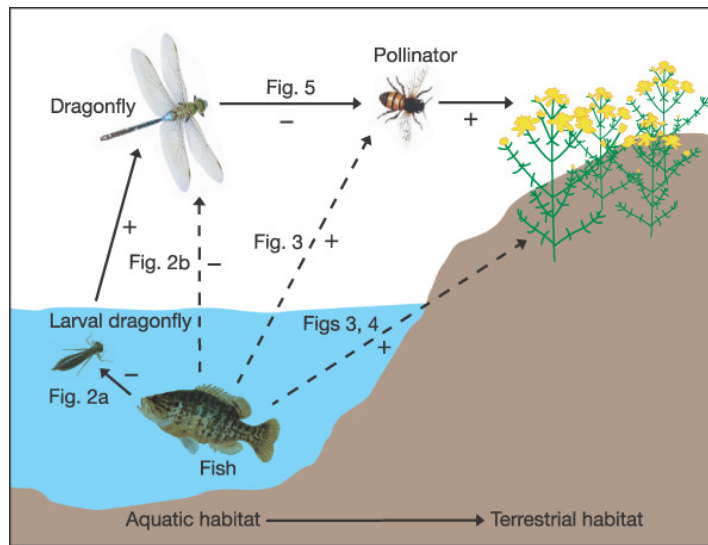[1]This leads nicely on to the scope of our research..

Figure 1.1: **An example of a trophic cascade** that crosses community boundaries. The presence of fish in ponds was empirically determined to indirectly benefit plant reproduction in neighbouring communities. Figure reproduced from Knight et al. [75].

argues [115] that the ecological community is an *epiphenomenon*, and that the strong focus of ecologists on local collections of species has hindered progress in our understanding of biodiversity at regional scales. Certainly spatial considerations are fundamental to our understanding of ecology. Whittaker showed that the concept of *biodiversity* must be considered on different spatial scales [144], and well known that species richness scales with spatial area [118]. More recently it has been shown that the choice of spatial scale also affects calculations of stability. Wang and Loreau [140] have shown that temporal variability can decrease with spatial scale, possibility due to averaging over asynchronous fluctuations at the landscape level.

In general we see that the ecological community is an abstraction of nature, that is sensitive to spatial scale. Geographic boundaries may exist which validate this abstraction. For example islands present useful study systems of relatively isolated natural communities. However in most cases the consideration of multiple spatial scales leads naturally to the concept of the meta-community [79]. At the landscape level one may think of a number of interacting communities, where local assemblages of species are connected via the dispersal of individuals. Meta-community modelling has increased in popularity [], and provides an important link between the local and the regional scales. However such models tend to use a simplistic representation of the local community []. Generally each locality is represented as a patch, containing information on species abundances but no spatial structure. Therefore meta-community modelling represents a trade-off in resolution at different spatial scales. For this reason *community modelling* remains useful for understanding the details of local dynamics and structure, but we must be aware of the wider context in which the local community exists.

1.2.1 Species interactions

In a local community, interactions occur between individual organisms. However it is common to use a condensed representation by defining which species interact. If the interacting individuals belong to the same species the interaction is referred to as *intra-specific*; if they belong to different species it is referred to as *inter-specific*. Inter-specific interactions broadly fall into three groups: *antagonism*, *mutualism* and *competition*, based on the effect that each species has on the other. An antagonism is an interaction where there is benefit to one species and harm to the other. A mutualism benefits both parties, whereas a competition harms both parties. Whatever the type of interaction being studied, it is possible to represent the pattern of interactions between the species in the community as a network. Such a network may be referred to as a *species interaction network*, or simply an interaction network, and they have proven a useful tool for community ecologists [14]. There is a widely held view that the *structure* of these networks provides insight into the function and dynamics of ecological communities (see section 1.2.2). Correspondingly an arsenal of network metrics have been developed, drawing on the mathematics of *network theory*, with which ecologists attempt to characterise meaningful aspects of network structure. Several of these metrics are introduced in section 2.7.4, and used in the analysis later in this thesis.

It has been, and largely remains, common practice to define a community by the way in which its constituent species interact. So in addition to the spatial delineation already discussed, a delineation exists according to interaction type, such that studies may refer to *antagonistic communities* [], *mutualistic communities* [] or *competitive communities* []. Antagonistic communities, in the form of food-webs, are perhaps the most general since all non-basal species must feed in some manner. However mutualistic communities have received much attention in the form of plant-pollinator communities, given the key role of pollination as an ecosystem function that helps maintain plant biodiversity []. Studies of competitive communities [], and host-parasitoid [] communities are also common. However in nature there exists no clear delineation based on interaction type. It is possible for all types of interaction to occur between species that co-exist in time and space. Therefore there has been a recent move towards studies that consider multiple types of interaction, or *hybrid communities* []. Such studies have brought into question previous results derived from communities with single interaction types (see section 1.2.2), and so represent an important development in the field.

Another recent development is the quantification of *interaction strengths* in ecological network studies. Early network metrics used by ecologists were based on binary networks [], i.e. networks without weights associated with the links. This is in part because it is easier to empirically identify the presence of an interaction (to define the existence of a link in the network), than it is to quantify the strength of the interaction (to define the weight of that link). However metrics have since been developed that incorporate interaction strength [], and several studies have highlighted the improved descriptive power of such *quantitative network metrics* over

their *qualitative* counterparts [] (see section 1.2.2)[2]. A key feature of ecological networks is their propensity to contain a few strong interactions and many weak interactions. Qualitative descriptors do not capture this structural feature [17]. It is common in empirical studies to use the *observed frequency* of an interaction as a proxy for its strength []. In many cases this interaction frequency is a good approximation of the biomass flow or energy transfer along a trophic link, and therefore serves as a useful measure for how important that link is in the network. However other metrics may be used to quantify link weight. For example plant-pollinator studies may measure pollen transport in order to quantify the amount of pollen that 'flows' along each interaction pathway [].

There are many reasons to *quantify interaction strengths*, aside from the assignment of link weights to interaction networks. For example, there are a number of reasons to believe that strong interactions between species are destabilising for a community. A seminal theoretical study on this topic is May's 1973 paper [88]. Using *random matrix theory* he derived results on the dynamic stability of interaction networks with random link weights. Specifically the weights were assigned randomly from a distribution with mean zero and variance σ^2. May concluded that the probability for such a system to be dynamically stable (in terms of the linear stability of the equilibrium) decreased with σ^2, and also with the *connectance* C (the fraction of non-zero link weights in the full coupling matrix). Subsequently a number of theoretical studies confirmed that strong interactions are destabilising in food webs [], and the effect has been empirically observed by O'Gormann [106]. From a dynamical systems perspective this result is intuitive. Strong coupling increases the dependence between variables. From a practical perspective the result is significant because by quantifying interaction strengths we may understand aspects of community stability.

Returning to the example of trophic cascades, we see further motivation for quantifying interaction strengths. In the case of the *Yellowstone cascade*, we may want to quantify the effect that a change in one population (wolves) has on the populations of other species (elk, aspen, bison, beavers). This is one definition of interaction strength, and we have seen that in Yellowstone it was spatially dependent. Similarly one may want to determine the effect that the removal of one species would have on a community. Extinction of one species may result in cascading extinctions [], which are likely determined by interaction strengths []. Extensive reviews on the subject of interaction strengths are provided in []. A general theme emerging from the two papers is that methods (both empirical and theoretical) for quantifying interaction strength are dependent on the question being asked. Various methods capture different aspects of the effect of one species on another, and any two metrics are not necessarily comparable. Wootton and Emmerson [] in particular call for more clarity from researchers on the metrics being used, and for an improved dialogue being theorists and empiricists regarding the issue of interaction strengths. In this thesis interaction strengths play a central role. The way in which they are defined is discussed in

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[2]And perhaps HL section with some discussion on Tyliankakis

section 2.7.4.3, and revisited in chapter **??**.

1.2.2 The role of network structure

Much work in community ecology has focused on the question: how does the structure of an interaction network relate to properties of the community. This is what we refer to as *the role of network structure*. Community properties that may be related to network structure include stability, diversity (species richness and abundances), and ecosystem functions such as pollination and nutrient cycling. We focus here on work relating to *stability* because it is of particular relevance to the current project. In later chapters we will be interested in how community stability is affected by habitat loss. In depth treatments of the role of network structure on community properties in general are provided in [133] and [117].

Community stability is a multifaceted and evolving concept [10, 83, 97, 141], that includes aspects such as *robustness*, *persistence*, *variability* and *resilience*. These are discussed further in section2.7.2, where definitions of associated metrics are provided. A general observation is that large and complex ecological communities can be remarkably stable given the extent of the external perturbations they face. There is an apparent contradiction between this empirical observation and some theoretical results regarding stability. May's work [88] showed that large and highly connected communities are unlikely to be stable. Subsequent work by Gross [51] has shown that indeed the probability of obtaining a stable network *at random* is vanishingly low for networks of many species ($P(stable) < 10^{-4}$ for networks of 50 species). Despite these theoretical results large and stable communities are observed in nature. Either there is something wrong with the way these studies compute stability, or there are some non-random properties of real-world network structures that confer stability on communities.

As we saw in section 1.2.1 community ecology has historically focused on communities with single interaction types. This focus has produced results that connect structural properties with stability in such systems. For example it is well documented that *compartmentalisation* promotes stability in antagonistic communities [131, 132]. Conceptually compartmentalisation is the tendency for groups of species to interact strongly within the group, while interacting weakly with species outside the group. This property has been observed in empirical food-webs [], suggesting that it may indeed play an important role in stabilising natural communities. Weak connectance [88, 132] and high variability in interaction strength [68, 137] have also been suggested to play a role. The structural properties of mutualistic communities appear to differ from those of antagonistic communities. Empirically it has been observed that mutualistic communities have a *nested* structure [15]. This property can be thought of as the tendency for specialist species to interact with subsets of the interaction partners of more generalist species. This concept is illustrated in figure **??**. The property of nestedness has been shown to promote stability in mutualistic communities, as has high connectance [132].

However more recent work on *hybrid communities* by Sauve et al [] has brought into question
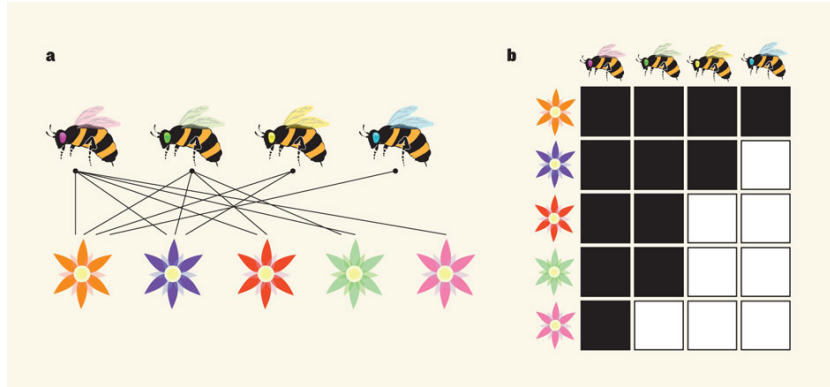
Figure 1.2: **Nestedness** is the property that the diets of specialist species are subsets of the diets of generalist species. It is common in mutualistic communities. Figure reproduced from [5]: '**a**, In the mutualistic interactions that occur between plants and their pollinators, some species (generalists, such as the pink-eyed bee) interact with many partners, whereas other species (specialists, such as the blue-eyed bee) have few partners. **b**, Such networks have been described as 'nested', as they produce a triangular pattern when the interactions (depicted by black squares) are arranged in a matrix. '

some of the structural properties commonly associated with stability. They modelled communities comprising mutualistic and antagonistic interactions, and demonstrated that the effects of modularity and nestedness on stability were strongly reduced. This controversial finding indicates the importance of the recent push to study hybrid communities (previously discussed in section 1.2.1). It has also been shown, by Mougi et al. [99], that the introduction of mutualism can stabilise antagonistic communities. The novelty of these results highlights how far there is to go in order to understand the role of different interaction types as they occur in nature: simultaneously. This thesis represents one step on that journey.

1.3 Habitat loss

A significant portion of this thesis (chapters **??** and **??**) is devoted to the study of community responses to habitat loss. As we saw in section 1.1, habitat loss is one of the leading causes of the extensive damage to ecosystems that we are witnessing globally. Therefore understanding the effects of habitat loss, and how to mitigate them, is more important now than ever. In this section we introduce the current state of knowledge regarding this issue, from a community ecology perspective. We cite certain key papers, however the field is too vast to provide a comprehensive overview. The reader is referred to reviews in [53] and [49] for such information. In section 1.3.1 we outline how habitat loss has been modelled previously, and discuss the results of this modelling. In section 1.3.2 we compare the modelling results to certain key empirical studies, and in section **??** we situate the current thesis within the body of literature presented. In the literature a range of related concepts are studied, including *habitat alteration*, *degradation* and

fragmentation. In what follows we use *habitat loss* to refer to all these concepts, except where a specific distinction is warranted.

1.3.1   Modelling studies

Historically studies of habitat loss have focused on species extinctions, since the loss of species is arguably the most visible consequence of any perturbation. Numerous theoretical studies have investigated how the species extinctions resulting from habitat loss depend on the spatial pattern of the perturbation [4, 36, 59, 67, 108, 134, 148]. The studies cited employ spatially explicit (either lattice-type or meta-community type) modelling, such that habitat can be destroyed according to different spatial patterns. In general these studies agree that species extinctions occur at a higher level of habitat loss when the destruction occurs in some spatially-correlated way, rather than at random.

Other modelling has indicated that the loss of species is mediated by properties of the interaction network structure. Fortuna and Bascompte [42] modelled the dynamics of mutualistic communities under habitat loss. They demonstrated that random network structures produced species extinctions at lower levels of habitat loss, compared to network structures empirically derived from real-world communities. Similarly Melian and Bascompte [94] used a meta-community model to demonstrate that certain network properties can help to prevent extinctions in simulated antagonistic communities. Both increasing levels of omnivory, and reducing top-down control by predators were shown to increase extinction thresholds. However both studies cited pertain to small model networks, and the results remain to be demonstrated empirically.

Understanding the full effects of habitat loss on a community necessarily requires the consideration of multiple trophic levels [31, 126]. We saw in section 1.2.1 that changes to a single species in a community can have effects that cascade across trophic levels. Modelling by both Dobson et al. [31], and by Sole and Montoya [126], suggests that species in higher trophic levels are most vulnerable to habitat loss. Dobson et al. describe how diversity, and associated ecosystem functions, are lost first from higher trophic levels. They refer to this effect as *trophic collapse* of the community.

We have previously noted a move towards the study of hybrid communities with multiple types of interaction (section 1.2). Since this is a recent trend, such communities have yet to be studied extensively in the context of habitat loss. The only relevant study we are aware of at the time of writing is by Evans et al. [37]. They empirically constructed a network of networks, spanning several habitats on a farm ecosystem and comprising multiple interaction types. A robustness algorithm was then used to determine how vulnerable the hybrid network was to the loss of different habitats from the farm. Interestingly they reported that two of the most important habitats, relative to their sizes, were hedgerow and wasteland. However their approach was spatially implicit and did not consider the *dynamics* of the farm community.

Species extinctions are not the only effect of habitat loss on communities. Other effects may

include changes in stability, in the distribution of species abundances and in network properties. These more subtle changes may be thought of, in some sense, as representing a decline in ecosystem 'health', and a loss of ecosystem function, which may occur prior to the loss of any species. Of particular concern are changes in species interactions resulting from habitat loss. We saw in section 1.2 that species interactions play a key role in generating community patterns and maintaining ecosystem function. This led Janzen to comment in 1974 that, when considering the effects of deforestation

> *"what escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions"* [69].

Modelling studies have investigated the loss of interactions due to habitat loss. For example Fortuna et al. [43] used a meta-community model to show that mutualistic interactions may be lost rapidly beyond a critical threshold of habitat loss. However we are not aware of any modelling that has attempted to reveal changes in network structure at the community level. Our knowledge of such changes under habitat loss comes from empirical studies.

1.3.2 Empirical studies

There are certain empirically observed responses to habitat loss that appear to be general. Namely habitat loss affects species in higher trophic levels more strongly than those in lower trophic levels [34, 114], it is generally de-stabilising, and beyond a certain level of destruction it results in the loss of species [49]. These effects are consistent with the theoretical studies cited in the previous section (1.3.1). Empirically studying the effect of the spatial pattern of habitat loss is a challenge because this requires controlled destruction. One such project, the *Stability of altered forest ecosystems* (SAFE) project [39], aims to do just that by agreeing a fixed spatial pattern for the logging of an area of rainforest in Borneo. This project is beginning to produce output. Of particular interest are the effects of fragmentation and the resulting edge effects, given that globally '70% *of the remaining forest is within 1km of the forest's edge'* [52].

One consequence of fragmentation results from the species-area-relationship (SAR). It appears that the number of species found within a given area, in a certain habitat, scales as a power law with the size of the area [118]. Therefore smaller fragments have lower species richness. Additionally it has been shown that smaller fragments may increase variability in species abundances [38, 140], and result in increased predation pressure due to spatial compression of the community [49]. Although the latter effect is only likely when the predator is mobile and can therefore exploit numerous fragments. On a regional scale fragmentation has been shown to dramatically reduce the biomass of terrestrial communities [52], due to a reduction in landscape connectivity.

Several recent studies have empirically detected changes in the structure of interaction networks due to habitat loss [53]. Tylianakis et al. [135] showed that empirical antagonistic

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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. 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. The changes detected represent subtle and 'hard to measure' impacts of habitat degradation, that may well be missed if only certain metrics are used. In particular this study highlights the importance of using quantitative network metrics. In contrast Albrecht et al. [3] detected a decline in antagonistic interaction diversity as a result of habitat alteration. They sowed that insect food webs in a grassland system lost interaction diversity faster than species diversity. Therefore, although species were lost, the extent of the community response would be underestimated if only metrics based on species abundance or richness were used. Both of these examples ([135] and [3]) highlight the sensitivity of results to the metrics used, when studying community responses to habitat loss. This sensitivity motivates the large variety of metrics used in our analysis (see section 2.7).

Further changes in network structure have been empirically detected. Habitat destruction has been observed to push mutualistic networks towards higher modularity, higher connectivity, and lower nestedness [128]. Such structural changes have traditionally been associated with reduced stability (see section 1.2.2). Similarly habitat loss has been shown to destabilise antagonistic communities by lowering modularity and increasing interaction strengths [53]. However Kaartinen and Tomas [72] observed that, although species composition of host-parasitoid communities varied between habitat fragments, quantitative network properties did not. This result suggests a possible generality of structural changes under habitat fragmentation. In general the literature suggests, as expected, that habitat loss reduces community stability, irrespective of the interaction type. However it is suggested that the underlying changes driving this loss in stability differs between mutualistic and antagonistic communities. It is not clear how these results generalise to the stability response of hybrid-communities. The observation of structural changes under habitat loss, sometimes without the loss of species, supports the conclusion that we must move beyond a focus on species richness. 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 [95]. The position is summarised nicely by Valiente et al. [136], who stress *"the importance of focusing on species interactions as the major biodiversity component on which the 'health' of ecosystems depends."*

1.4 Ecology *in silico*

Computational modelling has proven a useful tool in the mathematical sciences, and has become increasingly popular with the ever increasing power of modern computers. The field of ecology is no exception. In fact, given the difficulty and expense of ecological field work, computational modelling has provided a valuable complement to empirical studies. However it is important to note that *in silico* ecology is no substitute for ecology in the field. The review papers on species interaction strengths [], discussed in section 1.2.1, have already hinted at certain problems arising from a gulf between theory and experiment. Especially in the field of theoretical population dynamics there is a sense that some mathematical models are studied as objects in their own right, rather than with a purpose of rigorous application to empirical data. In such cases the term *ecological modelling* is incorrect. Barraquand is especially critical of this issue [13], and calls for better communication between theorists and empiricists. With this ~~is~~ in mind it is appropriate to define the scope and purpose of the investigation presented in this thesis.

The work undertaken for this thesis is purely theoretical. We do not fit our models directly to empirical data. However the modelling framework, which is fully specified in chapter 2.3, is grounded in ecological realism. We attempt to model *realistic* demographic processes and species interactions for multi-trophic communities. This is achieved by the use of bio-energetic constraints and, where possible, parameter values derived from the literature. However the simplifying assumptions required of any model inevitably mean that the simulated communities represent a departure from the communities of the natural world. As such the modelling serves as a tool for *hypothesis generation*. Results are analysed in detail, and presented in such a way that they may be subsequently tested against empirical observations derived from natural communities. Differences, if found, between simulated and natural communities would be suggestive of mechanisms that are either wrong or missing from the model. This is informative in itself. Equally, an apparent agreement between the model and reality does not necessarily indicate that the model accurately describes the true mechanisms of the natural world. We have already seen an example of such a case in the neutral models of biodiversity (section 1.2). Neutral models are able to produce realistic patterns, despite evidence that mechanisms in nature are not neutral [112]. Therefore the interpretation of our modelling results, as always, must be treated with caution[3].

The modelling framework employed in this thesis is *individual-based*. The model, which was developed by Lurgi et al. [], involves a two dimensional landscape on which individuals move around and interact according to certain rules. Such models have become increasingly popular in ecology [71], where they are known as individual-based models (IBMs), while in other fields they are often called *agent-based models* (ABMs). These two modelling concepts are equivalent, and represent a reductionist approach to the complex systems paradigm (introduced in section 1.1). The idea is that by explicitly modelling the behaviour of individual agents at a low level, one is

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[3]refer to limitations section in conclusion chapter?

able to study the aggregate patterns that emerge on a higher level as a result of the interplay between these agents. If the high level properties are realistic, this is evidence that the low level mechanisms in the model may be meaningful. Such modelling allows us to conduct experiments to determine how simulated communities respond to different perturbations. A challenge posed by the IBM approach is that the large number of parameters, and the complexity of the models, are such that simulations are capable of producing an overwhelming variety of output. The IBM model used in this thesis was previously parametrised in [], using some parameter values taken from the literature and other values tuned in order to generate realistic and stable community level patterns (see section 2.3.2). Our applications of the model are novel, and so a significant amount of the work in this thesis represents *stress testing* of the model under new parameter conditions (especially the work in chapter 4).

IBM models have been used previously in the study of habitat loss (see section 1.3.1). However our model combines certain key features that, taken together, represent a novel modelling framework. The model is spatially explicit, which is realistic since communities are naturally embedded in space. The spatially explicit treatment also allows us to study the effect of the spatial pattern of habitat loss, which as we have seen can determine the impact on a community. Previously models have focused on a small number of interacting species [], whereas our model simulates a multi-trophic community of many species. Such models are less common [50, 83], and partly facilitated by increased computational power. The multi-trophic aspect is key. We have seen that different trophic levels often respond differently to habitat loss [], and in fact the interplay between species in different trophic levels can mediate the response of the community as a whole [126]. As discussed in [], our *bioenergetic* model is more realistic than ~~previous~~ previous models of multi-trophic food web dynamics [20, 91, 109] in the following ways: 1) There is no need to define extinction probabilities (e.g. [43, 126]) since survival of individuals depends on available energy (non-basal species starve without food). 2) Complex demographic processes such as reproductive ability, are defined by energy availability. 3) Differential traits such as energy gathering efficiency model heterogeneity between trophic levels (but not within levels). Furthermore our model incorporates multiple types of direct interaction between species (antagonism and mutualism). The simulation of such *hybrid communities*, as we have seen, situates this work at the forefront of community ecology, especially in regards to theoretical treatements of habitat loss.

1.4.1 The role of immigration

A key feature of our modelling framework is *immigration*. The IBM is a model of *local community dynamics*, and as we saw in section 1.2 communities are embedded in a larger spatial context. Therefore we model an inflow of individuals from outside the local landscape. The mechanism for modelling this immigration is defined in section 2.3, and without it the simulations represent *closed communities* that are isolated from the wider landscape. In meta-community modelling the immigration (or dispersal/colonisation) mechanism is fundamental, and generally has positive

effects on biodiversity [22, 74, 80]. Experimentally immigration also been observed to increase the diversity of plant communities [100], and to buffer the risk of plant extinctions in tropical forest fragments [150]. In such studies the source of immigration is referred to as the *regional species pool*. Increased species diversity in the regional pool has been shown to increase diversity in local communities [44], and to reduce variability between different communities [2, 74]. In highly productive sites immigration has been experimentally shown to contribute less to community diversity than local ecological processes [44]. Whereas in sites of low productivity immigration is the more important factor, an observation referred to as *shifting limitations* on plant diversity along a gradient of habitat quality.

1.5 Inferring species interactions

Most of the work presented in this thesis consists of studying communities simulated using the IBM model. The full model specification is given in chapter **??**, but the basic idea is that we define which species are able to interact and the rules by which they interact, move around and reproduce. We then investigate the community level properties and dynamics that emerge from the local interactions of individuals belonging the constituent species. However, in the final chapter, we explore what might be considered the *inverse problem*. That is, given the observed community dynamics, is it possible to infer which species are interacting and how strongly. This problem finds parallels in other areas of science where high level aggregate properties of a system are relatively easy to observe, compared to the low level structural properties. For example the biochemical networks responsible for gene regulation in cells are highly complex and adaptive, and as such determining their topological structure presents an experimental challenge. Gene expression profiles (the high level result of the regulatory networks) are comparatively easier to measure via microarray experiments [141]. Therefore numerous methods have been developed to infer the structure of regulatory networks from gene expression profiles [85, 151].

Similarly in the field of ecology several attempts have been made to infer the network of species interactions from measurements of high level properties. Previous approaches may be thought of as falling into two categories: methods based on spatial data [55, 138], and those based on population dynamics [45, 48, 66, 102, 123]. Spatial approaches have looked at correlations in species spatial distributions. In the simplest approximation, if species affect each other negatively (for example via competition) then we may expect a negative correlation between species distributions in space. The converse would be expected for positive interactions (such as mutualism). However such an approach is hampered by *indirect effects* mediated by interactions with other species. More advanced statistical methods have attempted to overcome such problems (see [55]), with promising results. However in this thesis the focus is on the population dynamics approach. Although the empirical measurement of population dynamics requires a more sustained effort in the field, it does provide more information from which interactions may be inferred.

Some authors have attempted to detect signatures of species interactions via geometric analysis of observed population dynamics [45, 48, 123]. For example it may be possible, in certain contexts to detect predation or competition interactions from the phase relationships between species dynamics [123] (see section 5.4.6). However, as with the simplistic spatial correlation approach described above, phase-plane analysis neglects the dynamic complexities arising from indirect effects due to the presence of many interacting species. To give an ~~example~~ example, consider the case of *apparent competition*. In this scenario two prey species are fed upon by a single predator. Therefore there are two direct antagonistic interactions. However an *indirect competition* may emerge between the two prey species. If one prey species preforms well this confers benefit to the predator. The resulting increase in predator numbers may be detrimental to the second prey species, because of increased predation pressure. In a large and complex community the potential for such indirect effects increases dramatically. This problem may be overcome by the fitting of *population dynamics models* to empirical time series. Such models explicitly characterise the interactions between species, and their effects on dynamics. Therefore fitting population models, if successful, may account for all direct and indirect effects present.

Both Ives et al. [66], and Mutshinda et al. [102], have published similar methods that statistically fit variations of a *stochastic Gompertz model* [121] to time series data. The fitted models provide estimates of interaction strengths and other parameters. Ives et al. focus on the stability of the fitted models, while Mutshinda et al. attempt to quantify the relative importance of species interactions and compared to environmental forcing. However neither study stresses the importance of correct identification of interaction network topologies. The methodology we develop in chapter **??** is inspired by the paper of Shandylia and Timme: '*Inferring network topology from complex dynamics*' [125]. They present a method which is used to fit a system of differential equations to the dynamics of coupled chaotic oscillators. The results demonstrate that, in the presence of substantial noise, the method can successfully recover the structure of the network of coupling between the oscillators. Therefore the method appears well suited to the problem of inferring species interactions from population dynamics, which may be modelled by a system of differential equations and which are generally subject to noise. Our work represents a novel application of their method to this problem.

In [125] it is assumed that the form of the equations governing the dynamics is known, and particularly the coupling function between the oscillators is known and parametrised. Regarding our application of the method, this assumption raises a fundamental issue that has been the focus of much debate in the ecological modelling literature: what functions should be used to describe the interactions between species. When modelling the antagonistic interaction between a prey and a predator the key function is known as the *functional response* (FR). The FR defines the rate of consumption of prey pre-capita of predator (see section 5.2.1). Over the years theorists have proposed numerous forms for this feeding function [], and empiricists have endeavoured to determine its form experimentally []. Empirically the efforts to obtain a general form for the

FR have been hampered by context dependence in feeding relationships []. While theoretical investigations on the subject abound they suffer, in many cases, from a lack of experimental validation and weak dialogue with empiricists [13, 16]. Therefore no general consensus has been reached on the appropriate functional form for the FR in natural systems. The position was summarised by Wootton in 2005 [149], and has not changed greatly since:

> *"We still have a rudimentary understanding of which of the infinite possible forms of nonlinear interaction-strength functions we should attempt to apply a priori, particularly for interaction modifications. Identification of the most appropriate functional forms requires more extensive empirical exploration."*

Jost and Arditi have contributed to the debate [70] by fitting models with different forms of FR to population dynamics, and using model selection criteria to determine the 'best' form. Their results suggest that such an approach may be promising, although sufficient noise can easily lead to incorrect model identification. Another problem with their approach is highlighted by the quote from Wootton, since an *a priori* form of the FR must be defined before model fitting. In the context of inferring species interactions, it is likely that the use of an incorrect form for the FR will lead to errors in the estimated network topology. Therefore the choice of FR with which to fit to dynamics is a fundamental and non-trivial concern. However our choice is somewhat constrained by the model fitting method used.

The model fitting method of Shandylia and Timme [] requires an interaction function that is known and parametrised. The simplest modelling assumption is therefore to use an FR that is *linear and parameter-free*. The famous Lotka-Volterra equations [81, 139] contain such an FR (see section for more details). Therefore the model that we fit to population dynamics is the generalisation of these equations to systems of N interacting species. The additional benefit of this choice is that it makes no assumptions about species roles, or about the types of interactions between them. Therefore the fitting of this model enables the detection of antagonisms, competitions and mutualisms alike. A limitation of this modelling choice is that species interactions in nature are unlikely to take such a simple form (again see quote from Wootton). Therefore, in chapter **??**, the extent of this limitation is investigated. Also a novel method for the characterisation of the non-linearity in the interaction strength function between two species is proposed.

1.6 Outline of thesis

The thesis is structured as follows. In chapter **??** the individual based model (IBM) of community dynamics is defined. This model was previously used by Lurgi et al. [] to study the stability of hybrid mutualistic-antagonistic communities in space[4]. The IBM is central to this thesis, and is used for the majority of simulations conducted. In this chapter we also define, and provide

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[4]Need a section summarising the key feature of this previous work.

interpretations for, a range of ecological metrics that are used throughout the thesis for analysis of community structure and dynamical properties. Further methods and metrics are introduced throughout the subsequent chapters as they become relevant. Chapter **??** presents a detailed analysis of community responses to habitat loss, under the *default parameter values* of the IBM. In chapter 4 the properties of community dynamics under changing *immigration rates* are explored. The analysis in this chapter considers species persistence, and ways to quantify stationarity and determinism in the simulation output. We then return, in chapter **??** to a study of habitat loss, extending the scope of the analysis in chapter **??** by considering community responses under different immigration rates. At the end of this chapter we provide a summary of the findings regarding community responses to habitat loss, and discuss their ecological relevance. Finally in chapter **??** we move on to address the problem, introduced in section 1.5, of inferring species interactions from simulated population dynamics. The conclusion in chapter 6 provides a general summary of key results from all chapters, and suggests potential directions for further research.