Building Resilience: How do Species Interactions Shape Ecosystem Collapse?

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Summary

Natural ecosystems provide important services—like food and water—we humans depend on to a large extent. Much like the failure of a single key financial institution can trigger unexpected crashes on the stock market, human pressures—such as biological invasions and species extinctions—can cause sudden collapses that severely transform the way ecosystems function. However, despite its importance, we do not completely understand the dynamics that make ecosystems resilient to collapse. Because the functioning of ecosystems is largely determined by the network of interactions between the species that inhabit them, my proposed research aims to quantify the role played by species interactions in determining the resilience of ecosystems. To achieve this, I will focus on networks of mutually beneficial interactions, like those between plants and their pollinators, and use a combination of empirical data, computer simulations and ecological theory. Ultimately I want to understand why, when and how ecosystem collapses occur, and how to recover from them.

Introduction

From food and freshwater production, to recreation and carbon sequestration, ecosystems provide a wide range of services of considerable value to humans. Unfortunately, the frequency of undesired ecosystem collapses—like the (often sudden) shift from a transparent to a turbid lake or from a self-sustaining fishery to a collapsed one—is dramatically increasing worldwide(*1*). When ecosystem resilience is limited, breakdowns are more likely, and their ability to provide those services we depend on is endangered. Therefore, a necessary step to anticipate, prevent, and reverse ecosystem collapse is to understand the processes that support or undermine ecosystem resilience (*2*, *3*).

Resilience is related to the amount of disturbance that an ecosystem could withstand without collapsing, or, in ecological jargon, undergoing a regime shift—a large, persistent transformation in ecosystem functioning and structure (*4*, *5*). Moreover, substantial research indicates that ecosystem functioning and structure are largely determined by the network of interactions formed by species in an ecological community (*3*, *6–8*). Since these factors ultimately determine the ecosystem response to disturbances, **the overall objective of my proposed research is to quantify the role played by species interactions in modulating ecosystem resilience**.

To do so, I will focus on the network of mutualistic interactions between plants and pollinators (*6*, *9*, *10*). These networks, which form the base of pollination systems, play a globally important role in the maintenance of biodiversity and crop production (*9*, *10*). Pollination systems are locally important too; for instance two thirds of New Zealand plants are pollinated by birds or insects(*11*), and this includes iconic native plants (like kōwhai and pōhutukawa), and economically important crops (like kiwifruit, apples and grapes). However, pollination systems worldwide are currently being disrupted by multiple drivers of human-driven global change (*11*).

Pollination is being affected particularly affected by the simultaneous loss of previously important species, and the introduction of invasive species. My thesis will concentrate on the resistance and resilience of pollination systems to biotic invasions and defaunation—top components of human-caused global change. These two drivers have affected New Zealand with particular intensity, at the same time it remains notably vulnerable (*12*). For instance, 50% of plant species in New Zealand are introduced (*13*), and imported social bees are now an important component of pollinator fauna (*14*, *15*). Moreover, the depletion of native birds (*16*, *17*) is a prime example of how pollination systems in New Zealand are losing key pollinators, plants and habitats(*11*).

In the first chapter of my thesis I will concentrate on biotic invasions. Specifically I have a twofold objective **first, I aim to determine which network characteristics shape the its resistance and resilience to invasions**, and second **to determine how biotic invasions, by affecting existing interactions in the community, reshape network resistance and resilience**. Empirical, time continuous observations of ecosystem dynamics in networks that have been subjected to invasions are limited. Therefore, I will use computer simulated communities to estimate the population dynamics of the species in the community, and then I will directly quantify stability properties from fluctuations in the species populations (*18*, *19*). Specifically I will simulate communities with different network structures, and analyze which structures are more favorable for the coexistence of the invasive species to co-exist in the community. I will then in turn, see how the structure itself is changed by the invasive species, and whether the change in

structure has stability implications.

However, it has been shown that biotic invasions often occur in ecosystems that have already been degraded by species removal ([20]). Understanding how invasions interact with defaunation in ecological networks is a global research priority, and essential for conserving, restoring, and managing New Zealand ecosystems ([15]). In the second chapter, I will follow **by determining the compound effect of biodiversity loss and invasive species on the resilience of an ecosystem**. I will be extending the models developed in the first chapter, but focusing on how the loss of species—particularly those with a unique role in the ecosystem—make the ecosystem more or less susceptible to invasions. Simultaneously, the population models will also serve to determine the the patterns of species extinctions that follows after a successful species invasion.

The first two chapters of my thesis are designed to answer underlying questions of resilience theory, however the underlying aim of my third chapter is to translate the gained insight into useful lessons for ecosystem management. Ecosystems are complex, non-linear systems that are very difficult to control. However, recent work in theoretical physics has highlighted that is indeed possible to regulate them using targeted interventions ([21]). I propose to build upon these findings to **determine the optimal set of management actions—from both a theoretical and a feasibility perspective—that are required to modify an ecosystem state**. For that, using a previously collected empirical dataset that characterized the network of interactions before and after an ecological invasion ([22]), I will first find the set of species that can act as drivers of ecosystem state. Then, using an extension of the population model developed in the first chapter, I aim to determine the characteristics—like the degree of generalization of trophic position—that make an species more likely to serve as a driver of ecosystem state. Rescuing ecosystems from the brink of collapse and recovering them from undesired shifts is a major goal in conservation science. Finding a way in which actions targeted to specific species can maximize the ecosystem resilience, will bring us much closer to that goal.

In a world of constant change, building resilience is our best insurance against losing the ecosystem services we value and depend on. Although we have identified some of the pervasive effects of invasions and defaunation at the species level, we currently do not understand how the changes on ecosystem dynamics is affecting the resilience of the ecosystems as a whole. The research I propose intends to establish the general theory necessary to answer this question. Doing so is especially important when the ecosystem response might be inconspicuous until transformation is imminent. Only by better understanding the dynamics behind species interactions, can we hopefully be better prepared to anticipate, prevent and reverse undesired ecosystem collapses.

1 Ecosystems resilience to species invasions

The invasion of naturalized species is changing ecosystems worldwide. Fortunately, during the last four decades, there has been steady progress in understanding the causes and outcomes of biotic invasions. For instance, we now understand that the success of an ecological invasion depends on geographic, bio-climatic, and taxonomic factors, as well as aspects of reproductive biology and general ecology of the introduced organisms. However, we are still unable to successfully predict the outcome of species introductions in a large proportion of cases.

One of the potential explanations for this limited predictive success is that research on both the causes and consequences of invasive species, have focused on the negative interactions between species in the community (competition, and predator-prey relationships). However the establishment of an introduced species depends on, or at least is greatly enhanced, by the establishment of mutualistic relationships (*23*)—in which both interacting species have a positive outcome. In fact, there are multiple empirical examples of plants that only become successful invaders, when mutualistic partners that pollinate their flowers, or disperse their seeds, are available (*24–26*). Understanding the reciprocal relationship between biotic invasions and mutualism is a key step necessary to both improving current predictions of invasion outcomes, as well as evaluating how invasive species are modifying mutualistic systems (*23*).

1.1 Species coexistence theory underpins the invasibility of ecosystems

It has been recently shown that there exists a direct link between the structure of ecological networks and ecosystem stability (*6*, *18*, *27–32*). In particular stable species coexistence in mutualistic networks seems to be favoured by highly diverse, connected, and nested structures (*18*, *28*, *30*, *32*). For instance, the nested structure observed in many mutualistic networks—in which specialist species tend to interact with a subset of the species with which a generalist interact—support higher amounts of biodiversity, minimise competition among species in the community, and maximise the range of conditions necessary to have a stable community (*18*, *31*). The unambiguous link between ecosystem stability and the ecosystem response to disturbances is an important argument for investigating the implications of network structure and its vulnerability to drivers of global change.

Perturbations caused by global change are severely modifying the structure of mutualistic networks (*33*). Indeed, current evidence suggests that most of its effects are negative (*3*, *29*). Although our understanding of the effects of those perturbations is limited, we know that, for instance, climate change, and habitat modification can lead to shifts on species abundances, and mismatches of phenology, behaviour, or geographic ranges of the interacting species (*3*, *33–35*). Those changes can in turn disrupt the patterns of interactions that determine the structure of mutualistic networks. Some evidence suggest other factors of global change like biotic invasions can also modify the structure of mutualistic networks, for example trough changes in the strength of species interactions, and the degree of network nestedness and connectivity (*22*, *36–39*)

I hypothesise that network structure is not only modified by the succesive invasion of alien species, but it also plays an important role in determining the invasibility of the community. Two
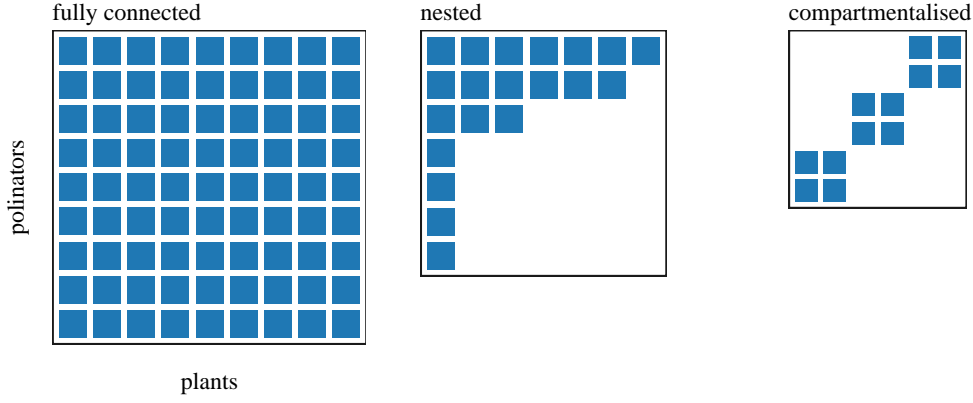
Figure 1: Each panel represents a plantanimal network with different network structures. Plants compete for resources such as nutrients, but also have indirect interactions mediated by their common pollinators. As the number of shared pollinators is higher, positive effects outweigh negative one. Current theory predicts a higher number of coexisting species as indicated by the size of the matrices.

facts provide support to this hipothesis. First, mutualistic interactions are key for the invasion success of introduced species because introduced species need to have suitable pollinators in the new habitat in order to establish themselves in the community (*23*, *40*). Second, the structure of mutualistic interactions is known to have direct implications for the number of coexisting species in the community (*6*, *9*, *18*, *41*). Specifically, structures that minimise plant competition seem to facilitate species coexistence and promote biodiversity (*18*). Therefore structural attributes— like the degree of specialisation/generalisation, and the contribution to nestedness, of available pollinators—should influence the likelihood an introduced species becomes invasive (*42*).

Previous studies have have found that simpler networks, with less species and less interactions between species, are easier to invade (*43*, *44*). However studies are strictly limited to trophic networks in which interactions are chiefly antagonistic (prey-predator) (*43–45*). Lamentably, these results cannot be easily extrapolated because mutualistic interactions introduce facilitation and competition feedbacks that are not present in antagonistic interactions. Here I will fill that gap, and study the link between different structural attributes of mutualistic networks—degree of nestedness, contribution to nestedness, and compartmentalisation.

The first step to achieve that is to construct simulated communities of mutualistic interactions. The structure of those communities will be determined by implementing the varying structure of empirically observed networks, as well as by constructing simulated networks with a wide range of structural parameters (Figure 1). This will allow me to evaluate if the network structures that have been found to minimise competition also make the community more vulnerable to invasions.

The second step is to develop models of the population dynamics in mutualistic communities in which the abundances of each species present on the community depends on their growth rate (*births − deaths*). These growth rates can in turn be affected by the feedbacks imposed by the interactions with other species. Previous theoretical work has largely assumed that the feedbacks of mutualistic interactions increase the growth rates of the focal species, while antagonistic interactions decrease it, which in turns allows the coexistence of a larger number of species (Figure 1) (*18*, *41*).
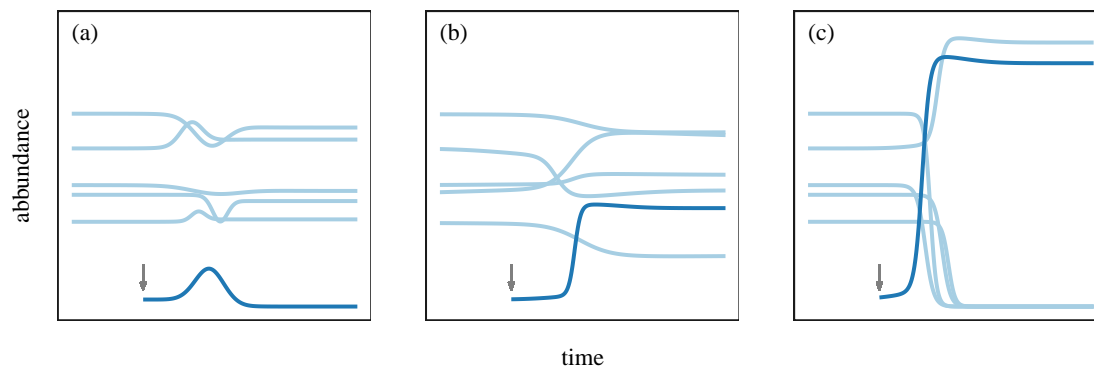
Figure 2: Three possible responses of ecosystems in stable coexistence to the introduction of an alien species (dark blue): (a) the alien species did not succeed to coexist, and caused only minor changes in the abundances of the species already present in the community (light blue); (b) the alien species persisted with the original species; or (c) the alien species became invasive, and five of the original species went extinct.

This assumption, however, ignores that in mutualistic systems, organisms might also compete to optimise the obtained benefits. Indeed evidence suggest that in plant-pollinator systems, the increase of mutualistic interactions caused by invasive species, does not translate in increased facilitation (*46*). Because plant reproduction depends strongly in the quality of the mutualistic service, mutualisms can be strongly altered when co-flowering species compete for the service of shared pollinators (*40*, *47*). This happens because the visit of a pollinator does not lead to reproduction if pollen is transfered between different species of plants (*48*). Even though there are some mechanisms to mitigate the impacts of competition for mutualism and inter-specific pollen transfer (*49*, *50*), it has been found that invasive species, at high densities, are able to co-opt pollinators from native species (*51*), dominate the networks of pollen transport (*46*, *52*), and ultimately decrease the seed output of native species (*53*).

The third step is to analyse the ecosystem response to an alien species. Depending on the network structure, and the traits of the native and alien species, the outcome of an species introduction can vary. One possible outcome option is that alien species is not able to invade the community(Figure 2a). Another possibility is that the alien species becomes an invader, which can, in some instances, have catastrophic consequences for other species in the community (Figure 2b, c). respond. Therefore, I will quantify the invasibility of the community as the likelihood that an invader is successful (*43*, *54*).

Because, as mentioned, a nested structure maximises the number of species that can stably co-exist (*18*), I predict that a similar relationship exists between invasibility and nestedness. However, I also argue that the competition for pollinators confers the community a resistance to invasions that has not been accounted for in previous theoretical or empirical research (Figure 3). These hypotheses link concepts of network structure, apparent competition/facilitation and ecosystem stability, and will allow us to put limited and somewhat disparate empirical observations in context.

Despite the general belief that successful invasive species tend to be super-generalists (*23*, *37*, *38*, *55*), a recent meta-analysis has shown that invasive species become very integrated in pollination networks (*42*). Specifically, invasive plants seem to interact preferentially with polli-
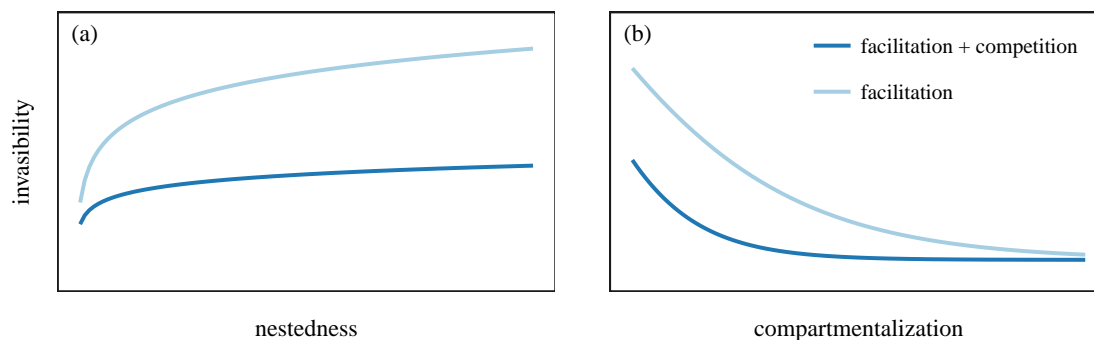
Figure 3: It has been found that (a) an increasingly nested structure enhances the number of species that can stable coexist, while (b) a compartmentalized structure decreases it. I hypothesise that a similar relationship exist between these attributes of network structure and the invasibility of the community. In addition, I argue that the apparent competition for pollinators increases the resistance of mutualistic communities to invasions by counteracting the positive feedbacks of apparent facilitation.

nators that are weak contributors to community nestedness, which have been shown to be the less vulnerable to extinction (*42*, *56*). However this empirical observation has not yet been explained mechanistically. By testing the hypotheses I propose, not only light will be shed on what makes ecosystem vulnerable to invasions, but also, because they deal with fundamental tenets in theoretical ecology, we will also gain a better understanding of the implications of network structure on the persistence of biodiversity, the link between stability and biodiversity, and the assembly of ecological communities.

1.2 Invasions change the structure of mutualistic networks

After analyising the structures that make an ecological network more or less susceptible to invasions, I then follow by investigating the consequences for the community when the invasion is successful (Figure 4). On one hand, I will explore the feedbacks on the structure of mutualistic network after an successful invasion; on the other hand I will explore when the invasions lead to a large number of secondary extinctions and ultimately ecosystem collapse (Figure 2c).

Successful invasive species have been shown to have pollination effects in the native species trough changes on pollinator populations and behavior (*38*, *57–59*). Although, as mentioned, they can have facilitative effects by increasing the total visitation rates (*40*, *58*), they can also have negative effects by decreasing con-specific or increasing hetero-specific pollen transfer (*59*). Therefore, changes on the structure of networks are expected.

Although there are few empirical studies that measure the consequences of ecological invasions in network structure, evidence suggest that invasive species have indeed the ability to modify the structure of mutualistic networks. In particular, invaded communities seem to be more nested (*22*, *42*) and less compartmentalised (*55*) than their un-invaded counterparts , while also having altered visitation patterns (*38*). However results are somewhat contradictory (*60*), and the limited amount of evidence precludes the generalisation of the patterns observed.

I will use the theoretical results obtained from the population dynamics model to fill the gap
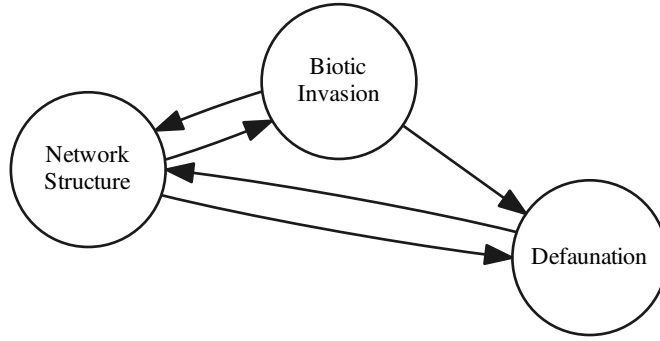
Figure 4: The network structure determines the invasibility of an ecological community. However, successful invasions also modify the structure itself, whether trough a shift in interaction partners or trough secondary extinctions in the community.

on empirical data. Specifically I will quantify the changes on network structure (nestedness, and compartmentalisation) induced by the invasive species, and the contribution to structure of both the invasive species, and the species it interacts with (*42*, *56*). Therefore, it will be possible to quantify how an initial successful invasion affects the future invasibility of the community. However a successful invasion can, not only affect future invasibility by causing changes on network structure, but also by causing extinction cascades that disrupt mutualisms in the community (*57*, *61*).

It is also possible to quantify the stability of an ecosystem by measuring the number of species extinctions that follow a successful invasion (*54*, *62*). Paradoxically, the same structures that I propose are the most vulnerable to invasions, have also been shown to be the most robust to cascading extinctions in ecological networks (*29*, *55*, *63*). The research I propose will help disentangle these two seemingly disparate observations.

2 Species redundancy promotes resilience

Random or top down, down-top, not functional

3 Controlling ecosystems for resilience management

A plethora of empirical and theoretic evidence suggest that ecosystems have stable states on which self-organised processes and structures persist in equilibrium (*5*, *54*). However, disturbances, when large enough, can cause the ecosystem to move to a critical transition point. When the ecosystem has reached this critical point, it can collapse, or more precisely, it can undergo a regime shift (a large, persistent transformation in ecosystem functioning and structure) after which the ecosystem enters an alternate stable state (*4*, *5*, *64*) (Figure 5a, 6).

Often, ecosystems enter into these alternate stable states in response to anthropogenic pressures of global change like climate, invasive species, overexploitation or habitat loss (Figure 5b). Unfortunately the frequency regime shifts is increasing, and this trend is likely to continue (*2*), which is severely compromising the provision of important ecosystem services we, and other species, strongly depend on (*65*). Some examples include the diminished production of fish after a food-web or habitat collapse in marine ecosystems (*66–68*), or failure of crops after a collapse on pollination services (*69*, *70*).

As evidenced by the limited amount of success of restoration projects, bringing back ecosystems to a pre-disturbance state, or even to a more 'desirable' state of ecosystem function, in which ecosystem services are somewhat recovered, is a particularly challenging endeavor (*71*). So far we have only small-scale and localised examples of recovery (*72*, *73*), and in many cases the ecosystem fails to recover even after the disturbances that caused the regime shift are removed (*2*). Moreover,some evidence suggest that recovery is at least partially determined by pre-disturbance structure of the community (*74*), but we do not understand the mechanisms behind. How to recover ecosystems from these undesirable alternate stable state is currently a major question in conservation and theoretical ecology.

The recovery of ecosystem depends strongly on the interactions between all species in the community and the dynamics that arise from these interactions. Therefore, there have been calls to replace the predominant species-level approaches by ecosystem scale approaches to management and conservation. However, perhaps with the exception of the mitigation of human-caused disturbances, ecosystem wide management can be expensive and difficult to attain. Contrastingly, even though the efficacy of conservation measures directed to individual species can be argued, they are more intuitive, tractable, and usually easier to implement. but we do not know how compatible they are with network theory ecosystem dynamics.

Unfortunately, we still do not understand how species-level interventions relate to the stability of the ecosystem as a whole. This is important because it will allow us to determine if current interventions are indeed pushing the ecosystem to recovery or not. Also, scaling the dynamics of individual species to the ecosystem level, will help to elucidate how to weaken the resilience of undesirable stable states, or strengthen the resilience of desirable states (*71*). What is more, it will also help to determine if ecosystem recovery to a pre-disturbance state is possible and feasible from a management perspective. Here, I propose to go one step beyond, and study the controllability of ecological networks.

Ecosystems are challenging to control because they are large, complex, inhomogeneous, and non-linear systems. However, recent work from theoretical physics has highlighted the possibility
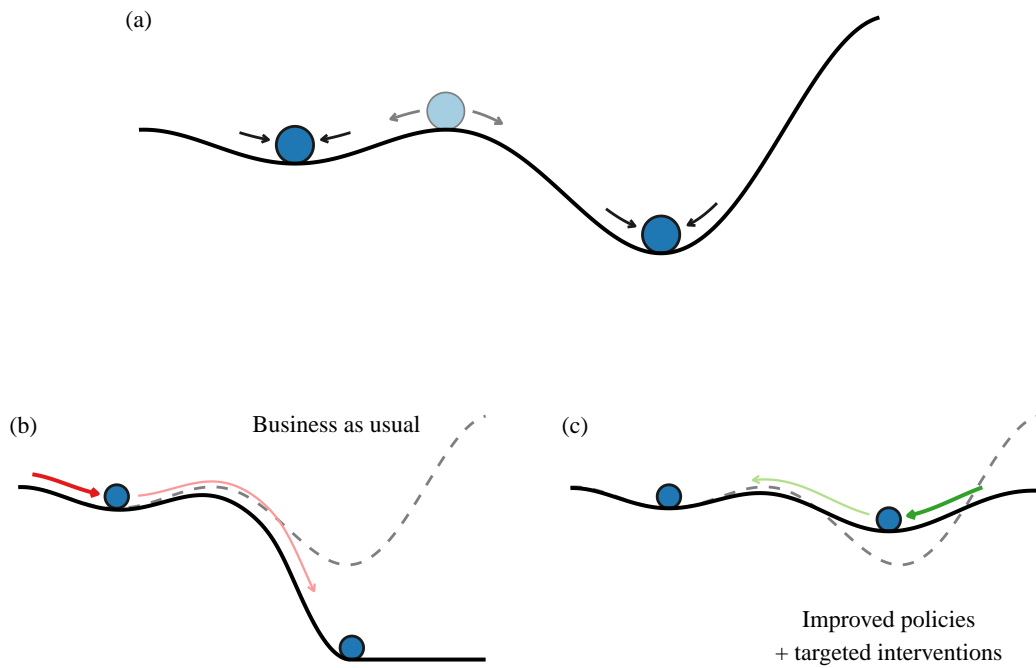
Figure 5: Ecosystems tend to converge into stable states (dark blue circles). (a) After a small disturbance, the ecosystem is likely to return to the original stable state (black arrows) at a rate determined by its resilience (depicted in the figure as the slope of the curve). However, large disturbance (or a combination of smaller ones) can bring the ecosystem into a critical transition point (light blue) from which the ecosystem can undergo a regime shift and enter into an alternate stable state. Under a "business as usual" scenario (b), the resilience of the desired state is diminished and human disturbances (red arrow) can push the ecosystem into an alternate stable state from which recovery is very difficult. By controlling the abundances of a set of key species (c), in theory, it is possible to induce a compensatory perturbation that weakens the resilience of the undesirable alternate stable state, and possibly push the ecosystem into recovery.

(a) Before (b) After

Figure 6: One example of alternate states in tropical coral reefs, (a) assemblages dominated by corals in the Caribbean in 1979, and (b) the same reef, degraded and smothered by fleshy seaweed two decades later. By definition, regime shifts among alternate states constitute profound and often sudden changes in species composition, with major economic and social consequences. Reproduced from Hughes et al. 2005(*2*).

of regulating ecological networks by using targeted interventions in just some key species. These species are not necessarily the most or least abundant, or invasive, but rather those that can drive the entire ecosystem dynamics (*75*) (Figure 7a). By modifying the abundances of driver species, is in theory possible to control the state of the ecosystem, and possibly push the ecosystem into a pre-disturbance state or at least a more desirable alternate state of ecosystem function (Figure 5c, 7b).

To achieve that, the first step is to determine the smallest possible set of driver species in which to apply conservation measures that modify their abundance (*75*, *76*). I will determine these species by using 'maximally matching' on the network of interactions—an algorithm that is already commonly used to find minimum sets in diverse areas of graph theory, image processing, and computational chemistry (*77*, *78*).

By applying this framework to six pairs of invaded and uninvaded pollination networks (*22*) I will examine the utility of this approach in a real world scenario. Specifically I will explore the characteristics that make an species (such as the degree of generalisation or it's contribution to nestedness) more or less likely to function as a driver of ecosystem state, and whether these characteristics depend on the presence of an invasive species in the ecosystem.

The second step is to determine which interventions on the driver species are necessary to guide the ecosystem to the desired state. Here I will use the subset of the population dynamics models developed for the previous research objective that show multiple alternate stable states. I will then employ a recently developed algorithm that accounts for the non-linear dynamics present in ecological community (*21*, *79*) to find the interventions that are necessary to modify ecosystem state.

However not all interventions are feasible; in reality, they are severely constrained by costs and scale. For example, the an intuitive intervention to restore a coral reef from an algal dominated stable state (Figure 6b) to a coral dominated stable state (Figure 6a) is to simply decrease the abundance of fleshy seaweed and increase the abundance of stony corals. This however is totally impractical; other interventions, for example those focused on species that predate on herbivore
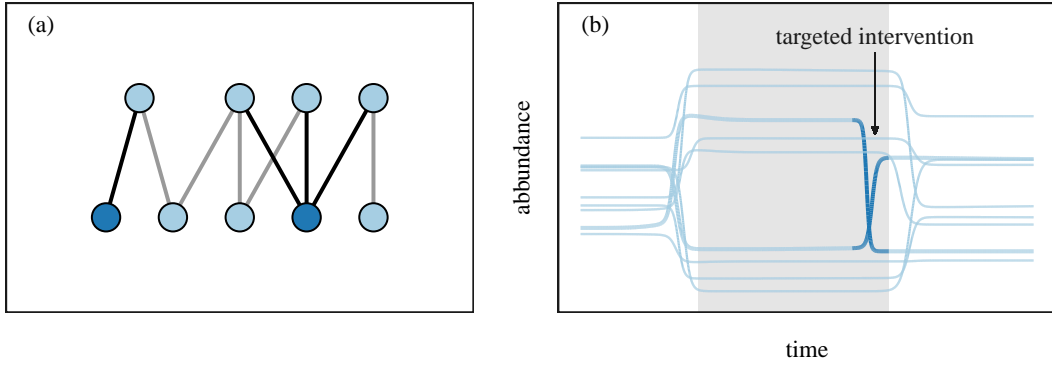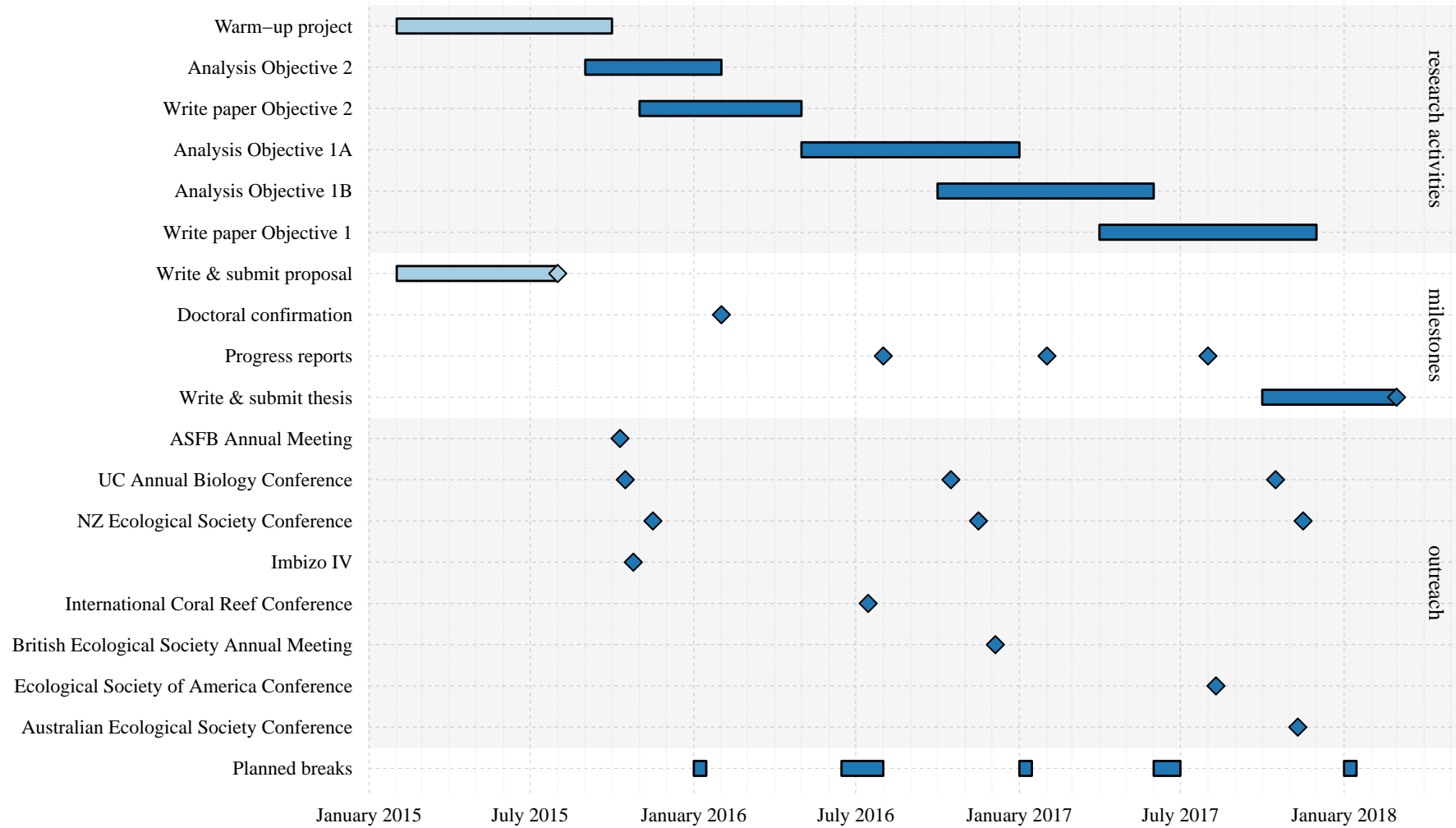
Figure 7: In an ecological network, due to the interactions between species, changes in the abundances of any species are necessarily reflected in the abundances of their direct and indirect partners. (a) It is possible to find a minimal set of species (dark blue), such that the abundances of all other species (light blue) can be modified by interventions on the minimal set. If targeted interventions on those species are feasible (b), it is, in theory, possible to regulate the state of the ecosystem, and therefore reverse a regime shift that has lead an ecosystem into an alternate stable state (shaded area).

fishes, are more practical and might lead to similar results ([20]). Therefore, I will focus on the feasible interventions that allow to modify the state of an ecosystem even when that state is not directly accessible. These interventions are tailored on weakening the resilience of the undesirable state ([71], [80], [81]).

Nevertheless, I anticipate to find empirical and simulated ecological communities in which none of the feasible interventions can lead to recovery to the original state. In these cases, I will focus on exploring the implications of accepting a 'novel ecosystem' ([82]). The concept of novel ecosystems highlights the possibility of an intermediate state, different from the original state, but one in which some ecosystem function and services have been restored ([83], [84]). As pristine environments become less and less common, restoring some altered ecosystems back seems unrealistic under escalating anthropogenic pressures ([84]) Therefore I will find the interventions that maximise one ecosystem service, like pollination, while maintaining novel components in the ecosystem like invasive species. Embracing change will "allows conservation and management efforts to be directed more appropriately towards goals that are achievable"([83]).

4   Research Plan

Warm–up project

Analysis Objective 2

Write paper Objective 2

Analysis Objective 1A

Analysis Objective 1B

Write paper Objective 1

research activities

Write & submit proposal

Doctoral confirmation

Progress reports

Write & submit thesis

milestones

ASFB Annual Meeting

UC Annual Biology Conference

NZ Ecological Society Conference

Imbizo IV

International Coral Reef Conference

British Ecological Society Annual Meeting

Ecological Society of America Conference

Australian Ecological Society Conference

outreach

Planned breaks

January 2015   July 2015   January 2016   July 2016   January 2017   July 2017   January 2018

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