Emergence and Implications of Conservation Opinion Propagation in Dynamic Coupled Socio-Ecological Systems

by

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of Contribution

- Chapter 2 : The work in this chapter was performed by Vivek Thampi (VT) under the supervision of Dr. Madhur Anand (MA) and Dr. Chris Bauch (CB), resulting in a co-authored paper published in *Nature - Scientific Reports* [209]. Contributions were as follows : VT conceived the study. VT developed MATLAB code, parameterized and analyzed the model, and wrote the first draft. All authors developed the model and revised the manuscript

- Chapter 3 : The work in this chapter was performed by VT under the supervision of MA and CB and published in *Ecological Modelling* [210]. The work was conceived and designed by MA and CB. VT developed parameter plane code, performed analysis and wrote the first draft. All authors developed the model and revised the manuscript.

- Chapter 4 : The work in this chapter is based on a manuscript in preparation for submission. MA, CB and VT conceived the study. VT developed the search terms, performed analysis of literature, and wrote the first draft. All authors revised the search terms and the manuscript.

Abstract

Human behaviour is rarely a static phenomenon. In life, individuals are presented with choices that define the trajectories they will experience days, weeks or months later. As an example consider farmer decision-making and orchard dynamics. If an avocado orchard is well taken care of, a bountiful harvest can lead to a lower price of avocados that will more easily attract grocers to stock the product. Alternatively, if the orchard is not properly cared for, avocado prices can surge (due to their low supply) and become a greater risk for grocers, causing them to seek other suppliers. If a particular 'care' routine is developed by the farmer, this can have a significant impact on the long-term trajectories of orchard dynamics. From this simple example, it is clear how dynamic human behaviour can interact with environmental system dynamics. This motivates the potential value of capturing this interaction in mathematical modelling. In this thesis, we develop two different coupled human-environment system (CHES) models that incorporate a dynamic feedback loop mechanism to link human impact and environmental system responses and *vice versa*. The first model is developed using a game-theoretic approach to describe dynamics of opinion spread. The model is then coupled to a previously established coral reef ecosystem model. We investigate the effects of key factors such as social learning, social norms, and exploitation rate on the trajectories predicted by the model. We discover stable regimes that are made possible by the presence of human coupling and we identify the potentially harmful role of social norms. In the second model, we utilize a similar game-theoretic approach to couple a dynamic human component to a previously established grassland model of the Southeastern Australian grasslands. The aim of this model is to determine conditions that suppress invasive exotic grasses, in the presence of human feedback that determines how strongly the local population mitigates its own pollution. Finally, we conduct a systematic review of the CHES modelling literature between May 2009 and April 2019 using the Web of Knowledge and PUBMED databases. Results reveal an increasing trend in the number of mathematical models using a CHES approach. Results also show that these models utilize a wide range of techniques of varying complexity. In general, most work focuses on agricultural systems. We postulate that application to other environmental systems is relatively unexplored and can be implemented using techniques similar to those of the models developed in this thesis, or via adaptations of other modelling techniques from different fields of research. We suggest that including dynamic human behaviour is necessary in order to improve existing environmental policies and improve the predictive power of mathematical modelling techniques in environmental systems research.

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Dedication

This thesis is dedicated to Romina Caraba-Thampi and Kiah Thampi, my partners in crime who are always looking after me on Earth and further beyond.

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Chapter 1

Introduction

Decision-making is an integral, foundational part of daily human life. Every day we are presented with problems of various complexity and our days are determined by the various choices we make. As an example, consider the COVID-19 pandemic. A simple choice would be to wear a mask (properly), and refrain from social outings. If, in such instances, the global population were to always conform to this, and if testing and contact tracing were more effective, this thesis could have been defended earlier. Through the simplicity of this example, the complexity and chain of reactions caused by simple decision making processes demonstrates how easily certain choices can affect our human environment. If spun into the context of natural environments, these decisions can lead to ecosystem resilience, catastrophic depletion of resources or the proliferation of invasive species [103, 188]. These choices, and their consequential effects, can induce a chain reaction creating a feedback loop mechanism where subsequent choices are impacted by the effects of one's previous actions.

On the topic of choices, individual decisions are not always independent from one another. While it is possible to act based on one's personal benefits, individuals are subjected to various forms of social interactions that can shape how personal beliefs and decisions are formed, and which in turn alter the impact of human choice on environmental dynamics. Exposure to various information channels can influence the global population in different ways. As an example, consider the persistent anti-vaccine movement caused by the spread of misinformation by Andrew Wakefield [170]. Despite the proven fabrication of the results, a small proportion of the global population remains committed to resisting vaccination based on the Wakefield study. These pockets of resistance are sometimes maintained by social forces such as peer pressure and social norms [77]. The result is local pockets of unvaccinated individuals that may serve as a reservoir for persistent infection [182]. As such, with the various effects of social influence on decision making, there has been a strong desire to implement mathematical modelling techniques to predict socially-informed decision making and the associated anthropogenic impacts on natural environments. This goal has been approached from various academic disciplines [193, 62].

Mathematical models have been developed to investigate the effects of human influence on natural systems in various fields of research. In classical Lotka-Volterra predator-prey models, human influence is often implicit through some form of constant pressure on one or both populations [171, 105, 7]. In the real world our actions are rarely constant. In the same way that eating the same food every day makes that food less desirable, humans will change certain choices we have made in the past to best satisfy current needs. These decisions can range from small choices to a full lifestyle change of becoming vegetarian, or to support conservation policies to promote sustainability of endangered populations. Human decisions are rarely static in nature and can change based on the current situation [63]. As such, the need to incorporate the dynamics of human behaviour has gained increasing traction, and has led to the development of coupled human-environment systems (CHES) models that incorporate dynamic human behaviour to capture the effects of anthropogenic stress on the modelled system. These models utilize feedback mechanisms (Figure 1.1) between both humans and the environment to investigate the more realistic interplay between human and environmental systems.

With the leap from static to dynamic modelling of human influence on natural systems, CHES models have slowly gained traction in the field of environmental sciences, leading to the development of mathematical models with varying levels of complexity [176, 166, 14]. This will be discussed in greater detail in Chapter 4. Prior to proceeding, some discussion is required on the game theoretical techniques used in this thesis, and the environmental systems on which our models are based.

1.1 Imitation of Human Behaviour through Game Theory

As described in the previous subsection, the choices we make can subsequently affect both our own outcomes as well as outcomes for other individuals. It is common to assume that individuals in a population act in their own best interest. To apply a game-like perspective on this, the higher the payoff of a given choice for an individual, the more likely the individ-

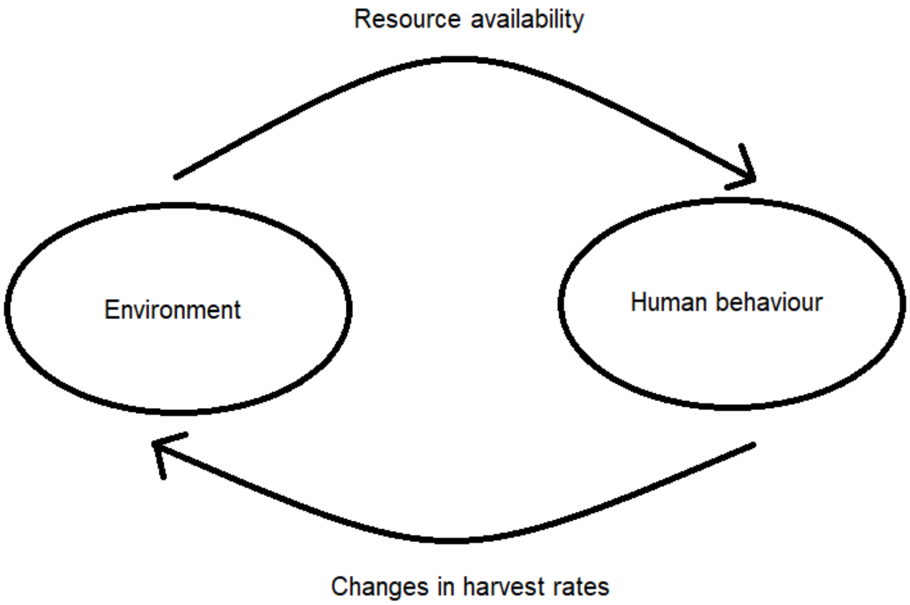

Figure 1.1: A simple flowchart to represent how human behaviour can change based on changes in the environment, and *vice versa*, in the context of resource harvesting.

ual will adopt it for that given situation. This concept of incentivization can drive multiple choices in the population, be it in an economics sense, such as the desire to buy promising stocks prices are low, or more subjective preferences such as the conservation value of a natural system. To accommodate this, mathematical models should also capture the dynamic feedback loops between changes in the environmental systems and human behaviour.

To help illustrate how mathematical models can quantify human behaviour, we consider the two-player prisoner's dilemma in Figure 1.2. This 'toy model' describes a situation where two individuals have been arrested for a crime and are being interrogated in separate cells. Each has the option to either 'cooperate' with the other individual by denying having committed the crime, or 'defect' against the other individual by admitting to the crime in the hope of a reduced sentence. The horizontal blocks in the figure represent the 'focal' individual, and that player's payoff is based on the choice of the second player. If both individuals were to adopt the same strategy (either cooperate:cooperate or defect:defect), the focal individual would receive a punishment, albeit a reduced sentence for honesty in the pure cooperate scenario. In contrast, if the focal individual betrays the second player, (this

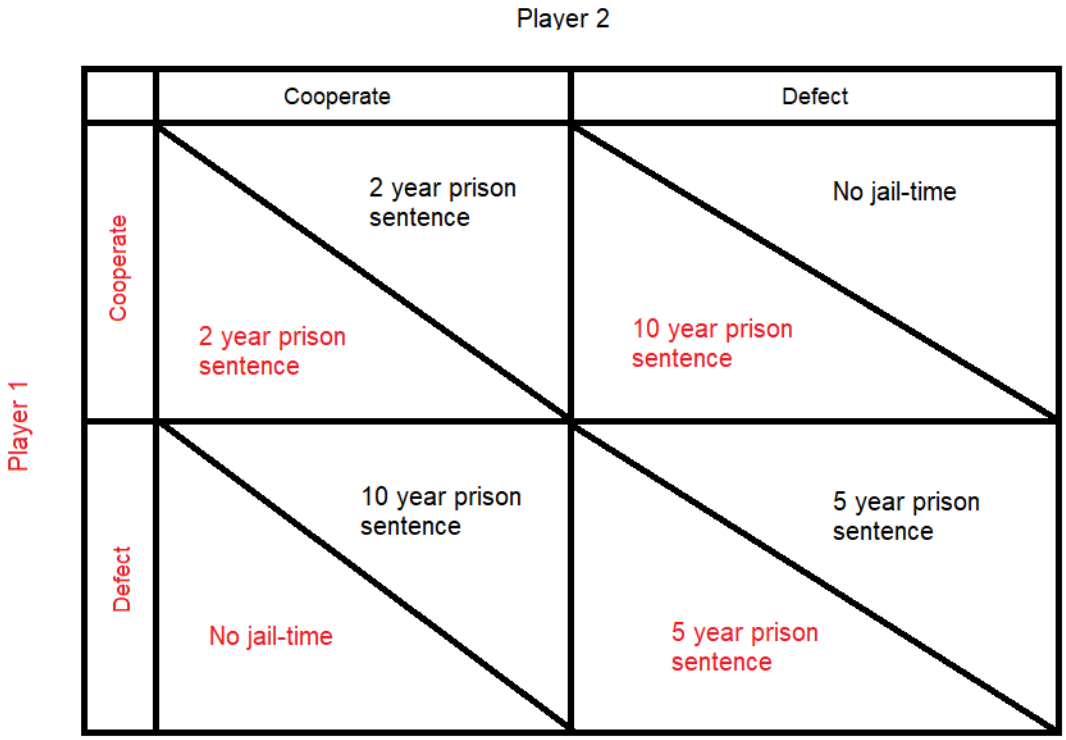

Figure 1.2: A 2-person prisoner's dilemma game, where each player's reward/punishment is based on the combination of the strategies both players have chosen. The judgment a player receives matches their player colour.

would be a defect:cooperate, scenario), the focal player would be absolved of all charges, whereas the second player would receive the maximum punishment and vice versa for the opposite scenario. In this sense, values can be assigned to measure the attractiveness of adopting a specific strategy. In general, the higher the payoff, the more likely that strategy is adopted. Recent modelling techniques have been developed to represent the utility of these choices in a functional form in games where an individual 'plays' against the average behaviour of the population. As an example, consider the two-strategy scenario developed by Oraby et al [159], where V represents a pro-vaccinator strategy and A represents an anti-vaccinator strategy. Now, let z represent the proportion of pro-vaccinators (V) in this arbitrary population at some given time t (and consequently $1-z$ represents the remainder of the population adopting strategy A). Using a functional form, the respective payoff for a pro-vaccinator is given by:

$$\mathcal{P}_V = -c + \phi z(t) \tag{1.1}$$

where c represents an associated cost or risk if choosing vaccination such as taking time to receive the vaccine. If an individual chooses to vaccinate, that individual will gain the support of the local community ϕ. This term is synonymous with peer pressure or social norms, which can influence individuals to either keep or switch their strategy based on its relative strength and the proportion of pro-vaccinators in the population. In contrast, the payoff function for an anti-vaccinator is given by

$$\mathcal{P}_A = -qI(t) + \phi(1 - z(t)) \tag{1.2}$$

where q represents the likelihood of being infected and its impact on the player's utility, scaled by the proportion of the population that is infected $I(t)$. Similar to pro-vaccinators, anti-vaccinators are also supported by local community members who adopt the same strategy (also represented by ϕ). Note that the greater the proportion of anti-vaccinators in the population, the more likely it is that an individual will transition from a pro-vaccinator strategy to an anti-vaccinator strategy, and *vice versa*. Using evolutionary game theory and techniques developed by Hofbauer and Sigmund [93] (explained in more detail for each model in Chapters 3 and 4), the dynamics of pro-vaccinators is given by:

$$\begin{aligned} \frac{dz}{dt} &= kz(1-z)(\mathcal{P}_V - \mathcal{P}_A) && (1.3) \\ &= kz(1-z)(-c + qI(t) + \phi(2z-1)) && (1.4) \end{aligned}$$

where k represents social learning in the population.

In the context of vaccination, individuals may not feel the need to vaccinate if their perceived risk of infection is sufficiently low, such as due to herd immunity. The concept of *herd immunity* has been used an excuse for unvaccinated members of the population, where they perceive their safety is ensured, provided that the surrounding members of the population are vaccinated [66]. This mentality, in conjunction with anti-vaccine beliefs [109], has caused a significant delay in the eradication of treatable diseases. In the context of mathematical modelling, using Equation 1.3, if the payoff to vaccinate is sufficiently low ($\mathcal{P}_V$), the population can be influenced to transition into an anti-vaccinator state. Alternatively, if the payoff to vaccinate is sufficiently high, the population will likely adopt a pro-vaccinator strategy. Thus, using this simple methodology, mathematical models can capture the dynamic interplay between human behaviour and disease dynamic systems.

In the following chapters, we transition to environmental scenarios, where we observe the effects of incorporating a dynamic human behaviour component into coral reef and grassland ecosystems, in order to study their human-environment sustainablity. The structure of the human components will change based on the studied ecosystem, but will maintain a similar structure to the example above. Using this coupling, we can formally define our models as "coupled human-environment systems" which include a dynamic human behaviour compartment that changes based on the relative payoffs and incentives derived from the status of the environment. Prior to moving forward, some preliminary knowledge of each environmental system is required.

1.2 Caribbean Coral Reef Ecosystems

A coral reef can be described as a slowly growing ecosystem that is dependent upon mutualistic interactions to sustain itself. Each coral reef ecosystem is comprised of multiple coral polyps that have grown on the exoskeletons of a previous generation of polyps [153]. Reefs in general require a large amount of time to grow [215]. Upon each polyp's death, algal turf grow over the exoskeleton where, similar to weeds in a garden, they must be removed in order for new polyps to settle on these sites. In the Caribbean Sea, resident grazers such as the *Diadema antillarum* sea urchins would graze the turf prior to their mass mortality in 1983, and have since been mostly replaced with resident parrotfish. This process is illustrated in Figure 1.3.

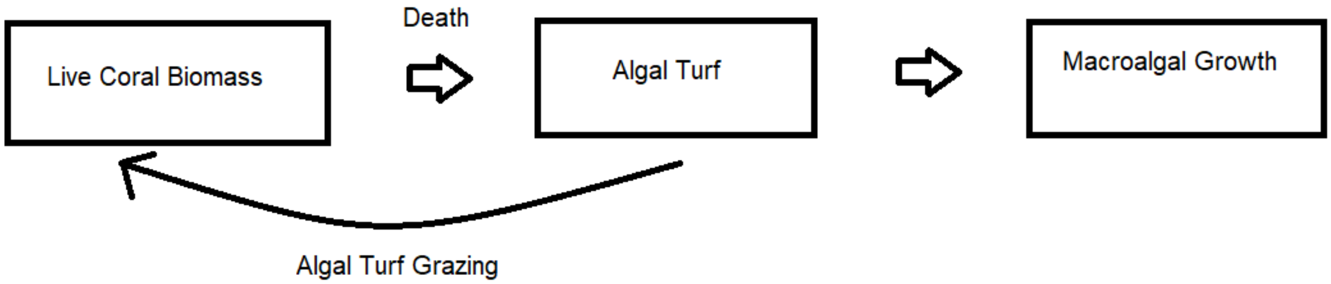

Figure 1.3: A simple diagram to visually represent the growth of coral reefs.

As stated earlier, corals require a large amount of time to grow and establish themselves into a reef formation. Due to their stationary nature, corals are heavily reliant on the mutualistic relationship with resident Zooxanthellae (algae) [163]. These organisms provide growth and nourishment to corals via photosynthetic processes. In return, excreted coral waste acts as nutrients for the Zooxanthellae. Corals are extremely sensitive organisms, where small changes in water quality can cause them to dispel Zooxanthellae, leaving reefs bleached and impairing internal coral functions [25]. Numerous factors have been known to cause bleaching events, such as excessive sediment deposition, acidity levels, or increases in water temperature. Similar effects have been documented by simply touching a coral [69].

Overfishing has led to severe depletion of the parrotfish population. With reduced grazing activity, significant levels of turf can develop, preventing new polyps from establishing. Efforts have been made to protect these ecosystems, such as through implementing fishing limitations. In addition, crude forms of exploitation have been outlawed, such as "blast fishing" which utilizes explosive devices to stun or kill fish redand also incurs significant damage to the ecosystem [**?**]. Despite the implementation of policies and fines, exploitation continues to persist.

In Chapter 2, modelling of this ecological system will be presented and discussed in greater detail. We utilize a natural system model that was previously developed for the Caribbean reef system and introduce a dynamic human behavioural coupling. We explore the changes in predictions for reef recovery and sustainability utilizing a game-theoretic scenario between exploiters and conservers. We contribute to the discussion on habitat preservation with our CHES model to closely observe the effects of interactions between exploiters and conservationists on the integrity of the reef ecosystem.

1.3 Southeastern Australian Grassland Ecosystem

A grassland ecosystem can be defined as an ecosystem that is dominated with herbaceous vegetation and shrubs [226]. Grasslands contribute to the maintenance of plant and animal species, provide grazing material for livestock, and have sometimes seen transitions into other types of land. Maintenance can be performed pastorally using livestock, but have been demonstrated with naturally occurring fire or extreme temperate conditions.

Degradation of Australian grasslands has already been well documented. Research performed by Williams and Cary highlighted the human threat to the ecosystem [232] due to aesthetic preferences regarding urbanization. Alongside human desires, industrial services need to be established in order to promote growth and development of the human population. Land transformation and pollution can lead to changes in ecosystem dynamics. As an example, consider lake dynamics with excessive pollution. If pollution is minimal, lake ecosystem services can mitigate the damage. Alternatively, if pollution is sufficiently high, a threshold can be crossed, causing a clouding process known as eutrophication that significantly disrupts lake dynamics [85]. Although this example is simplistic, it is representative of the trajectories ecosystems can take under the impact of human actions.

In some cases, ecosystems can be threatened due to the competitive interactions caused by the introduction of exotic pests. A simple example would be to consider the invasive agricultural pest known as the Japanese beetle (*Popillia japonica*) which was introduced to Canada in 1939 [5]. Following its introduction, numerous infestations have occurred, threatening vineyards, croplands, etc., while treatment programs have been unable to completely eradicate the pest. Similarly, exotic grasses have been introduced to the South-eastern Australian grasslands, threatening the native species. Due to the ability of exotic grasses to capture sunlight more efficiently they can outcompete native species [210].

In Chapter 3, we investigate the competitive interaction between exotic and native grass biomasses when coupled to a human behaviour component characterizing local efforts to mitigate industrial nutrient deposition. Development of the human component is similar to its formulation in the coral reef model. Using this model, we explore the parameter space to find socio-ecological conditions that lead to the preservation of the native species. Furthermore, we obtain qualitative insights on the efficacy of local interventions based on the costs attributed to adopting these mitigatory techniques.

1.4 Thesis Outline

In this thesis we first illustrate the predictions and explore the insights provided by two different CHES models focused on two different ecological systems. In the first environmental system, we investigate the effects of dynamic human interactions on a Caribbean coral reef ecosystem. Specifically, we study the effects of varied levels of exploitation of local reef-grazing fish (parrotfish) on the growth and recovery trajectories of coral reefs. In the second system, we study the effects of local nutrient deposition on south-eastern Australian grassland ecosystems and its effects on the competitive nature of exotic and native grass biomasses. These systems were both obtained by modifying existing ecosystem models to incorporate a human behavioural dynamics compartment. We observe the changes in the predictions of each model based on a range of parameter values for the human system. Finally, we explore the definition of CHES models and provide a review of the different modelling approaches that have been developed over the span of a decade. The thesis is organized as follows:

In Chapter 2 a CHES model is developed using a previously established model by Blackwood et al. [27]. The formulation of the human component is shown in detail, outlining the assumptions for each payoff function alongside the calibration of the human parameters. Once our baseline parameter settings are established, we use our model to generate simulations of reef ecosystem state based on different parameter ranges. Furthermore, we explore socio-ecological conditions that promote reef recovery. This chapter has been published in *Scientific Reports* [209].

In Chapter 3 we develop another CHES model based on the framework previously published by Chisholm et al. [45]. We transition to grasslands, but use similar techniques to develop the behavioural components of grassland preservers and polluters. We establish the costs and benefits associated with adopting each strategy and develop the human component of the model. The human component was calibrated and the baseline parameters established after correspondence with Dr. Ryan Chisholm. We explore how model dynamical regimes depend on the parameter space and we develop socio-ecological insights for successful native grassland preservation. This chapter has been published in *Ecological Modelling* [210].

In Chapter 4, we continue the discussion of human behaviour and its implementation in modelling through a systematic review. Chapters 2 and 3 utilize differential equations (DEs) to model CHES, but many other modelling approaches are possible and we explore them in this chapter. This chapter serves as a review of CHES models from 2009 to 2019. We discuss each approach in detail, potential avenues of future research, and limitations of each approach. Work from this chapter is in preparation for submission to a peer-reviewed journal.

In Chapter 5 we conclude with a discussion of the CHES models developed in this thesis. The results of our models are compared, discussed in more detail and their limitations are stated. We tie our discussion of these two models together with our review on CHES modelling techniques and discuss future plans to build on and improve our implementations, and extend it to the growth and development of future CHES models in the field of environmental science.

Chapter 2

Socio-ecological Dynamics of Caribbean Coral Reef Ecosystems and Conservation Opinion Propagation

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This Chapter is based on the paper : Thampi, Vivek A., Madhur Anand, and Chris T. Bauch. “Socio-ecological dynamics of Caribbean coral reef ecosystems and conservation opinion propagation.” Scientific reports 8.1 (2018): 1-11.

2.1 Abstract

The Caribbean coral reef ecosystem has experienced a long history of deterioration due to various stressors. For instance, over-fishing of parrotfish – an important grazer of macroalgae that can prevent destructive overgrowth of macroalgae – has threatened reef ecosystems in recent decades and stimulated conservation efforts such as the formation of marine protected areas. Here we develop a mathematical model of coupled socio-ecological interactions between reef dynamics and conservation opinion dynamics to better understand how natural and human factors interact individually and in combination to determine coral reef cover. We find that the coupling of opinion and reef systems generates complex dynamics that are difficult to anticipate without the use of a model. For instance, instead of converging to a stable state of constant coral cover and conservationist opinion, the system can oscillate between low and high live coral cover as human opinion oscillates in a boom-bust cycle between complacency and concern. Out of various possible parameter manipulations, we also find that raising awareness of coral reef endangerment best avoids counter-productive nonlinear feedbacks and always increases and stabilizes live coral reef cover. In conclusion, an improved understanding of coupled opinion-reef dynamics under anthropogenic stressors is possible using coupled socio-ecological models, and such models should be further researched.

2.2 Introduction

Coral reef ecosystems are complex aquatic systems structurally composed of scleractinian (hard or stony) corals situated on the accumulated dead exoskeletons of their ancestors [23]. Coral reefs are host to a diverse combination of organisms while offering a multitude of services to the population surrounding them. Each coral reef consists of the multiple base units–polyps–that over a large period of time develop into large coral reef ecosystems which often act as a magnet for both tourism and fishing.

A key asset for coral growth is the zooxanthellae (algae), which is a unicellular organism capable of performing photosynthetic processes. In coral reefs, zooxanthellae exist in a symbiotic relationship with coral polyps (although we note that zooxanthellae can also exist in isolation). In order to acquire nutrients, corals secrete a chemical signal causing the zooxanthellae in the coral tissue to release organic compounds created during photosynthetic processes [148]. In return, zooxanthellae acquire nutrients such as nitrogen in higher densities via the coral excrement [148]. This mutual feedback cycle promotes growth and development of both species.

Historically, Caribbean coral reefs have been subjected to various stressors, such as coral disease and hurricane-induced destruction [153, 74]. Despite the influence of these and other stressors, Caribbean coral reefs have demonstrated considerable resilience against past disturbances. For instance, Caribbean coral reefs began recovering quickly after Hurricane Allen over a 3 year period from 1980 to 1983 [74, 153]. This resilience is widely attributed to the presence of its dominant grazers, the *Diadema antillarum* sea urchins [74, 102, 153]. The mutualistic relationship between the urchins and the coral reefs provided the urchin population with nourishment in the form of algal turf (Figure 4.2) [153]. However, the mass mortality of *Diadema antillarum* in 1983, possibly on account of multiple stressors [2], appears to have reduced the resilience of coral reefs and caused a period of decline in the face of stressors that reefs previously demonstrated resilience against, such as hurricanes [153]. Parrotfish are now considered the primary grazers of the ecosystem, but overfishing of parrotfish has further reduced coral reef resilience, underscoring the need for effective conservation measures [211, 102].

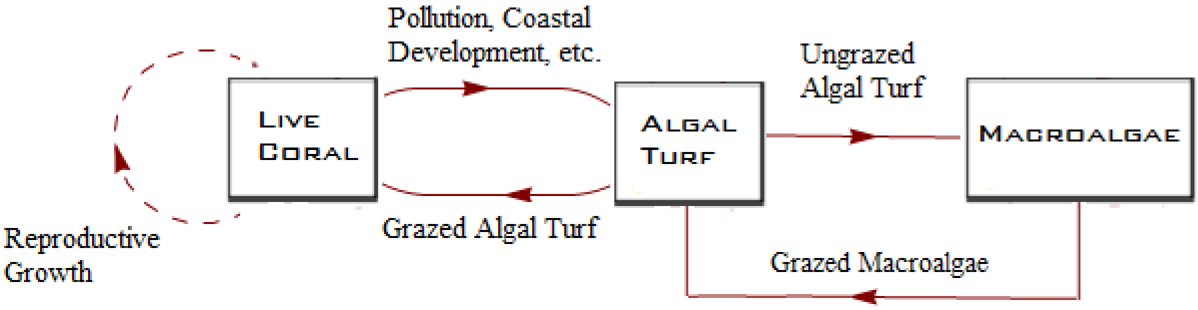

Figure 2.1: Flowchart illustrating the basic dynamics of the coral reef ecosystem

Algal formations are detrimental to the integrity of coral reefs. Invasion of macroalgae is known to prevent reef growth due to their colonization of potential growth sites for new polyps. In the absence of grazing, macroalgal contact with corals has been known to cause higher levels of coral mortality and bleaching [102]. Multiple genera of these algae exist, but for this chapter we only consider two species of macroalgae–*Lobophora variegata* whose effects on the reefs induce heightened levels of coral mortality and an extended state of coral bleaching, and *Dictyota* species which cause heightened coral mortality and rapid coral tissue deterioration [234, 64].

Mathematical modelling has been an invaluable tool for many decades, offering insight into real-world systems with applications ranging from classical predator-prey dynamics [127], to infectious disease dynamics [160]. Relatively detailed mathematical models with empirically-informed model structure and parameter estimates can be useful for predicting future population dynamics under various possible scenarios. However, even simple models can be useful for gaining potential insights into the dynamics of ecosystems where the component species interact nonlinearly [143]. Research on coral reef ecosystem dynamics has included mathematical models that explore the impact of various stressors on the coral reefs, including the effect of exploitation [153, 27]. Among other findings, these models predict that when predation and/or fishing of grazers is sufficiently low, the system exhibits a critical transition beyond which the growth and recovery of the ecosystem are possible [27, 153].

Models typically treat human influence on coral reefs as constant and incorporate it through a fixed model parameter, such as fishing intensity. In contrast, coupled socio-ecological models (or equivalently, human-environment system models or coupled human-and-natural system models) formulate a separate dynamical equation for humans, and allow for human systems and ecological systems to influence one another. To capture the effect of dynamic human social behaviour, elements of evolutionary game theory have been previously employed in order to capture social learning dynamics, in which human opinions or strategies actively change based on the current condition of the environment [18]. Humans are assumed to follow an imitation dynamic whereby individuals imitate more successful strategies that they observe in other individuals. Socioecological models have already been established in ecosystem management [17, 115], forestry/grasslands [99, 89, 115, 124], land-use change [90] and vaccination [18, 160] but have not been utilized modelling the dynamics of coral reef ecosystems, to our knowledge. For many systems, interactions between humans and natural systems is complex and does not need to be unidirectional [71]. This approach of coupling human social dynamics to environmental or ecological dynamics contrasts with treating human behaviour as a fixed parameter, as in much previous research on coral reef dynamics, enabling us to model how human opinion about reef conservation and fishing restrictions responds to changes in coral reef cover and vice versa.

The impact of dynamic human behaviour on coral reef sustainability therefore requires further investigation via theoretical modelling. With evidence of various anthropogenic impacts reflected in current research together with ongoing efforts to promote reef conservation through marine protected areas and other measures [9], mathematical models of coral reef ecosystem dynamics can benefit from including a coupling to a human population with evolving opinions. By modelling human behaviour as an adaptive, dynamically evolving phenomenon, a deeper and richer understanding of the anthropogenic stresses in a given system over longer time horizons — including potential surprises due to nonlinear interactions – can be achieved. With further development, this approach has the potential to assist developing more effective coral reef conservation by helping policymakers avoid counter-productive response by human populations and/or by harnessing processes like social learning to optimize conservation.

Here, we create a coupled socio-ecological coral reef model by combining an existing model of a Caribbean reef ecosystem including parrotfish fishing, with an imitation dynamic model of human opinion spread and behaviour. Our objective is to explore how adaptive human feedback influences the viability of coral reefs, and also to explore the potential dynamics that may emerge in a socio-ecological reef-opinion system that may not be recognized from studying these systems in isolation from one another. We use the model to explore the impact of social norms, sensitivity of the human population to coral loss, and social learning on the coral reef ecosystem. Through these investigations we are able to explore conditions that could improve the long-term viability of the Caribbean coral reef ecosystem.

2.3 Model

2.3.1 Model Overview

We built our socio-ecological model by expanding a previous coral reef ecosystem model by Blackwood *et al.* [27]. We used this model because it is relatively recent and well-documented, and because it is formulated as a system of ordinary differential equations, which facilitates its incorporation into a socio-ecological model based on replicator (imitation dynamic) equations — a type of differential equation model. This model was in turn a modified version of the mathematical model developed by Mumby et al. [151]. The latter authors observed a hysteretic feedback loop based on the dynamics of three key components of the ecosystem — macroalgae (M), live coral (C) and algal turf (T). The model was expanded by Blackwood *et al.* to include parrotfish density (P) — a key component of the ecosystem–into the model. By incorporating parrotfish grazing dynamics into the model, with loss based on a fixed fishing pressure, the authors were able to determine trajectories for recovery based the fishing pressure. Originally, Blackwood *et al.* extended the model to include grazing based on the relative density of parrotfish which was affected by the overall fishing pressure in the system [27].

We extended the Blackwood *et al.* model by adding a fifth equation representing the proportion x of the human population currently adopting an opinion in favour of coral reef conservation by reducing parrotfish fishing (we will call these individuals "protectors" for brevity). We consider a human population at the level of local organizations or national populations who can influence decisions about fishery regulation in national waters. The resulting system of five equations for the proportion of macroalgae, live coral, algal turf, parrotfish density, and human opinion is given by:

$$\frac{dM}{dt} = aMC - \frac{PM}{M+T} + \gamma MT \tag{2.1a}$$

$$\frac{dC}{dt} = rTC - dC - aMC \tag{2.1b}$$

$$\frac{dT}{dt} = \frac{PM}{M+T} - \gamma MT - rTC + dC \tag{2.1c}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{P}{K(C)}\right) - \sigma P(1-x) \tag{2.1d}$$

$$\frac{dx}{dt} = \kappa x(1-x)(-1 + J(1-C) - \sigma P(1-x) + \phi(2x-1)) \tag{2.1e}$$

The first four equations above are identical to the model of Blackwood *et al.* except that constant parrotfish fishing intensity has been replaced by the coupling term $\sigma P(1-x)$ which reflects the influence of public opinion. We do not explicitly model the mechanism by which public opinion influences fishing intensity, but in real populations it could be applied through public pressure and/or special interest group pressure in support of legislation for a marine protected area, for instance. Public opinion (x) in turn is influenced by the coral reef cover C (the $J(1-C)$ term); the economic and social benefits of parrotfish fishing (the $\sigma P(1-x)$ term); a fixed cost of reducing parrotfish fishing through marine protected areas (this is represented by the -1 term since the x equation has already been rescaled in the above equations; see Methods for details); and the effects of injunctive social norms (the $\phi(2x-1)$ term). The parameter ϕ represents the strength of injunctive social norms which creates an incentive for individuals to switch to the dominant strategy in the population (i.e. when $x > \frac{1}{2}$ the net incentive from social norms favours switching to conservationism since that is the majority behaviour, and vice versa for $x < \frac{1}{2}$).

The model assumes that macroalgae overgrow coral at a rate of a per year and spread over ungrazed algal turf over a rate of γ per year. In addition, corals overgrow grazed algal turf at a rate of r per year and have a natural mortality of d per year. Since parrotfish have become the primary grazers in these ecosystems [102, 154], the model focuses on parrotfish population dynamics, grazing and fishing. The model assumes logistic growth of the parrotfish population, proportional to the amount of algal turf and macroalgae grazed, with a growth rate of s per year; a carrying capacity term reflective of the current proportion of live coral, $K(C)$; and a fishing rate based on the number of protectors, $\sigma(1-x)$ [27], in the population where x represents the proportion of protectors in the population and $1-x$ represents the proportion of the population opting to continue fishing and, effectively, increase the total fishing pressure. Details pertaining to the development of the model and the human dynamic, and the definition of the parameters are discussed in Section 2.3.2.

Our model used the same baseline parameter values for the coral reef component as the models of Blackwood *et al* and Mumby *et al* [153, 27], and have been included in Table 2.1 below. In particular, we assumed the rate of macroalgal overgrowth of corals, $a = 0.1$ yr^{-1}, the rate of macroalgal growth over ungrazed algal turf, $\gamma = 0.8$ yr^{-1}, the rate of coral growth over grazed algal turf $r = 1$ yr^{-1}, coral mortality rate, $d = 0.44$ yr^{-1}, and the parrotfish growth rate, $s = 0.49$ yr^{-1}, consistent with the previous models. The parameter representing the per capita (exploiters) rate of human-induced parrotfish mortality σ can vary over a range of [0,1], but baseline was assumed at 0.5 yr^{-1}. Values for κ, J and ϕ were calibrated to yield biologically and sociologically plausible behaviour as follows. Coral reefs associated with various Caribbean islands were impacted differently by stressors. However, overall live coral cover declined significantly across the Caribbean region over several decades, causing macroalgal formations to dominate many Caribbean coral reef ecosystems [102]. Degradation of the coral reefs stimulated conservationism and a demand for marine protected areas [151]. Hence, we sought values of κ, J and ϕ such that coral cover declines from an initially high level to be replaced by growing macroalgal turf due to parrotfish over-fishing, which in turns stimulates a growth in protector opinion that restrains parrotfish fishing and stabilizes coral cover. The resulting model trajectory for coral reef cover from $t = 5$ to $t = 45$ years (Figure 2) is qualitatively similar to the decline in coral reef cover reported by Jackson *et al.* over three successive time intervals (1969-1983, 1984-1998 and 1999-2011) from 34.8% to 19.1% to 16.3% [102]. Longitudinal data on coral reef conservation opinions in Caribbean populations are not available, so as a proxy we used longitudinal data on conservation opinions on a range of issues in the United States from 1965 to 1990, a time period corresponding to a significant shift in attitudes regarding conservation. Our baseline change in coral reef conservation opinion from $t = 20$ to $t = 45$ years (Figure 2.2) was likewise calibrated to the observed changes in the United States data.

Model simulations at the baseline parameter values follow a trajectory of live coral cover similar to that observed in populations where coral decline has stimulated successful conservationism (Figure 2.2) [102]. Parrotfish start out initially low due to overfishing and lack of conservationism, which causes a gradual decline in coral cover. However, when coral cover gets too low, human opinion shifts in favour of conservationism.

2.3.2 Model Construction

As mentioned previously, a Caribbean coral reefs compartmental model by Blackwood et al [27] was extended to a coupled human-environment system. The original model is represented by the following system of differential equations:

$$\frac{dM}{dt} = aMC - \frac{PM}{M+T} + \gamma MT \tag{2.2a}$$

$$\frac{dC}{dt} = rTC - dC - aMC \tag{2.2b}$$

$$\frac{dT}{dt} = \frac{PM}{M+T} + \gamma MT - rTC + dC \tag{2.2c}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{P}{K(C)}\right) - fP \tag{2.2d}$$

The effect of human influence in the original model is represented by the fixed parameter *f*. However, human opinion is as dynamic as ecosystem dynamics and can change based on

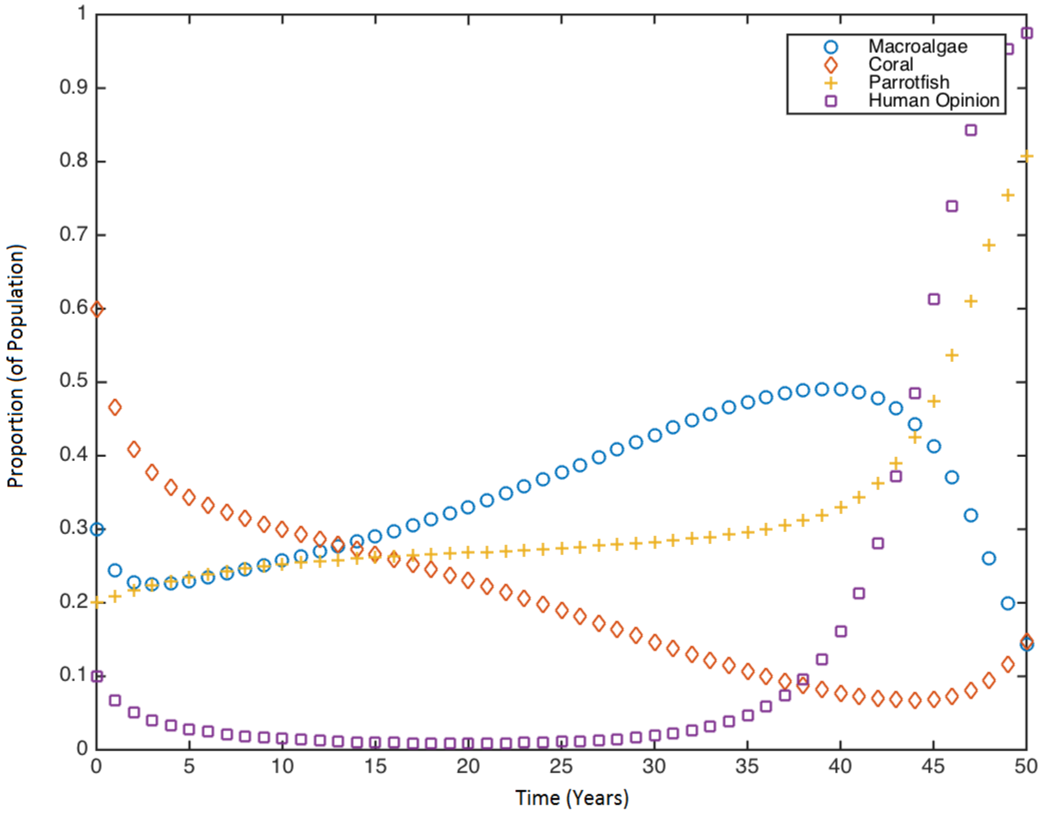

Figure 2.2: Time series of reef-opinion dynamics at baseline parameter values, showing the response of the human population to declining coral reef cover. Baseline parameter values are $\kappa = 1.014\ yr^{-1}$, $J = 1.68$, $\phi = 0.2$. Initial conditions are $M(0) = 0.3$, $C(0) = 0.6$, $P(0) = 0.2$, $x(0) = 0.1$.

the various policies and laws implemented in order to promote conservation, as well as by responses to coral reef endangerment. Thus, in order to introduce human strategies into the model, we introduce a human-behavioural differential equation in the system.

It is well-known that the coral reefs are highly regarded as a tourist attraction [39, 43]. As their condition diminishes, the reef loses value, both ecologically and economically. In order to increase their utility, conservation strategies can be implemented to promote recovery and increase the value of the resource [1]. To generate the basic human behaviour dynamic, utility equations are developed, modelling individuals residing in the above regions, adopting either the “protector” strategy or the “exploiter” strategy.

Similar to vaccination dynamics, we use utility functions to quantify human preferences [160]. We consider a population making decisions about whether to exploit parrotfish or protect the coral reef. Let U_P represent the perceived utility for protecting coral and U_N represent the perceived utility for not protecting coral (i.e. parrotfish exploitation). Let x represent the proportion of the population who support coral protection. Consequently, $(1-x)$ represents the proportion of the population who do not want to protect the coral reefs (and, thus support parrotfish fishing). We assume that the utility function for protectors is given by the following equation.

$$U_P = -q + m(1 - C) + \delta x, \tag{2.3}$$

Where q represents the cost to protect coral (for instance, the cost to set up and monitor a protected area); m is a proportionality constant that controls the sensitivity of the protector utility to coral density C; and δ controls the strength of injunctive social norms, as in similar behavioural models [160]. This utility function captures how the utility (or motivation) for protection increases as coral C becomes rare.

Similarly, the utility function for non-protectors is given by:

$$U_N = \sigma P(1 - x) + \delta(1 - x). \tag{2.4}$$

where σ is the maximal fishing rate and P is the density of parrotfish in the ecosystem. This utility function captures how the utility of parrotfish exploitation is higher when more parrotfish are exploited, however, a high proportion of protectors in the population will reduce exploitation.

When $U_P - U_N > 0$ coral conservation is a more valuable strategy, whereas if $U_N - U_P > 0$, parrotfish exploitation is preferred. Let k represent the time rate at which individuals sample others in the population [18]. If $U_P - U_N > 0$, then the rate at which non-protectors switch to a protector strategy is given by

$$\frac{dx}{dt} = (1 - x)kx(U_P - U_N). \tag{2.5}$$

and if $U_P - U_N \leq 0$ then non-protectors never switch. Alternatively, if $-(U_P - U_N) > 0$, then the equation of motion is represented by:

$$\frac{dx}{dt} = -kx(1 - x)(U_N - U_P), \tag{2.6}$$

and if $U_P - U_N \geq 0$ then protectors never switch. We sum these two processes to get the total rate of change of x:

$$\frac{dx}{dt} = kx(1-x)(U_P - U_N). \tag{2.7}$$

Let $\kappa = kq$, $J = \frac{m}{q}$ and $\phi = \frac{\delta}{q}$ be the rescaled social learning rate, sensitivity term and strength of injunctive social norms respectively. The human behaviour equation thus becomes:

$$\frac{dx}{dt} = \kappa x(1-x)(-1 + J(1-C) - \sigma P(1-x) + \phi(2x-1)). \tag{2.8}$$

In addition to incorporating the human behaviour model, the compartment describing the dynamics of the parrotfish density must also be modified so that parrotfish exploitation slows down when conservationists are more dominant. This change results in the system:

$$\begin{aligned}
\frac{dM}{dt} &= aMC - \frac{PM}{M+T} + \gamma MT && \text{(2.9a)}\\
\frac{dC}{dt} &= rTC - dC - aMC && \text{(2.9b)}\\
\frac{dT}{dt} &= \frac{PM}{M+T} - \gamma MT - rTC + dC && \text{(2.9c)}\\
\frac{dP}{dt} &= sP\left(1 - \frac{P}{K(C)}\right) - \sigma P(1-x) && \text{(2.9d)}\\
\frac{dx}{dt} &= \kappa x(1-x)(-1 + J(1-C) - \sigma P(1-x) + \phi(2x-1)) && \text{(2.9e)}
\end{aligned}$$

Note that the rednatural death rate term is omitted from the parrotfish dynamics model as its effect is inherited by the loss rate due to predation. Parameters and their baselines values are provided in Table 2.1 below.

Parameter	**Definition**	**Value(s)**	**Units**	**Source**
$\mathbf{a}$	rate of macroalgal overgrowth over corals	0.1	year^{-1}	[27]
γ	rate macroalgal growth over ungrazed algal turfs	0.8	year^{-1}	[27]
$\mathbf{r}$	rate of coral growth over grazed algal turf	1	year^{-1}	[27]
$\mathbf{d}$	coral mortality rate	0.44	year^{-1}	[27]
$\mathbf{s}$	growth rate of parrotfish	0.49	year^{-1}	[27]
$K(C)$	non-dimensional term which limits the carrying capacity of parrotfish as a function of coral cover	1-C	–	[27]
σ	maximum parrotfish mortality rate due to overfishing	0.5 $(0 \leq \sigma \leq 1)$	year^{-1}	[27]
$\kappa(= kq)$	the product of the combined imitation rate (k) at which people sample others and switch strategies, and the cost of adopting a protector strategy q	1.014	year^{-1}	calibrated
$\mathbf{J}$	sensitivity of humans to current density of coral cover	1.68	–	calibrated
ϕ	The rescaled strength of injunctive social norms	0.2	–	calibrated

Table 2.1: Table of parameters along with their baseline values and sources

2.4 Results

Time series of the model dynamics across a selection of parameter values illustrate the range of possible dynamics of this socio-ecological system. For instance, when the parrotfish growth rate s is zero (Figure 2.3 **a,b**), the system enters an undesirable equilibrium state of high macroalgal cover and no live coral without (a) or with (b) parrotfish survival. In both cases conservationism eventually becomes strong, but because the parrotfish population is insufficient, the coral reefs cannot survive. However, under parameter conditions where parrotfish growth rate is sufficiently high, the system is predicted to recover and achieve (Figures 2.3 c,e,f). The system stabilizes as a 'Macroalgae-Free Equilibrium' (MFE). This can occur without anthropogenic assistance, if the fishing rate (even at maximal levels) is less than the parrotfish growth rate even in the absence of marine protected areas — MFE-NA ($s = 0.3$,$\sigma = 0.05$), Figure 2.3 **c**), or with human assistance — MFE-A, (Figure 2.3 **e,f**).

It is also possible for the model to exhibit oscillations over long time horizons. During periods of sufficient conservationism in the human population, the system successfully recovers. During periods of sustained recovery, coral reef cover becomes high again, which means that parrotfish exploitation becomes attractive compared to continued conservationism (the human population becomes complacent about conservationism). As a result, conservation eventually becomes less popular and coral reefs correspondingly begin to decline again ($s = 0.5$, $\sigma = 0.2$) (Figure 2.3 **d**). In some cases, this oscillatory behaviour is predicted to wane, and the utility to protect permanently outweighs the utility to not protect, yielding an MFE-A over the long term (Figure 2.3 **e**). Additional time series depicting other, less common dynamical regimes of the model appear in Appendix B, including variations of the catastrophic equilibrium for parameter values away from baseline values.

To explore model dynamics more systematically we generated a series of parameter planes. A parameter plane shows how model dynamics vary under changes in two different model parameters. The plane has a model parameter on each axis, and indicates the dynamics that occur for each possible pair of parameter values. For each parameter plane, all parameters were held at their baseline values except for the two parameters being varied in the plot. Solutions were generated using MATLAB. Time series were generated for each pair of values under a range of initial conditions for M, C, P and x, and their long-term states were identified. Gnuplot was used to render the parameter planes.

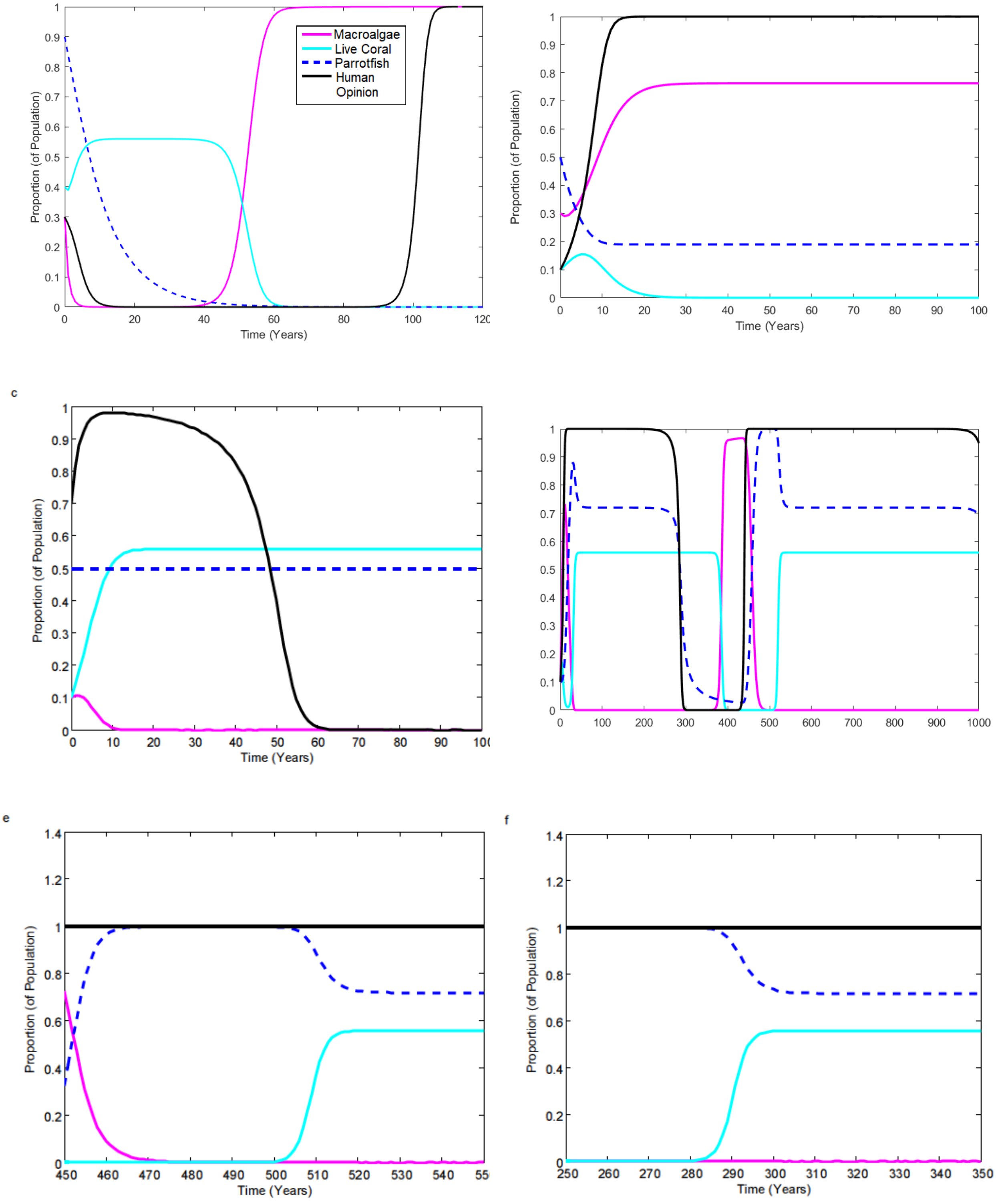

Figure 2.3: Time series depicting : **(a)** - The catastrophic equilibrium with complete parrotfish eradication, where $s = 0$, and $\sigma = 0.1$. **(b)** - the catastrophic equilibrium with parrotfish survival, where $s = 0$, and $\sigma = 0.15$. **(c)** - the unassisted macroalgae-free equilibrium, where $s = 0.3$, and $\sigma = 0.05$. **(d)** - oscillatory behaviour, where $s = 0.2$, and $\sigma = 0.5$. **(e)** oscillatory behaviour which eventually converges to the assisted macroalgae-free equilibrium, where $s = \sigma = 0.4$. **(f)** - the assisted macroalgae-free equilibrium, $s = 0.35$, and $\sigma = 0.5$. Note that these time series have different endpoints in order to observe their described behaviour. All other parameters remain at baseline values.

Using the range of parrotfish population doubling time reported in FishBase [70], we derived a range of realistic growth rate values s from 0.16/year to 0.50/year. Hence, parameter planes varying s were taken to range from 0/year to 0.6/year. Fishing rates are highly variable and since our objective was to gain qualitative insights, we chose the fishing rates to capture the full range of possible outcomes from very little fishing to fish population collapse. Population collapse in the model occurs when the maximal fishing rate exceeds the population growth rates (if conservationist opinion is weak and the fish population is low). Hence, the range for the maximal fishing rate σ also runs from 0/year to 0.6/year. Ranges for κ, J and ϕ were chosen to include enough representation of values on either side of the baseline value to capture a variety of possible dynamics.

The dynamical regimes we discovered through this process are summarized in Table 2.2 where they are divided into three primary regimes corresponding to healthy coral reefs without the need for human assistance (which is the least realistic scenario, given modern-day maximal fishing intensities); healthy coral reefs with human assistance; and dead corals. Other less common dynamical regimes are described in Table 2.3 as well.

Classification	Description
Healthy Corals - Unassisted	The most desired result. The system follows a trajectory which stabilizes in the regime governed by the human - unassisted macroalgae-free equilibrium (MFE-NA). Achieving stability within this regime implies conservation does not need to be permanently employed. The system will preserve its resilient state despite individuals not opting to promote conservation, minimizing the total costs and achieving the most desirable state of the ecosystem
Healthy Corals - Assisted	Another desired result. Similar to the MFE-NA, under certain initial conditions the system will stabilize to the human-assisted macroalgae-free equilibrium (MFE-A). Contrary to the MFE-NA, the system is incapable of maintaining its resilience without conservation. Despite the additional costs incurred to stabilize the system, this is still a desirable state as the recovery of the ecosystem has successfully been achieved, increasing attractiveness for tourism.
Dead Corals	The most undesirable result. The system converges to a state dominated by macroalgae and dead coral. The system admits 4 different variations of this result: **(i)** - A bistable regime where the system converges either to a macroalgal dominant state with complete conservation, living parrotfish and coral death or a macroalgal dominant state with complete conservation, parrotfish death and coral death. **(ii)** - Convergence to a state of complete coral death with complete macroalgal overgrowth and live parrotfish density without conservation. **(iii)** - Convergence to state of complete coral and parrotfish death and complete macroalgal overgrowth without conservation. **(iv)** - Convergence to a state devoid of macroalgae and corals, with conservation practices in motion and live parrotfish density (shown in Appendix B).

Table 2.2: Parameter plane regions and descriptions for healthy corals and dead corals.

Region	Behaviour
A	Bistable regime, converging to either a coral death equilibrium with sustainable parrotfish density or the unassisted macroalgae-free equilibrium.
B	Behaviour stabilizes to either a limit cycle or the assisted macroalgae-free equilibrium.
C	Tristable regime, stabilizing to either: **(1)** a coral death equilibrium with parrotfish survival and full conservation cooperation, **(2)** a catastrophic equilibrium with parrotfish extinction with full conservation cooperation or **(3)** the assisted macroalgae-free equilibrium.
D	Bistable regime, stabilizing to either the assisted macroalgae-free equilibrium or a state of coral and macroalgal decimation, with human-assisted parrotfish survival.
E	Tristable regime, stabilizing to either: **(1)** the unassisted macroalgae-free equilibrium, **(2)** the assisted macroalgae-free equilibrium, or **(3)** a state governed by a human-unassisted coral death equilibrium, with sustainable parrotfish density.
F	Bistable regime, stabilizing to either the unassisted macroalgae-free equilibrium or a state governed by the human-unassisted coral death equilibrium, with sustainable parrotfish density.
G	Tristable regime, with behaviour converging to either behaviour of **(D)**, or a state governed by the human-unassisted coral death equilibrium, solely governed by macroalgae.
H	Convergence to limit cycles.

Table 2.3: Additional parameter plane regions

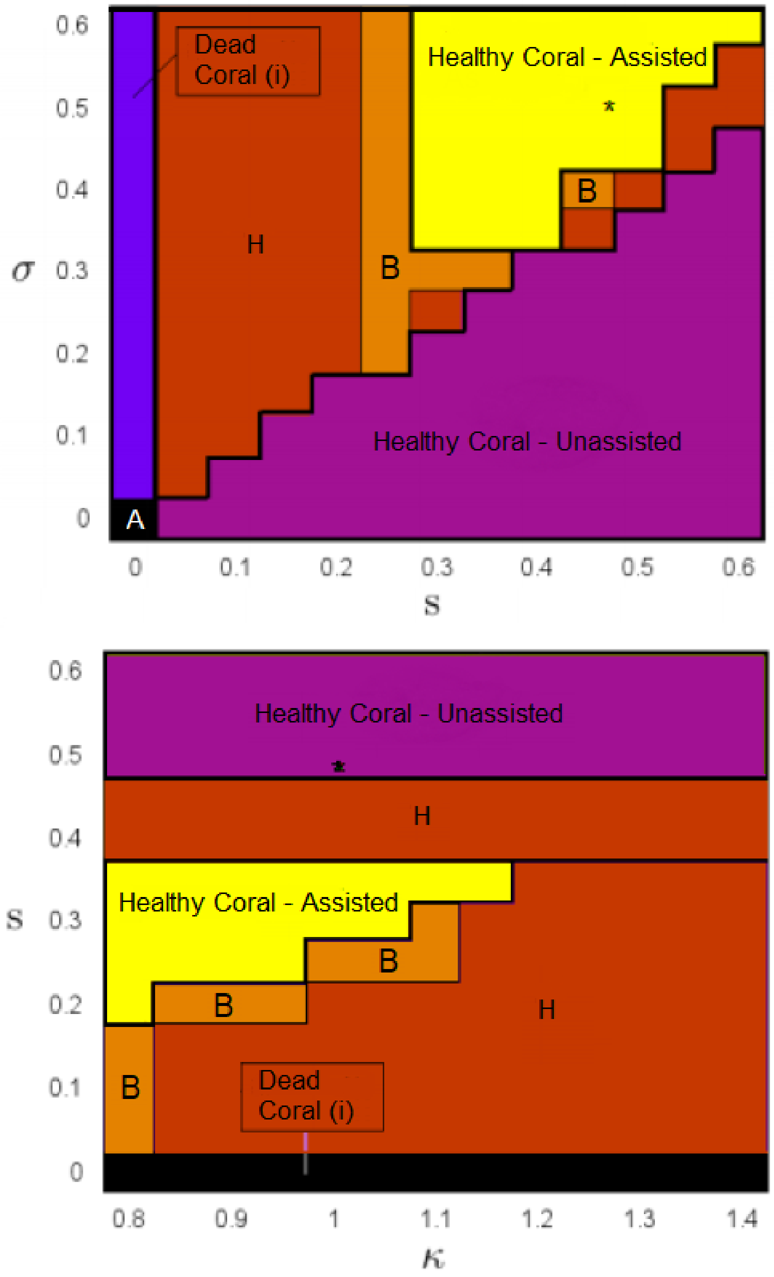

Figure 2.4: Parameter planes depicting the model dynamical regimes under parameter variations in, **(a)** - the parrotfish growth rate s and the maximal fishing rate σ, with all other parameters held at baseline values, **(b)** - the social learning rate κ and the parrotfish growth rate s, with all other parameters held at baseline values. (*) denotes the baseline value of the parameter. See Tables 1 and 2 for the interpretation of the dynamical regimes.

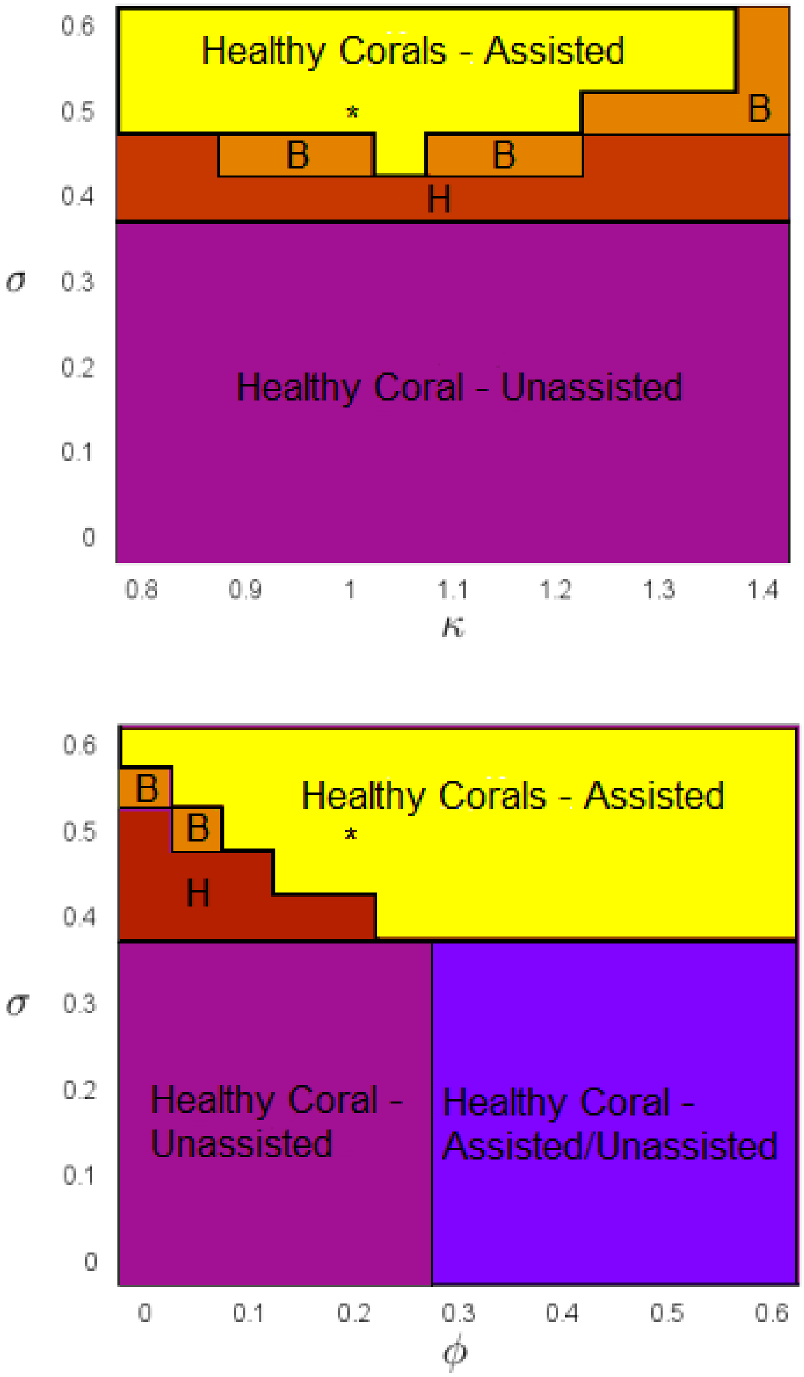

Figure 2.5: Parameter planes depicting the model dynamical regimes under parameter variations in, **(a)** - the social learning rate κ and the maximal fishing rate σ, with all other parameters held at baseline values, **(b)** - the effect of social pressure ϕ and the maximal fishing rate σ, with all other parameters held at baseline values. (*) denotes the baseline value of the parameter. See Tables 1 and 2 for the interpretation of the dynamical regimes.

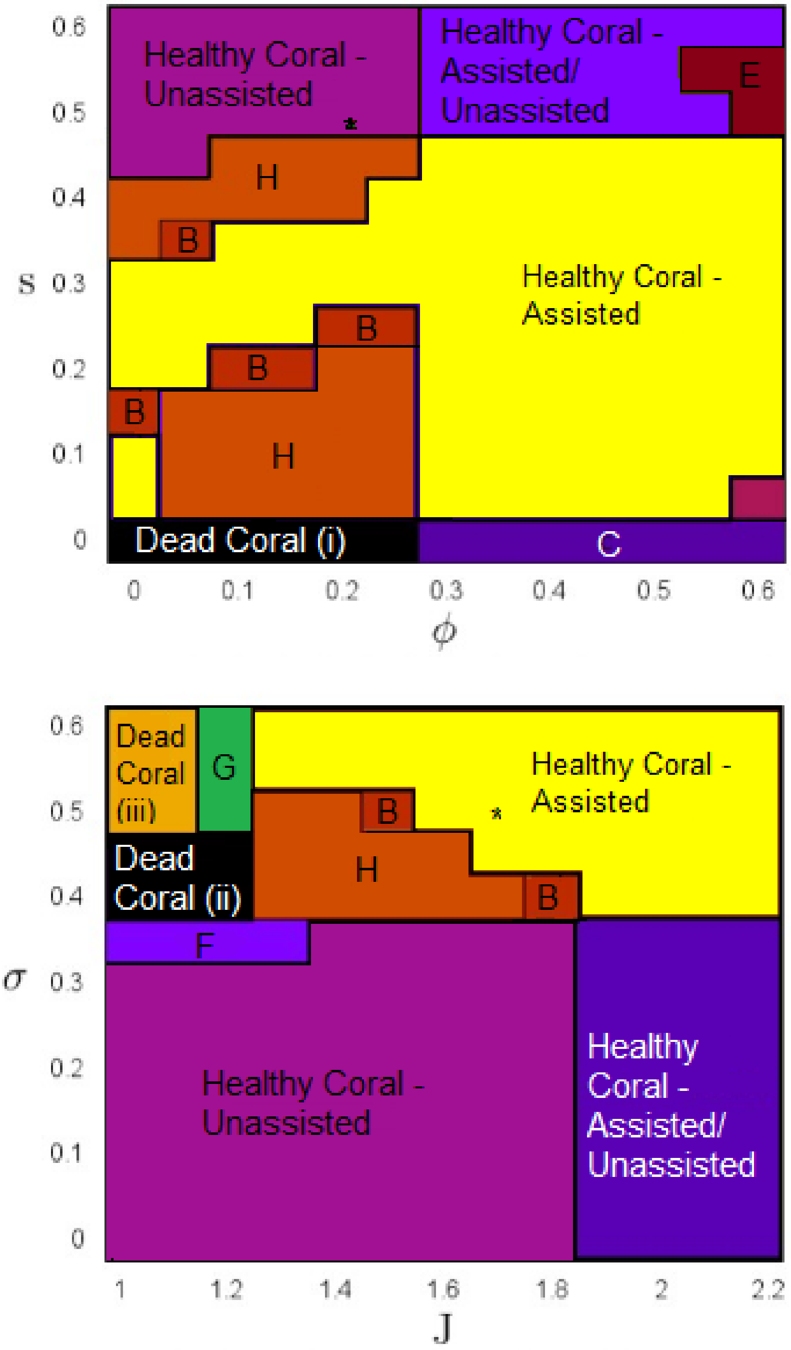

Figure 2.6: Parameter planes depicting the model dynamical regimes under parameter variations in, **(a)** - the effect of social pressure ϕ and the parrotfish growth rate s, with all other parameters held at baseline values, and **(b)** - the coral density sensitivity J and the maximal fishing rate σ, with all other parameters held at baseline values. (*) denotes the baseline value of the parameter. See Tables 1 and 2 for the interpretation of the dynamical regimes.

Model dynamics under variation in the maximal fishing rate σ and the parrotfish growth rate s depend on the relative size of these two competing parameters (Figure 2.4**(a)**). When the growth rate exceeds the fishing rate, then the coral is able to maintain itself in a healthy state without human influence, and the system follows a trajectory stabilizing to the unassisted macroalgae-free equilibrium (MFE). However, when the fishing rate exceeds the growth rate, a number of outcomes are possible. For instance, when the growth rate is too low, the coral simply dies off completely, or the system oscillates in all of its variables (regime H). When the parrotfish growth rate is higher, it is possible for coral to persist in a healthy state with human assistance, but other dynamical regimes also occur in this part of parameter space, such as oscillations once again (regime H, B). Finally, regardless of the fishing rate, when the growth rate is too small ($s \approx 0$), the corals collapse along with the parrotfish population. If the fishing rate σ is also too small, the final state of the ecosystem becomes solely dependent on the initial state, converging to the bistable regime.

Under varying levels of the social learning rate κ, the model dynamics indicated strong dependence on the relative sizes of the maximal fishing rate σ and the parrotfish growth rate s. At the baseline value of the fishing rate, when the parrotfish growth rate is sufficiently high, coral is able to follow a trajectory towards the unassisted macroalgae-free equilibrium (Figure 2.4**(b)**). Conversely, at the baseline value of the growth rate, low fishing rates cause the system to follow a trajectory to the unassisted macroalgae-free equilibrium (Figure 2.5**(a)**). In the absence of growth, the model predicts coral collapse (*Dead coral (i)*), regardless of the initial conditions of the ecosystem. Alternatively, at the baseline growth rate, a significant increase in maximal fishing intensity causes the ecosystem to transition from unassisted macroalgae-free equilibrium to assisted macroalgae-free equilibrium (Figure 2.5**(a)**). In addition, if the system exhibits small (but not too small) parrotfish growth, it does not predict coral collapse. So long as growth is present, conservation causes the ecosystem to adopt an oscillatory trajectory (regime H) or the MFE-A equilibrium (Figure 2.4**(b)**).

Variation of the strength of injunctive social norms ϕ revealed its impact on model dynamics in the context of varying the maximal fishing rate σ (Figure 2.5**(b)**) and parrotfish growth rate s (Figure 2.6**(a)**). At baseline parrotfish growth, when the maximal fishing rate sufficiently overwhelms the strength of social norms, corals are able to survive under human assistance, following a trajectory towards the assisted macroalgae-free equilibrium (Figure 2.5**(b)**). This occurs because social norms in support of conservationism can maintain the popularity of conservationism, as the population tends to conform to the majority opinion. When fishing rates are lower, then the coral is able to survive either with or without human assistance, depending on the value of ϕ. Alternatively, at baseline fishing rates, a wide variety of possible outcomes are observed for various values of the strength of social norms ϕ and the growth rate s (Figure 2.6**(a)**). For sufficiently low strength of social norms, the corals maintain a trajectory towards the unassisted macroalgae-free equilibrium. As the strength of social norms increases, the model predicts ecosystem dynamics to shift towards a bistable regime governed by either the assisted or unassisted macroalgae-free equilibrium. This occurs because social norms can also operate to suppress conservationism, if it was not sufficiently popular at first in the population. This effect can be clearly observed where a significant increase in the strength of social norms at sufficiently high levels of parrotfish growth (but not maximal growth) can force the system into a tristable state, following a trajectory towards either macroalgae-free equilibrium, or towards a catastrophic state with live parrotfish density (Regime E). The opposite effect can observed under periods of low parrotfish growth. Under certain initial conditions, social norms can operate to enhance conservationism, causing ecosystem dynamics to shift towards the assisted macroalgae-free equilibrium. Finally, for sufficiently effective social norms, and sufficiently low parrotfish growth, corals are still able to thrive with human support. If social norms become too influential, the ecosystem can either maintain its coral integrity, or be driven into a state completely devoid of macroalgae or corals, with efforts in conservation protecting the parrotfish community (Regime D), but unable to restore corals.

Model dynamics under variation in human sensitivity to coral reef rarity J and the maximal fishing rate σ depend on the relative sizes of these two parameters, and dynamics again display a complicated dependence on the parameter values (Figure 2.6**(b)**). When the fishing rate and sensitivity terms are sufficiently low, corals are able to dominate and the ecosystem converges to the unassisted macroalgae-free equilibrium. As the maximal fishing rate increases, the system produces different behaviour. For sufficiently small sensitivity, corals die out and the ecosystem follows a trajectory to either a catastrophic equilibrium with living parrotfish and no protection *(Dead coral (ii))* or the catastrophic equilibrium with no parrotfish, and no protection *(Dead coral (iii)*. For sufficiently high sensitivity, corals are able to sustain themselves in a healthy state due to human intervention, and the ecosystem stabilizes at the assisted macroalgae-free equilibrium. Lastly, for sufficiently low fishing rates and sufficiently high sensitivity, the system transitions into a bistable regime governed by both macroalgae-free equilibria. High sensitivity can force the population to adopt conservationism, despite the resilient state of the coral reefs. Depending on the initial state, efforts in conservation can become perpetually enforced, driving the system to converge to the assisted macroalgae-free equilibrium.

2.5 Discussion

We coupled an existing model of Caribbean coral reef ecosystem dynamics to a model of human opinion dynamics. The resulting coupled socio-ecological model was used to explore how coral reef viability depends on nonlinear interactions between the combination of social and ecological factors. To our knowledge, this is the first mathematical model to capture coupled socio-ecological dynamics of a coral reef ecosystem. Our model suggests that increasing human sensitivity to declining coral reef cover (for instance, through awareness programs) is the best way to support live coral and parrotfish densities. This model result is consistent with empirical findings that increased awareness of coral decline can help stimulate coral reef protection [230].

The added benefit of developing models in addition to using empirical studies is that models can help develop intuition for nonlinear feedbacks; test the logic of existing hypotheses that concern nonlinear feedback mechanisms; and suggest new ideas and new hypotheses. Here, we found that higher levels of injunctive social norms (i.e. social pressure) can also support conservationism, if the initial state of the population and other natural and economic factors already tend to support it. The system also tended to oscillate in boom-bust cycles, as human populations become complacent when coral reefs are robust, but react to support conservationism when they become endangered again. Such boom-bust cycles are commonly observed under higher rates of social learning, especially in replicator dynamics models. As such, the cyclic behaviour predicted by the model exemplifies a dynamic that could not be identified without constructing a nonlinear mathematical model. Finally, the harmful effects of increasing the maximal fishing intensity were often partially counteracted by the conservationist response that higher fishing intensities stimulated in the population, such that conservationism was able to help sustain live coral cover even at high maximal fishing rates under some conditions.

Results of sensitivity analyses revealed trends similar to that of earlier models developed by Mumby et al. and Blackwod et al. [153, 27]. When grazing is at a minimum, the models predict convergence to an equilibrium of algal overgrowth. Alternatively, when grazing is sufficiently large and critical fishing thresholds are not exceeded, all three models predict convergence to a desirable, coral-dominated state (the MFE-A is admitted in our case). In comparison to the previous ecological models, by coupling a human dynamic to the model, we have achieved a novel condition for recovery whereby both fisheries and corals are capable of thriving and coexistence is achieved (MFE-NA).

It is well-known that Caribbean coral reefs have suffered an extreme decline over the past few decades [102]. Declines in the parrotfish population have already been identified as a core concern, but additional stressors have also been identified, such as sedimentation and coral bleaching [153, 74]. The Caribbean coral reef ecosystem has shown little to no resilience since the decline of the *Diadema antillarum* sea urchins despite the implementation of conservation strategies. This is not to say that conservation has not been fruitful, as it has been documented that within smaller sanctuaries such as marine protected areas (MPAs), live coral cover has greatly increased due to conservation efforts compared to unprotected areas that can be targeted by fisheries [40, 152]. Thus, a stronger focus on parrotfish protection policies can be implemented to promote parrotfish growth and, consequently, promote recovery of the Caribbean coral reefs [225, 144]. Our results agree with these proposed actions, where increasing awareness and concern for declining coral reef cover in the general population might be the most effective and feasible way to achieve coral reef recovery.

The model assumed only two types of macroalgal growth that are the preferred food source of the dominant grazerred, but other algal growths have been documented in the reef ecosystem. Multi-species structure can influence model predictions. Hence, future models could include multiple species of algal grazers with differing effects on coral cover, different life histories, and different fishing rates. In the context of Caribbean coral reefs, it was noticed by Mantyka and Bellwood in 2007 [132] that parrotfish specialize in the consumption of calcified macroalgae, whereas another local grazer–siganids–were typically much more selective. Experimental results by Burkepile and Hay [40] illustrated the advantage of species diversity on herbivory, where a combination of parrotfish and surgeon fish can produce a stronger positive response on reef recovery compared to an ecosystem redcomprised solely of parrotfish. Specifically, within a ten month period, it was discovered that regions with greater herbivorous fish diversity increased coral cover by over 20%, whereas regions maintained by one or less herbivorous fish experienced declines in coral cover of up to 30%. The current model can be improved to incorporate this diversity.

It is a common practice in theoretical biology to start with simple models and progress to more complex models over time [143]. The reasons are that (1) simpler models are easier to analyze and require less data to develop, (2) in many situations, simpler models can provide accurate predictions even though they do not include all the details of the system being modelled, and (3) lessons learned in developing the simpler model are helpful when developing more complex models that are harder to analyze and understand. However, simplifying assumptions can influence model predictions and must be highlighted for improvement in future models. For coral reefs, there is limited availability of long-term coral cover data, so the primary use of our model was to generate insights into possible nonlinear feedbacks, suggest new hypotheses and topics for further empirical research, and test the logical validity of hypotheses. For instance, a survey that compares the effects of social learning rates (rate at which individuals read or talk about coral reefs); injunctive social norms; and sensitivity to the amount of coral reef cover (i.e. how concerned individuals become as coral becomes rarer) on attitudes toward coral reef conservation might help refine the model. Not all stressors that currently affect the reefs have been explicitly incorporated into the model, such as sediment contamination. Similarly, the model does not explicitly account for climate change (coral bleaching) in the sense that the modelled human population does not respond adaptively to coral bleaching to take steps to prevent climate change. This was excluded as a state variable because the local and national populations we are modelling can influence parrotfish fishing in their waters, but cannot take effective unilateral action on climate change. However, climate change effects can be captured partially and implicitly in our model by varying parameters such as the coral death rate, d. In the future, more sophisticated models could include specific climate change aspects such as interactions between multiple stressors like coral bleaching and growth of algal turf. Other extensions could include spatial structure, multi-species interactions, Allee effects, and more sophisticated fishery dynamics.

While opportunities for future research are clearly numerous, the incorporation of human-environment feedback into a coral reef model showed how ecological and human factors act both individually and in combination to determine coral reef health, and also showed that these interactions can be surprising and nontrivial. Overfishing and reef degradation persists, despite efforts to mitigate them [8], hence more research on the socio-ecological of coral reef ecosystems and public opinion is urgently needed. Such opportunities to expand this research offer great potential for generating biologically relevant results that can reshape and influence the dialogue around coral and parrotfish conservation in the Caribbean and elsewhere. Hence the model has generated compelling evidence that theoretical approaches to understanding socio-ecological interactions would be helpful in the efforts to restore coral reefs to their former, resilient status.

Chapter 3

Socio-ecological Mechanisms For Persistence of Native Australian Grasses Under Pressure from Nitrogen Runoff and Invasive Species

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This chapter is based on the paper : Thampi, Vivek A., Chris T. Bauch, and Madhur Anand. "Socio-ecological mechanisms for persistence of native Australian grasses under pressure from nitrogen runoff and invasive species." Ecological Modelling 413 (2019): 108830.

3.1 Abstract

Nitrogen runoff in certain southeastern Australian grasslands promotes the invasion of exotic grassland species at the expense of native species. Mitigation programs can reduce runoff and thus support native species, but they may require public awareness and support of local populations for their success, depending on how much runoff is due to local pollution. This situation represents a coupled socio-ecological system, since human activity can enable the invasion of exotic grassland species, which can in turn stimulate a social response to support the native species. Our objective is to use a mathematical model to identify potential socio-ecological mechanisms for the persistence of native grassland species, and the parameter regimes for which these mechanisms operate. We couple a model of southeastern Australian grassland dynamics with a model of human social dynamics concerning runoff mitigation. Nitrogen runoff can enter the ecosystem either through local sources under control of a human population, or through global sources not under their control. Humans learn mitigating behaviour socially, and respond to the prevalence of native and exotic grassland species. We find that socio-ecological dynamics introduce broad parameter regimes that are not present in the ecological system in isolation from the human system. We identify two mechanisms for native grassland persistence: one is associated with significant reductions in both runoff rates and/or cost of runoff reduction programs, resulting in a stable state where the native grassland species exists or dominates. A weaker mechanism associated with less favourable conditions supports persistence of the native grassland species through oscillations in species abundance and mitigation behaviour in the population. However, in some parts of this parameter regime, oscillations become too extreme to support persistence. Moreover, we find that increasing the cost of mitigation programs can decrease mitigating behaviour in the population and–more surprisingly–increase the tendency toward unstable native grassland dynamics. We conclude that multiple socio-ecological mechanisms could potentially support native species in grassland ecosystems under stress from nitrogen runoff and invasive species. Further research can refine such models to inform policy in the face of nonlinear socio-ecological responses.

3.2 Introduction

Numerous ecosystems around the world are negatively impacted by deposition processes that input excessive nutrients, pollutants, or sediments into the ecosystem through processes such as runoff. For instance, lake ecosystems are adapted to natural background rates of nitrogen input, but excessive nitrogen loading due to runoff from industrial or agricultural sources can cause lakes to flip from a clear oligographic state to a eutrophic state where the lake is overgrown by algae, causing fish populations to suffer [194, 186]. Similarly, excessive sedimentation impedes the growth and function of coral reefs [178]. Detrimental effects may spread to neighbouring ecosystems, such as when forests go through acidification [168, 92]. Rehabilitating these degraded systems and restoring the ecological balance requires significant effort over long periods of time, depending on the severity of the degradation [54].

A further example of these effects has been observed in grasslands subject to excessive levels of nitrogen deposition. For instance, exotic grassland species primarily originating from Africa and Europe are capable of invading native southeastern Australian grasslands at sufficiently high rates of nitrogen deposition [233, 45]. Exotic grasses and plants are often better competitors for sunlight and, with sufficient soil nitration, can out-compete native grassland species. This alters the biodiversity in these ecosystems and also causes a decline in grassland productivity [34, 101], while also affecting neighbouring ecosystems [233]. Some of these exotic species are more flammable than native species [55], causing fire to encroach on nonflammable regions, and/or increasing the intensity of fires. In other cases, invasion can cause other changes to the local ecology, where once open water systems are subsequently colonized by the exotic grass species, creating wetlands in their place [55]. Although exotic grassland species are not without benefits, such as providing grazing [55], the touristic, agroeconomic, and cultural benefits of native grassland species are considerable and wide-ranging [233, 232, 91, 49]. As such, many stakeholders wish to maintain and preserve grassland ecosystems based on native grassland species.

Programs such as Australia's Environmental Stewardship Program utilize incentive-based payments and promote a sense of stewardship to persuade landowners to protect and rehabilitate native ecosystems, and have shown successes in protecting Australian grasslands through landowner participation [41]. The development this and other environmental protection programs in other countries are generally stimulated by the degradation of natural ecosystems, and require public support for environment protection, expressed either through grass roots efforts or through pressure for government interventions. Hence, many natural ecological systems and human systems can be conceptualized as coupled socio-ecological (human-environment) systems: human activities impact ecological systems, and the resulting changes in the ecological system in turn influence human opinion and behaviour, often to the point of altering the trajectory of these ecosystems toward restoration of their natural states [128, 99, 112]. This human response to anthropogenic changes in natural systems is generic and is expressed in a range of systems, including forest-grassland mosaics[90], old growth forests[57, 19, 142], fisheries[46], coral reef ecosystems[209], elk-human interactions[24] and the earth's climate[96]. The human response may or may not be adequate to save the natural system concerned, however.

Many of the natural systems subject to damage from deposition processes exhibit alternative stable states, where the ecosystem can persist in one state or in a dramatically different state depending on initial system conditions [186]. An implication of alternative stable states is that gradually changing environmental conditions may push the ecosystem past a threshold, beyond which the state of the system flips abruptly to a new and contrasting state[22]. These sudden regime shifts have been observed in the cases of lake eutrophication[194, 186] and invasion of exotic grassland species in Australia[45], for example. As a result of these nontrivial dynamics, alternative stable states in ecological systems is a frequent subject of ecological modelling efforts[186, 22, 196, 45]. Human influence in most of these ecological models is treated as a fixed input parameter, but in fact these ecosystems are often part of a tightly coupled socio-ecological systems. This has simulated the development of mathematical models of coupled socio-ecological systems, wherein a dynamic human system influences a dynamic environmental system and *vice versa* [128, 99, 112]. Coupled socio-ecological models typically consist of an ecological model coupled with a human model derived from economic, social or psychological assumptions. These socio-ecological models can be used to study how nonlinear ecological and social feedbacks modify the effectiveness of policy interventions, among other phenomena. Some examples of socio-ecological models include forest harvesting[185]; forest pests[17]; forest-grassland mosaics[91, 90], common pool resource problems[115, 175]; water sharing[156]; vaccination preferences [160] and coral reef ecosystems[209]. However, a coupled socio-ecological model of alternative stable states of native and exotic grasses in a system subject to excessive nitrogen deposition has not been explored in the literature, to our knowledge.

Here we extend an existing ecological model that captures the effects of excessive nitrogen deposition on southeastern Australian grasslands[45]. The model predicts that these grasslands can exhibit bistability, with grasslands being dominated either by the native grassland species, or an alternative state dominated by the exotic grassland species due to higher nitrogen input. Nitrogen pollution in such systems may be broken down into contributions from global sources not under the control of local populations (such as atmospheric deposition from distant industrial sources) versus contributions from local sources that can be controlled by local populations (such as runoff from local fertilizer usage in agricultural lands or local industries) [216, 199]. Hence, we create a socio-ecological model of this system by coupling a model of a human social subsystem that can control the contribution of local (but not global) nitrogen sources with the existing grassland model[45]. The prevalence of mitigating behaviour in the human population depends on mitigation costs, social learning, social norms, and the current ecosystem state. Unlike most previous socio-ecological models, this allows us to model a population where only a certain proportion of environmental impact can be controlled by the local population. We formulate the model using known features of our socio-ecological study system and other similar systems. We analyze it numerically to identify asymptotic dynamical states and their dependence on model parameters. Our objective is to identify potential socio-ecological mechanisms for the persistence of native grassland species, and the parameter regimes for which these mechanisms operate. This allows us to address research questions such as: what are the impacts of changing the cost of nitrogen runoff mitigation, and what kind of dynamical regimes are observed in the socio-ecological model that would not be observed in an ecological model assuming a fixed human influence? Our approach is to explore the model's parameter space in order to gain qualitative insights into possible dynamical regimes and their dependence on parameter trends, rather than fitting the model to empirical data in order to obtain quantitative predictions for a specific population and time. In the next section we construct the model and explain its parameterization. This is followed by the Results section where we analyze model time series and parameter planes, which in turn is followed by a Discussion.

3.3 Methods

3.3.1 Model overview

The socio-ecological model divides the human population into a proportion x who support conservation of natural grasslands by reducing nitrogen runoff ("mitigators") and a proportion $1 - x$ who do not ("non-mitigators"). Support may be through individual actions to reduce runoff, or through supporting the implementation of local mitigation programs or bylaws. Individuals switch between these two strategies according to a social learning process determined by the cost of conserving native grasslands, the prevalence of native grasslands, and social norms. Grassland dynamics are determined by an existing model[45], wherein native and exotic species of grass compete, and nitrogen input may cause a critical transition from native-dominated to exotic-dominated grassland states. In our socio-ecological model, the input rate of nitrogen from local sources is reduced according to the current proportion of mitigators in the population. Additional details about the model structure and assumptions appear in redSection 3.3.2 where we first explain the existing grassland model, and then build on this to introduce the coupled socio-ecological model. We then explain our parameterization and approach to model analysis.

3.3.2 Model Construction

A previous model[45] was extended to a coupled socio-ecological system. We built on this model because it is relatively simple, exhibits alternative stable states according to nitrogen runoff rates, and was developed for the southeastern Australian grassland ecosystem. The previous model is represented by the system of differential equations:

$$\frac{dB_n}{dt} = B_n(\omega_n \nu_n A - \mu_n - m_n f_n(B_n, B_e)), \tag{3.1a}$$

$$\frac{dB_e}{dt} = B_e(\omega_e \nu_e A - \mu_e - m_e f_e(B_n, B_e)), \tag{3.1b}$$

$$\frac{dA}{dt} = I - kA - P - Q, \tag{3.1c}$$

where

$$P = B_n\left(\nu_n A - (\mu_n + m_n f_n(B_n, B_e))\frac{1-\delta_n}{\omega_n}\right), \tag{3.2}$$

$$Q = B_e\left(\nu_e A - (\mu_e + m_e f_e(B_n, B_e))\frac{1-\delta_e}{\omega_e}\right), \tag{3.3}$$

$$f_n(B_n, B_e) = g_n(B_n, B_e) + \alpha_{ne} g_e(B_n, B_e), \tag{3.4}$$

$$f_e(B_n, B_e) = \alpha_{en} g_n(B_n, B_e) + g_e(B_n, B_e), \tag{3.5}$$

$$g_i(B_n, B_e) = \frac{B_i^p}{h^p + B_n^p + B_e^p}. \tag{3.6}$$

for $i = n, e$. Here, B_n and B_e represent the biomass of native and exotic species respectively, and A represents the environmental nutrient level. The model assumes a fixed nutrient loading rate I. In addition, the model the assumes light competition terms f_i between plants of the same and the other species, which are determined using cover of both the native (g_n) and exotic (g_e) species. The parameters α_{en} and α_{ne} determines the light competition effects of the native species on the exotic species, and *vice versa*. The cover of a given species type g_i is a Hill function of the biomass of both species in order to account for spatial overlap[45]. The environmental nitrogen level is determined by the nutrient

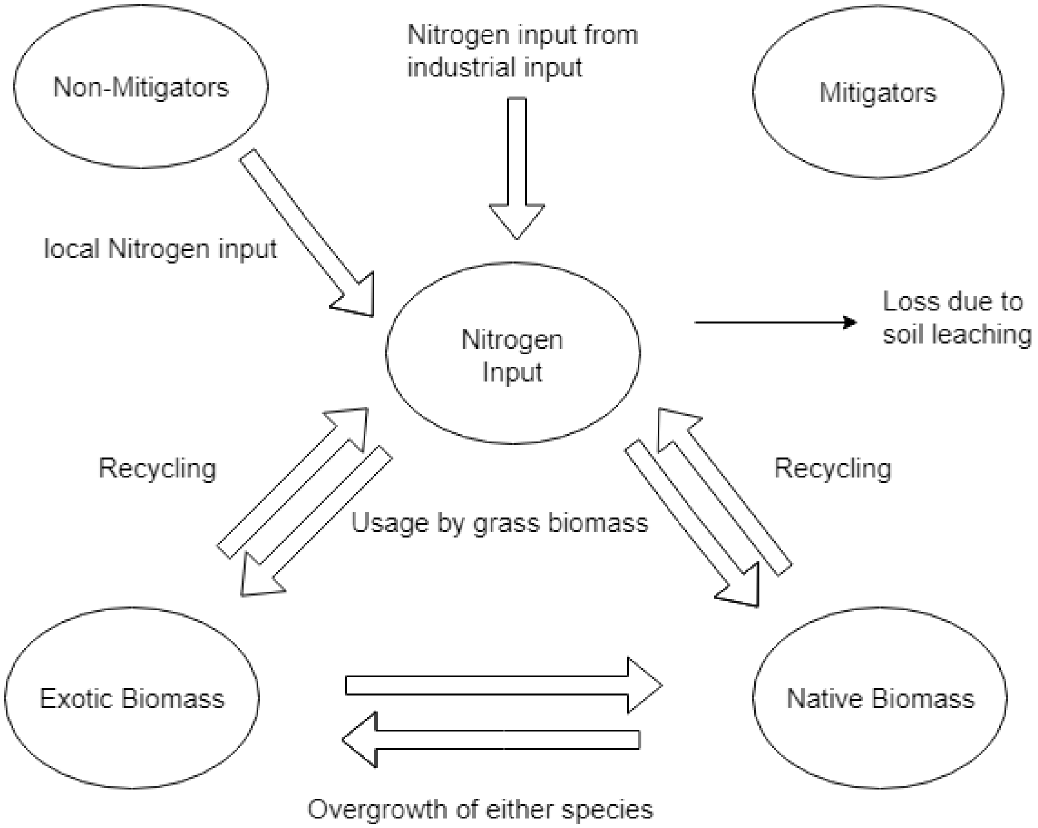

Figure 3.1: Schematic diagram of the socio-ecological model, combining an existing model of exotic and native grassland species under nitrogen loading[45] to a model of human social learning dynamics.

deposition constant I, less absorption by native and exotic biomass. Parameters and their respective baseline values are detailed in Tables 3.1 and 3.2 and the model is depicted in Figure 3.1.

This model represents human impact through a fixed parameter I representing the rate of nitrogen input. However, social behaviour is dynamic and varies based on perceptions and sensitivity to economic and ecological conditions. Hence we seek to write down a governing dynamic equation for x, the proportion of the population who support nitrogen runoff mitigation to preserve native grasslands. Members of the population who do this are assumed to be adopting a 'mitigator' strategy. Conversely, the remaining proportion $1 - x$ who do not are assumed to adopt a 'non-mitigator' strategy. We use utility functions to quantify the human motive to mitigate, or not to mitigate. We let U_C represent the utility for protecting native grassland species and U_P represent the utility for non-mitigators. We assume that the utility function for mitigators is given by:

$$U_M = -z + \eta \left(\frac{B_e}{B_n + B_e} \right) + \phi x, \tag{3.7}$$

where z represents the cost to protect native grassland species by reducing personal contributions to nitrogen runoff or personal efforts to support bylaws and mitigation programs that reduce runoff; η is a proportionality constant that controls the sensitivity of the mitigator utility to the amount of native grassland cover; and ϕ controls the strength of injunctive social norms, as in similar socio-ecological models [17, 160, 209]. This utility function captures how the utility for mitigation increases as the native grassland cover B_n becomes rare. Similarly, the utility function for non-mitigators is given by:

$$U_{NM} = w + \phi(1 - x). \tag{3.8}$$

where w is the individual cost associated with producing nitrogen runoff, such as fines paid for bylaw violations.

When $U_M - U_{NM} > 0$ preservation of native grassland species becomes a more valuable strategy, whereas when $U_{NM} - U_M > 0$, the population starts to abandon conservation. We assume that each individual 'samples' other individuals at rate κ_0 (social learning) and that, upon encountering someone with a different strategy, the individual switches strategies with a probability proportional to the difference in utility (with proportionality constant p_0). This sampling process generates dependence on the strategy frequencies x and $1 - x$. Hence, after re-scaling, the differential equation governing x is given by

$$\frac{dx}{dt} = \kappa x(1 - x)(-W + \left(\frac{B_e}{B_n + B_e} \right) + \epsilon(2x - 1)). \tag{3.9}$$

where $\kappa \equiv \kappa_0 p_0 \eta$ is the rescaled rate of social learning; $W \equiv (z + w)/\eta$ is the rescaled net cost of mitigation; and $\epsilon \equiv \phi/\eta$ is the effect of social norms. Despite this rescaling, changes in rescaled parameters have a clear interpretation in terms of the original parameter definitions. For instance, an increase in W corresponds to an increase in the cost of mitigation, hence we will continue to refer to this as the (rescaled net) mitigation cost. Similar interpretations apply to κ and ϵ, although changes in η correspond to simultaneous changes in W, κ and ϵ. We note that these equations are identical to the replicator dynamics used in evolutionary game theory [93, 52]. Further examples and full derivation of this differential equation in the context of social learning and imitation dynamics can be found elsewhere [18, 88, 99, 90].

Changes to the existing grassland model[45] are required in order to incorporate human mitigation dynamics. In particular, the model must account for the fact that only a proportion of nitrogen runoff is under the control of local human populations such as municipalities, while the remainder can be due to upstream sources or atmospheric deposition. Hence, we assume that total nitrogen is inputted into the grasslands comes from global sources that are not under the control of the local population at a rate J, as well as from local sources at a rate ρ that is reduced by a factor $1-x$ in proportion to the prevalence of mitigators, x. The socio-ecological model for the southeastern Australian grasslands is thereby given by the following system of non-linear differential equations:

$$\frac{dB_n}{dt} = B_n(\omega_n \nu_n A - \mu_n - m_n f_n(B_n, B_e), \tag{3.10a}$$

$$\frac{dB_e}{dt} = B_e(\omega_e \nu_e A - \mu_e - m_e f_e(B_n, B_e), \tag{3.10b}$$

$$\frac{dA}{dt} = J + \rho(1-x) - kA - P - Q, \tag{3.10c}$$

$$\frac{dx}{dt} = \kappa x(1-x)[-W + \left(\frac{B_e}{B_n + B_e}\right) + \epsilon(2x-1)], \tag{3.10d}$$

where

$$P = B_n \left(\nu_n A - (\mu_n + m_n f_n(B_n, B_e))\frac{1-\delta_n}{\omega_n}\right), \tag{3.11}$$

$$Q = B_e \left(\nu_e A - (\mu_e + m_e f_e(B_n, B_e))\frac{1-\delta_e}{\omega_e}\right), \tag{3.12}$$

$$f_n(B_n, B_e) = g_n(B_n, B_e) + \alpha_{ne} g_e(B_n, B_e), \tag{3.13}$$

$$f_e(B_n, B_e) = \alpha_{en} g_n(B_n, B_e) + g_e(B_n, B_e), \tag{3.14}$$

$$g_i(B_n, B_e) = \frac{B_i^p}{h^p + B_n^p + B_e^p}. \tag{3.15}$$

All parameters and variables are as defined previously in this subsection and in Tables 3.1 and 3.2. The difference between equations (3.1c) and (3.10c) is that nitrogen input simply occurs at a fixed rate I in equation (3.1c), whereas in equation (3.10c), nitrogen input is the sum of a fixed input rate J and a new input term $\rho(1-x)$ that depends upon x; hence total nitrogen input is not fixed due to coupling with the time-varying dynamics of the x

equation. We note that this model assumes the effects of the human population on nitrogen runoff to unfold continuously in time through the $\rho(1-x)$ term. Hence, this approach could capture situations where existing bylaws, recommendations or guidelines can wax or wane smoothly depending on factors such as individual participation in programs and public support for enforcement of existing bylaws. However, it would not capture discrete events, such as a sudden drop in nitrogen runoff after introducing a new bylaw.

3.3.3 Parameterization

Model parameters concerning the grassland subsystem were taken from the previous grassland model[45]. The additional model parameters govern human social dynamics and the coupling between the human and grassland subsystems. These additional parameters were calibrated to satisfy two conditions that met our objective of obtaining qualitative insights into dynamics rather than fitting empirical data from a specific study site and time. Firstly, we required that application of human effort to curb nitrogen input should cause a decline in exotic grassland species and an increase in the native species (and *vice versa*). Secondly, we chose a region of parameter space in which native and exotic species could co-exist and the proportion of mitigators and non-mitigators were nonzero. These two conditions ensured that parameter variation away from the baseline values produced a meaningful change in model dynamics that could be explored through time series and parameter planes. The resulting baseline parameter values appear in Tables 3.1 and 3.2.

3.3.4 Baseline Simulation

The model was numerically simulated in Matlab using the ode23 solver. A time series of the model simulation at the baseline parameter values provides insight into how the model assumptions translate into the observed dyanamics and especially the interactions between natural and human variables (Figure 3.2). The time series shows damped oscillations leading to an interior equilibrium where native and exotic grass co-exist (with the native species being most prevalent); mitigators constitute 10% of the population; and nitrogen input is nonzero. As the proportion of mitigators increases and decreases, nitrogen input evolves accordingly, which in turn forces changes in the grassland composition. A sufficient increase in the native grassland species increases causes the proportion of mitigators to decrease, which in turn eventually causes a resurgence of the exotic species. However,

Parameter	**Definition**	**Value(s)**	**Units**
ω	nitrogen use efficiency of each species	(n) = 39.6, (e) = 27.1	$\frac{kgC}{kgN}$
ν	nitrogen uptake rate of each species	(n) = 0.0211, (e) = 0.0877	$\frac{ha}{kgCyr}$
μ	biomass turnover rate of each species in the absence of light competition	(n) = 0.14, (e) = 0.81	yr^{-1}
m	the maximum increase in biomass turnover rate for each species due to interspecific light competition	(n) = 0.17, (e) = 0.32	yr^{-1}
k	soil leaching rate of plant-available nitrogen	0.4	yr^{-1}
δ	proportion of nitrogen in literfall lost from the system in plant-unavailable forms	(n) = 0.06, (e) = 0.06	–
α	light competition coefficients	(n) $\rightarrow$ (e) (19), (e) $\rightarrow$ (n) 0.05	–

Table 3.1: Continued on the next page

Parameter	**Definition**	**Value(s)**	**Units**
h	half-saturation constant for the Hill function for coexistence equilibria	3890	$\frac{kgC}{ha}$
p	parameter controlling sharpness of transitioning from low to high cover of the Hill function	3	–
J	global nitrogen input rate	2	$\frac{kgN}{hayr}$
ρ	maximal local nitrogen input rate	3	$\frac{kgN}{hayr}$
κ	social learning rate	1.5	yr^{-1}
W	net cost of supporting runoff mitigation programs	0.1	–
ϵ	strength of injunctive social norms	0.001	–

Table 3.2: Parameters and their definitions and baseline values. (n) denotes a parameter value specific to the native grassland species, while (e) denotes a parameter value specific to the exotic species. Parameters were obtained from the previous grassland model[45] except for ρ, J, κ, W and ϵ which were calibrated as described in the Methods section.

the overall free nutrient availability is relatively constant through these cycles, since free nitrogen is rapidly assimilated into plants and thus cycles in nitrogen input are translated directly into cycles in species abundance.

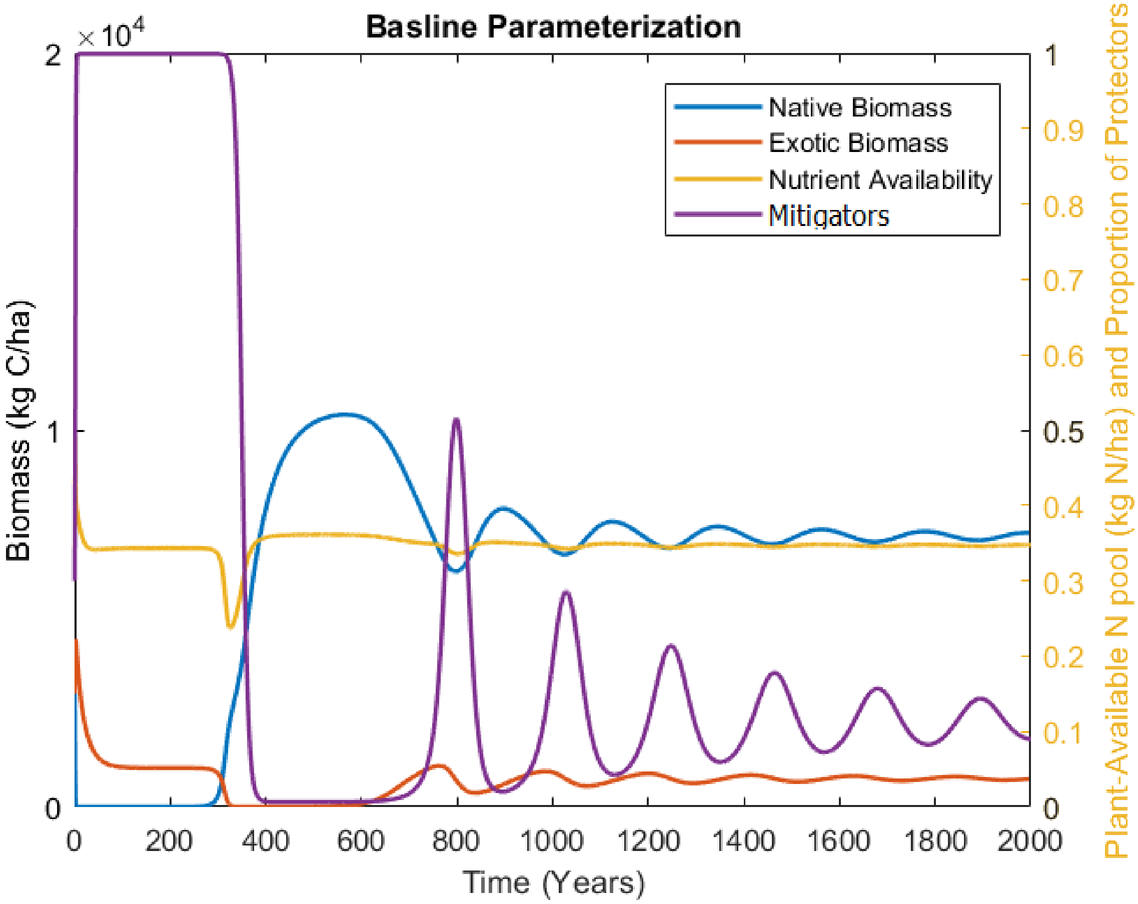

Figure 3.2: Dynamics of the model at baseline parameter values, showing damped oscillations converging to an interior equilibrium where native and exotic species co-exist and where the proportion of mitigators is nonzero. Parameter values come from Tables **3.1 and 3.2**.

3.3.5 Time Series and Parameter Planes

Simulations in parameter regimes away from the baseline parameter values indicate the potential for a wide range of outcomes with respect to both natural and human dynamics. We illustrate some of these regimes in the Figures 3.3–3.5, through time series of simulated model solutions. Parameter planes describing the model's dynamical regimes as a function of two model parameters were also generated in order to understand how model dynamics depend on parameter values. The planes illustrate the impact of changes in parameter values on asymptotic states of the model (Figure 3.6). To construct the parameter planes, two parameters were selected to be varied around baseline, while all other parameters were held constant at baseline. Initial conditions for B_n, B_e, A and x far from equilibrium values were randomly chosen and the model was run for 3,000 simulated years. Exploring a large number of random initial conditions allowed us to detect alternative stables states and thereby completely characterize the asymptotic states of the model at any given set of parameter values. Approximately 30,000 time series were thereby generated over 256 different initial conditions and the asymptotic state(s) of the system at each parameter pair on the plane were determined from the numerical results. These were results were then compiled into an $11x11$ grid to form the parameter plane. All figures were generated using Matlab.

3.4 Results

3.4.1 Time Series

Exotic Grassland Eradication or Dominance

Under a parameter regime where the global input rate J and the net cost to support mitigation W are lower than baseline values, the model predicts suppression of the exotic species (Figure 3.3a). In this regime, the proportion of mitigators is initially high but eventually declines to zero during a period when the native grassland species are still recovering. Despite the collapse in support for the native grassland species, the native grasses are still able to recover and establish dominance on account of the reduced global nitrogen input. In this case, the net costs of mitigation make it unattractive to the population, but the native species can re-invade anyway because J is sufficiently low. (We note that the cases where $x = 0$ and $x = 1$ at equilibrium reduce to the model of Chisholm *et al.* [45] where

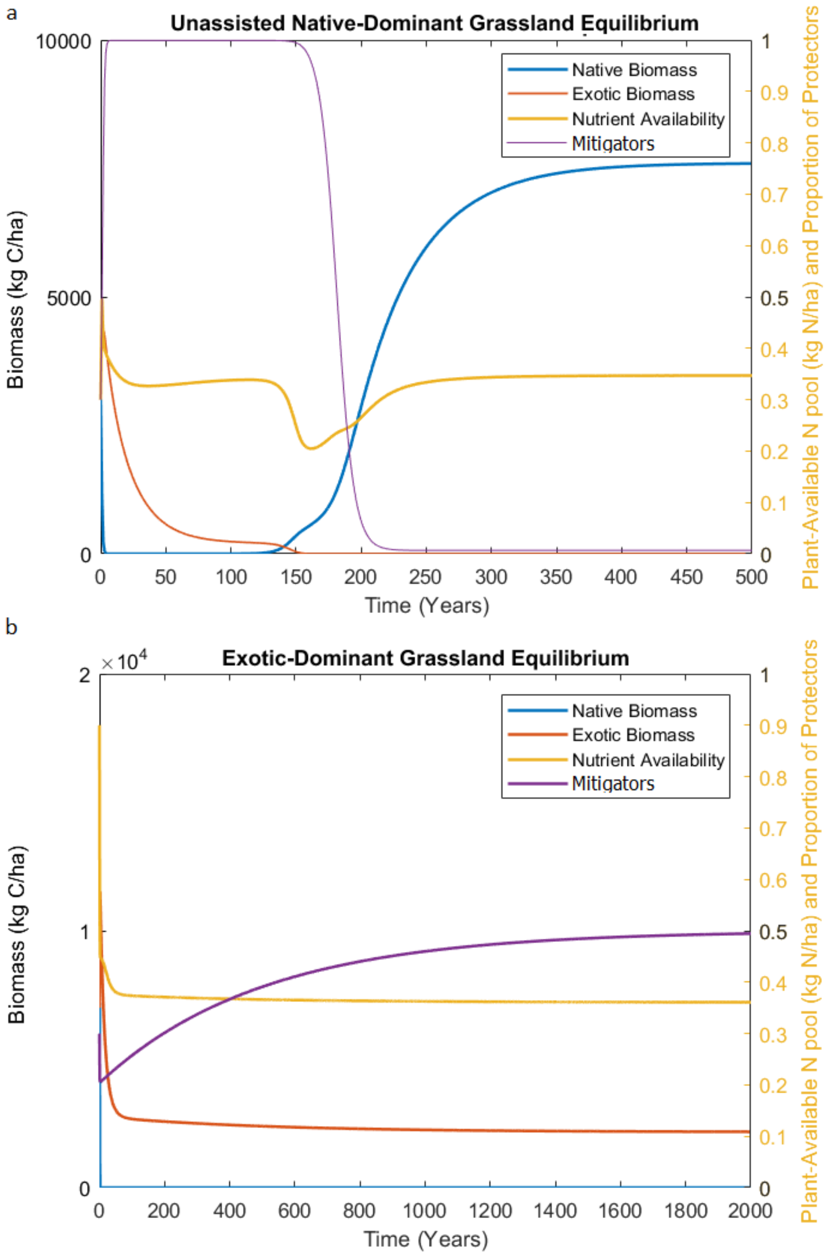

Figure 3.3: Time series representing the (a) native grassland dominance without human assistance, assuming $J = 0.5$, $W = 0.1$ and all other parameters held at baseline, and (b) representing the exotic grassland domination under the assumption that $\rho = 4.5$, $W = 1$ and all other parameters held at baseline values.

nitrogen input is fixed.)

In contrast, a scenario where the maximal local nitrogen input ρ and the net utility for mitigation W are heightened relative to baseline values illuminates a second dynamical regime (Figure 3.3b). In this simulation, we observe that the exotic species invades rapidly in the first few years, stimulating a rapid shift to the mitigator strategy in the human population to an equilibrium proportion of 50 %. This surge of interest in mitigation is inadequate to allow the native species to re-invade, however, and the population eventually converges to an equilibrium where the exotic species is dominant.

Oscillations in species abundance and mitigating behaviour

Limit cycles are states of oscillatory behaviour in which a system exhibits transient behaviour, cycling over some period of time. During conditions of sufficiently high social learning rate κ and sufficiently large cost of supporting these reduction programs W, the model predicts the ecosystem to undergo limit cycles of extreme amplitude (Figure 3.4a, 'extreme oscillations' scenario). The oscillations reflect the same underlying dynamic as observed in the baseline scenario of Figure 3.2, where support for mitigation becomes widespread in time periods when the exotic species is dominant, which eventually causes a return of the native species and, in turn, a decline in support for mitigation. These extreme cycles are driven by the high social learning rate, which has also been observed to destabilize equilibria in this and other socio-ecological models [18, 90]. We note that introducing institutions might modulate these extreme cycles. For instance, if support for mitigation was translated into law, then nitrogen input would be modulated despite changes in public support for it, at least until the law is repealed. We postulate that this would cause the amplitude to be less extreme. In contrast, under a parameter regime of sufficiently low costs of protection (W) and a lower social learning rate (κ), the model predicts stable limit cycles of moderate amplitude that correspond to enduring coexistence between native and exotic grassland species, with a similarly moderate cycling in the proportion of mitigators (Figure 3.4b, 'oscillatory coexistence' scenario).

Stable Coexistence

Under optimal conditions of sufficiently low local input and sufficiently low costs to conserve relative to baseline values, the system predicts convergence to an asymptotic regime

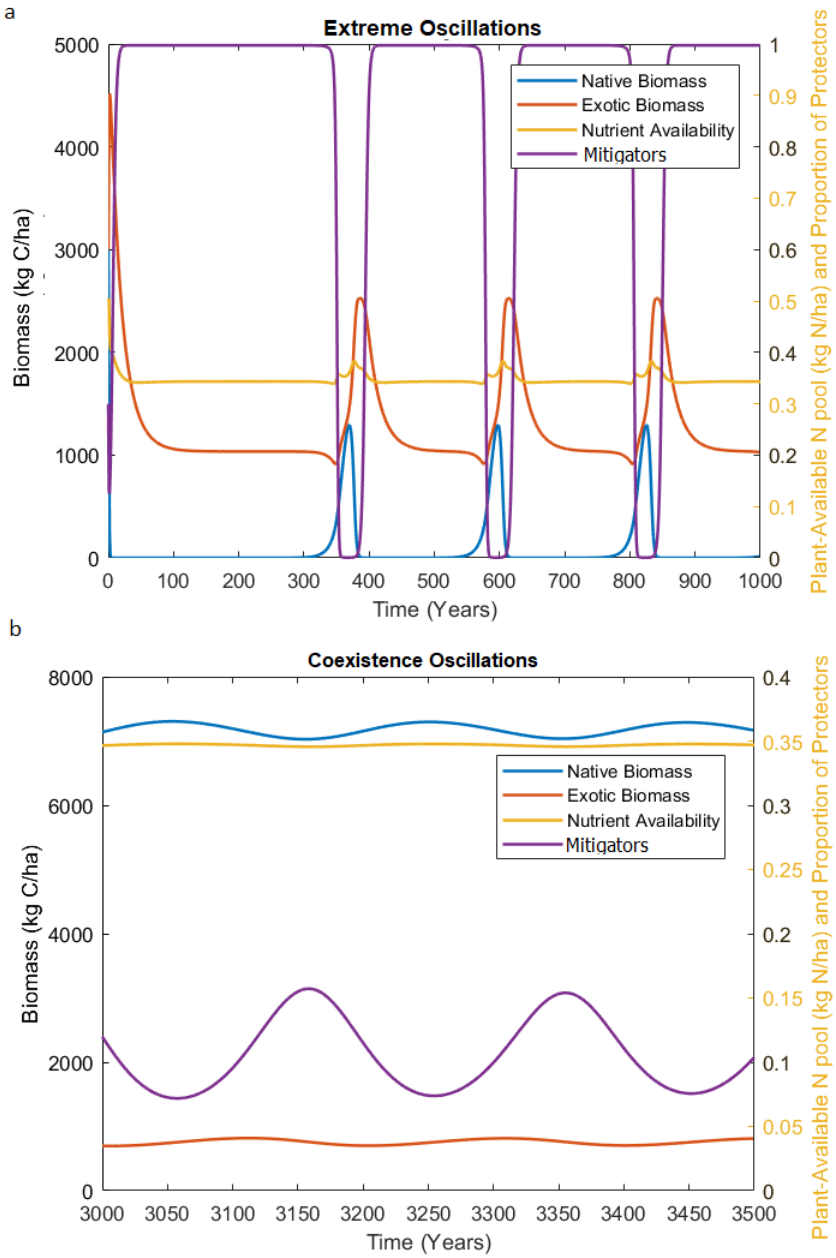

Figure 3.4: Time series representing oscillations (stable limit cycles) predicted by the model, either (a) extreme oscillations that support species eradication in the troughs ($\kappa = 4$, $W = 0.9$) or (b), more moderate oscillations that support coexistence of the two species ($\kappa = 2$, $\rho = 3$). All other parameters were held at baseline values.

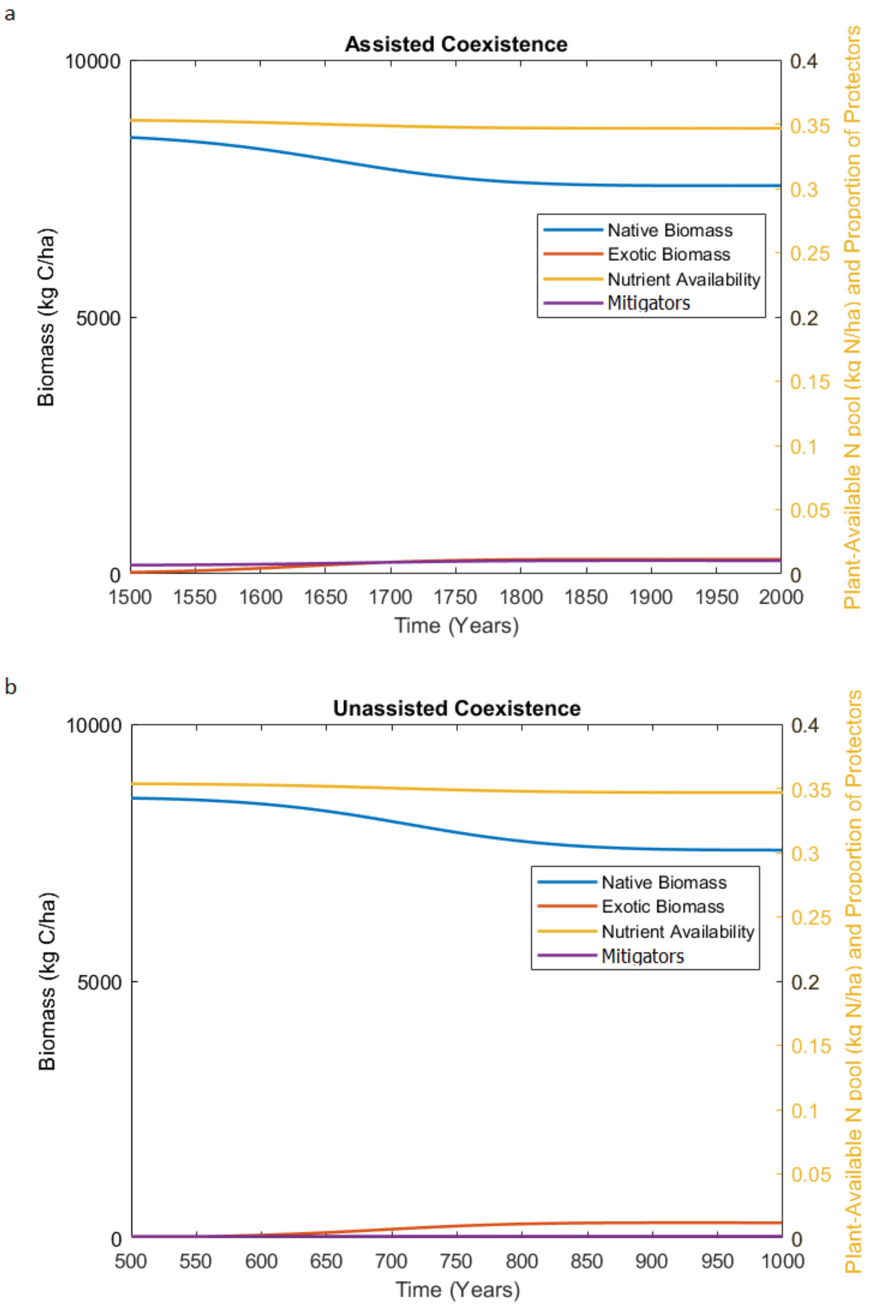

Figure 3.5: Time series representing stable coexistence. The results were generated under the assumption that for assisted coexistence (a) $J = 1$, $W = 0.1$ with other parameters at baseline values. For the unassisted coexistence scenario (b), $J = 1$, $W = 0.5$ and all other parameters were held at baseline values.

governed by stable coexistence of both grassland species . As such, the system is not significantly perturbed by the level of nutrient input as low levels of human-controlled nutrient input drives the persistence of native grassland species at much higher levels than the exotic species (Figure 3.5a). Conversely, if the cost to protect is increased and industrial pollution is sufficiently low, the population can become more reluctant to protect. Yet, despite the population opting to abandon mitigatory strategies, nutrient deposition levels are sufficiently low, such that the model can predict grassland coexistence without additional anthropogenic intervention Figure 3.5b. Both species of grasslands remain present, although the native species is much more abundant.

3.4.2 Parameter Planes

Parameter planes were generated for the parameter pairs $J-W$, $\rho-\kappa$, $\kappa-W$ and $\rho-W$ (Figure 3.6, and see Table 3.3 for a detailed legend describing the numbered regions). It should be stated that these regimes were determined via randomization over multiple initial conditions. Using this scenario analysis, conditions (if they exist) were determined for which the model would potentially stabilize into alternative asymptotic regimes. These parameter planes show that the exotic species can invade and entirely replace the native species when the global input J is sufficiently high, as expected. Conversely, when J and/or the local input ρ are sufficiently low, the native species excludes the exotic species and is at a stable equilibrium, with or without human assistance. However, dynamics outside of this regime depend on nonlinear interactions between social and natural dynamics. We observe that a sufficiently small mitigation cost W not only promotes persistence of the native species, as expected, but it can also stabilize dynamics in most parameter regimes tested. We also observe that even when ρ is very high, a decline in biomass of the native species can stimulate a mitigation response in humans and thus prevent eradication of the native species, resulting in oscillatory coexistence. Finally, limit cycles are pervasive, suggesting that stable persistence of the native species is only possible for very favourable environmental conditions, and that outside of these parameter regimes, they persistence relies on the continued threat of the exotic species in order to simulate a mitigating response. We discuss each of the four parameter planes in turn in the following subsections.

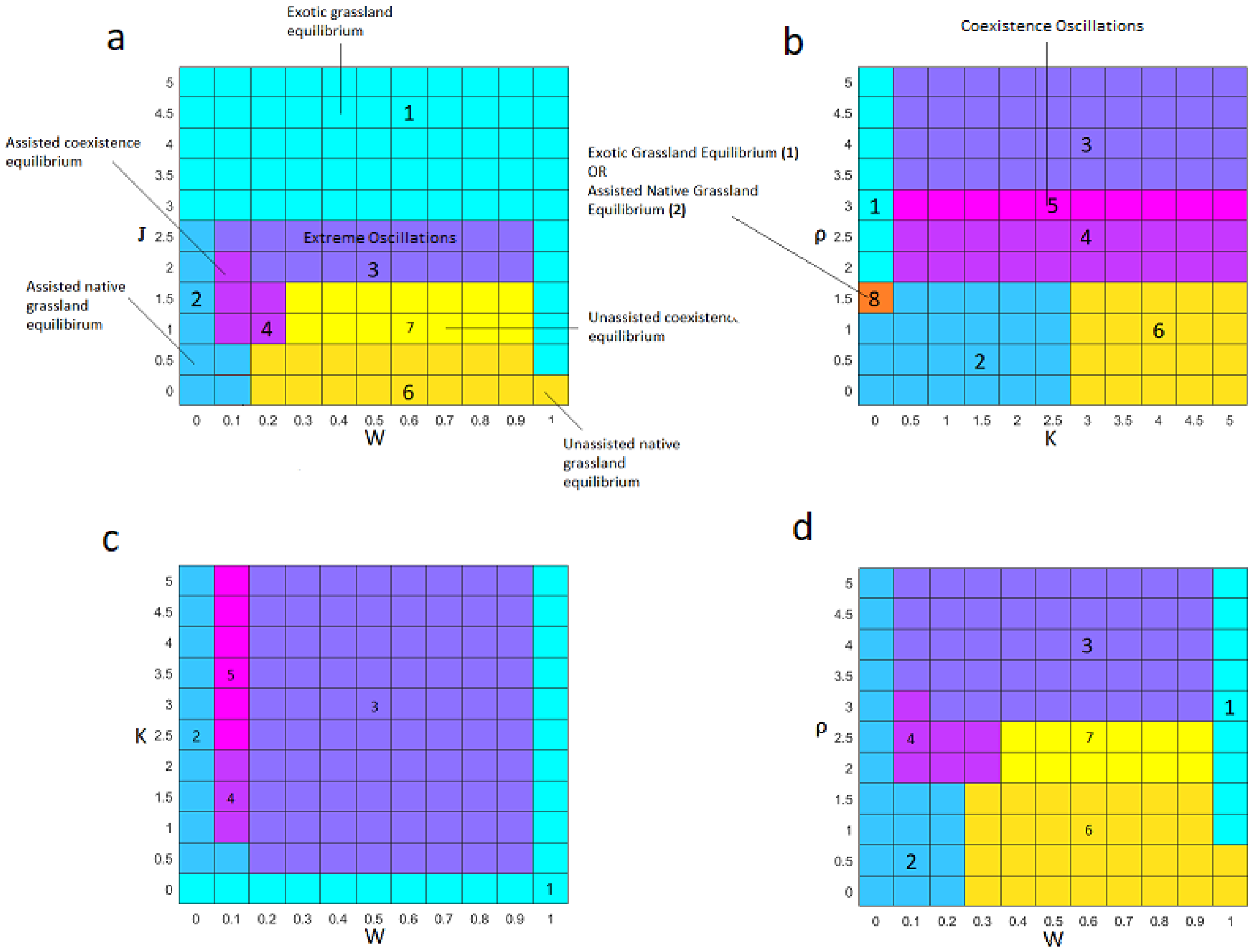

Figure 3.6: Parameter planes indicating model dynamical regimes with respect to variation in parameter pairs: **(a)** J-W, **(b)** κ-ρ, **(c)** κ-W, **(d)** ρ-W. All parameter values are at baseline values except the two being varied. Further details on the dynamics of the numbered regions are provided in Table 3.3.

Local socio-ecological dynamics become important when global nitrogen input is sufficiently small

In the J-W parameter plane, we observe that high values of J favour dominance of the exotic species and low values of J favour dominance of the native species as expected, but there is also an intermediate regime in J where the two species coexist as a result of mediation by the human population, where mitigating activity can respond to changes in the native grassland biomass (Figure3.6a). Coexistence in this intermediate regime occurs either through a stable equilibrium or (extreme) oscillations (stable limit cycles). The dynamics are less variable along changes in W. When J is very large, the exotic species excludes the native species regardless of the mitigation cost W–in this regime, global nitrogen input overwhelms any attempts to restrict local input. However, when J is small, reducing W below 0.05 replace all three regimes of coexisting limit cycles, coexistence equilibrium, and the unassisted native dominance equilibrium with a single regime of an assisted native dominance equilibrium.

Local socio-ecological dynamics remain important even for high rates of maximal local nitrogen input

In the ρ-κ parameter plane (Figure 3.6b) we observe that a low local nitrogen input capacity ρ supports dominance of the native species, yielding a stable native species equilibrium that excludes the exotic species. However, unlike the case for larger values of the global nitrogen input J, larger values of ρ continue to permit the existence of the native species through coexistence regimes of both equilibria and stable limit cycles where native and exotic species undergo oscillations due to mediation by the human social response. Hence, even at very high values for local nitrogen input to the grasslands, feedback from the human subsystem is sufficiently strong to prevent eradication of the native species, although it is not strong enough to eradicate the exotic species. In contrast, changing the social learning rate κ has relatively little impact on dynamics, except when κ is very low and ρ is relatively large–in this parameter regime, increasing the social learning rate can shift the system from regime governed by exotic species to coexistence states (either equilibrial or oscillatory). This occurs because if the social learning rate is too small and the initial proportion of mitigators is also very small, the mitigating behaviour does not spread sufficiently quickly. Whereas for higher κ, individuals are more likely to adopt new strategies, converting non-mitigators into converters, and thus the system transitions into a state with a presence of the native species.

Region	Behaviour
1	Stable equilibrium where exotic grassland species dominate, with a human population fully dominated by mitigators.
2	Stable equilibrium where native grassland species dominate, with a human population fully dominated by mitigators.
3	Extreme oscillations: A state governed by limit cycles where native and exotic grassland biomass can vary drastically between levels of near extinction and of high density. One can thrive if the other approaches ≈ 0 kh C/ha biomass.
4	Stable equilibrium where both native and exotic grassland species coexist, with minor assistance from mitigators.
5	Coexistence oscillations: a state where the model predicts cyclic coexistence of both native and exotic grassland species, with fluctuating proportion of mitigators. In contrast to region [**3**], both exotic grass and native grass biomass are always $>> 0$ kg C/ha and thus not in danger of elimination during troughs of oscillations.
6	Stable equilibrium where native grassland species dominate in a human population without mitigators.
7	Stable equilibrium where both native and exotic grassland species coexist, with no assistance from mitigators.
8	A bistable region, where system dynamics predict convergence to either the exotic grassland equilibrium **(1)** or the assisted native grassland equilibrium **(2)**.

Table 3.3: Legend for dynamical regimes exhibited by the model and illustrated in the parameter planes.

Social learning can yield coexistence, but increasing mitigation costs destabilizes the ecosystem

The parameter plane for the social learning rate κ and the cost of supporting reduction programs W illustrates the pervasiveness of limit cycles (extreme oscillations) in the system (Figure 3.6c). Starting from low levels of W, the effect of increasing W is immediately apparent: unless the social learning rate is extremely low in which case mitigator behaviour cannot spread, an increase in W shifts the system from a dynamical regime where the native species dominates with the assistance of humans, to a regime of oscillatory behaviour, where both exotic and native species are present. Hence, increasing the mitigation cost not only allows the exotic species to be introduced, but also destabilizes the ecosystem. Increasing W still further to extremely high values (thus making ecosystem conservation too expensive) predicts native eradication and convergence into a regime dominated by the exotic species. Increasing the social learning rate has little effect on qualitative dynamics, except when κ is very low in which case an increase in κ will allow the mitigatory behaviour to spread in the population. Limit cycles dominate the dynamics for almost all of the κ-W parameter combinations in this parameter regime. Hence, the model predicts that a dominant mechanism for persistence of the native grassland species is a social dynamic that responds nonlinearly to the prevalence of native versus exotic species in the ecosystem and adjusts local nitrogen input accordingly.

High maximal rates of local nitrogen input prevent homogeneous population behaviour

The parameter plane for ρ and W yields similar insights to the other parameter planes: higher rates of ρ stimulate limit cycles, except when W is very small or very large, in which case the population is characterized by stabilization into regimes for native or exotic species dominance (Figure 3.6d). As before, coexistence is possible in broad intermediate parameter regimes, often through limit cycles. When ρ is smaller, dynamics are at equilibrium and may be characterized by presence or lack of assistance from a mitigating human population. Of note is the fact that here (as in other parameter planes), the maximal local nitrogen input rate ρ–which represents the level of economic development (higher ρ means greater local industrial capacity)–influences social dynamics very strongly. In particular, when ρ is small, the cost W determines whether a population is characterized by complete dominance by mitigators (region 2) or complete dominance of non-mitigators (region 6) where the boundary between these two redregimes is a sharp transition. Hence, when ρ

is small, population behaviour can be homogeneous. But when ρ is larger, population behaviour swings back and forth in conjunction with grassland dynamics. This difference is also observed in other parameter planes (e.g. Figure 3.6a,b).

3.5 Discussion

A model of southeastern Australian grassland dynamics subject to excessive nitrogen deposition was coupled with a model of human behaviour to explore potential dynamics that could arise in the socio-ecological system. In particular, we wished to explore conditions that supported the persistence of the native grassland species in the face of an invasive grassland species assisted by nitrogen pollution. The model predicted two mechanisms for persistence of the native species. Firstly, a combination of reducing the cost of mitigation programs that reduce runoff (thus making uptake more desirable in the population) and decreasing local and/or global sources of nitrogen pollution could create an environmental regime that supports grassland convergence to an asymptotic regime dominated by native grasslands species, with or without assistance from mitigation activities in the human population. Secondly, for somewhat less favourable environmental conditions where nitrogen input is higher, persistence of the native species was still possible but it occurred through oscillations in the biomass of the native species, exotic species, and mitigation support in the human population. These oscillations were driven by our assumption that the prevalence of mitigating behaviour in the population depended on the current state of the grasslands (mitigation behaviour is reinforced when the native species is rare, but are relaxed when the native species is common).

Under the second mechanism for support of the native grassland species, persistence of the native species is gained at the cost of admitting dynamics where the prevalence of both native and exotic species oscillate. The danger of such oscillations is the possibility of extinction of other native species (plant or animal) that depend on the native grasslands, at times when native grassland biomass is at a low point in the cycle. Although some parameter regimes corresponded to coexistence oscillations through relatively gentle limit cycles, most of the oscillations we observed in the parameter planes corresponded to extreme oscillations where the native species are almost eradicated in the troughs of the cycles (Figure 3.4a versus Figure 3.4b) [60]. We also found that decreasing the cost of a runoff reduction program not only increases the prevalence of mitigators in the population, but more surprisingly it is also predicted to stabilize both social dynamics and grassland dynamics. Hence, the benefits of subsidizing runoff mitigation programs could be twofold.

These results are relevant to concepts of ecological[94] and socio-ecological resilience[67]. The traditional conception of resilience in ecology is the ability of an ecosystem to return to its original, pre-disturbed state [94, 83, 26]. Mathematically, this behaviour is connected to the asymptotic stability of a model's steady state solution[94]. However, subsequent conceptual development has emphasized that dynamical systems can exhibit a wide variety of attractors in addition to steady states, such as complicated cycles or chaotic dynamics, suggesting a need for a more nuanced definition of socio-ecological resilience[67, 68]. Other research has noted how instability in real socio-ecological systems, such as elk-human interactions in Yellowstone National Park, could manifest as oscillations but may also appear as other irregular patterns [24]. Accordingly, our model could be argued to manifest two forms of resilience, whereby the oscillations generated by socio-ecological feedback in our model represent resilience in a looser sense, since they allow persistence of the native grassland species. However, on account of generating oscillations with sometimes dramatic swings in species abundances, this resilience is arguably less desirable than the conventional resilience associated with a stable, high cover of native grasses that occurs in favourable environmental conditions in a different parameter regime. Real populations may not exhibit such smooth limit cycles on account of stochasticity, population structure, and other heterogeneities, but the precise form of instability is secondary to the prediction that a socio-ecological equilibrium will destabilize into a less resilient dynamical regime.

Our model assumes incentives can increase the proportion of the population engaging in mitigating behaviour that reduces local sources of nitrogen runoff. This pattern appears to be consistent with field data from Australia's Environmental Stewardship Program [41]. In particular, native plant species richness is significantly higher in grasslands under the Environmental Stewardship Program, while exotic plants species richness does not differ significantly between sites (although it does vary regionally) [125]. This regime corresponds to a region of coexistence where native species are supported by mitigation efforts, as exemplified in Figure 3.5 for instance.

Socio-ecological models can be useful to identify possible sources of 'policy resistance' whereby the response to an intervention tends to undermine the intervention [198]. Some previous models have suggested that outcomes may improve by applying interventions in tandem so that the weaknesses of one intervention are compensated by the strengths of another [17]. In a related vein, nonlinear socio-ecological systems characteristically exhibit thresholds at which the effectiveness of an intervention changes qualitatively (Figure 3.6), which implies that cost-effectiveness of the interventions will vary depending on the system's location in parameter space. We assumed that all mitigators in the population mitigate runoff to the same degree. However, efforts to mitigate can vary between individuals in real populations. In experimental settings, this has led to the observation of a trade-off whereby some interventions can increase individual effort to mitigate at the expense of decreasing population participation in mitigation programs [189]. A worthwhile approach for future research would be to allow mitigation effort to vary between individuals in the model.

Another simplifying assumption that we used to facilitate gaining insights through model analysis included the assumption of a constant global source of nitrogen availability. In fact, this quantity can vary over time and influence system dynamics. If governments implement policies to penalize excessive industrial pollution, this can cause industrial sources of nitrogen deposition to decline. An extended model with multiple populations representing both local and global sources of nitrogen could be developed to explore this scenario. We also note that we restrict our attention to a limited portion of a high-dimensional parameter space and rely upon analyzing two-dimensional cross-sections of that parameter space. Hence, there might be other relevant dynamical regimes that our analysis does not reveal. However, finding more dynamical regimes that correspond to persistence of the native species would not qualitatively alter our conclusion (although it could expand our findings).

Similarly, a previous model of southeastern Australian grassland dynamics illustrated the effect of pulsing the system with significantly higher rates of nutrient input for a specific period of time, causing dominance of the exotic species [45]. Nutrient spikes such as these in lake systems are associated with a regime shift to an undesirable state of eutrophication [157] although in grasslands these nutrient spikes can play a beneficial role in abandoned lands [183]. We did not explore the effect of exogenous nutrient spikes in our model, although extreme oscillations in the proportion of non-mitigators in the local population has a similar effect. Future research could explore the impact of spikes in the globally sourced nitrogen deposition (model parameter J). We expect this extension to have nontrivial effects, given the tendency of equilibria in our socio-ecological model to destabilize into limit cycles. The timing of spikes could interact with the limit cycles to produce very different outcomes depending on the timing of the spike (e.g., very long transient dynamics [87]).

In summary, there exist many opportunities to pursue research in the mathematical modelling of socio-ecological dynamics. In this case, the incorporation of human social dynamics into the model has revealed more than one mechanism to support persistence of a native grassland species, although the mechanisms relying upon socio-ecological oscillations can be less desirable. Reducing the cost of mitigation not only increases the proportion of individuals who participate in mitigation but can also stabilize socio-ecological dynamics. In the future, multiple opportunities can be explored to expand the current research to provide a deeper understanding of socio-ecological mechanisms for reducing nitrogen pollution and restoring human-affected grassland ecosystems.

Chapter 4

Trends in Coupled Human-Environment Systems Modelling: A Scoping Review

4.1 Abstract

Classical environmental models assume the influence of humans on environmental systems is constant. However, human and environmental systems respond to one another. As such, coupled human-environment systems (CHES) models have been developed and are becoming more widely studied. In this review, we analyze CHES modelling techniques and study systems over a decade (May 2009-April 2019). We utilized the PRISMA method to filter publications from both Web of Knowledge and PUBMED, yielding 92 relevant papers for our review. Publications more than doubled from the 5-year interval May 2009-December 2013 (28/92) to the 5-year interval January 2014-April 2019 (64/92). CHES models typically used either differential equations (DEs) (44/92) or agent-based models (ABMs) (28/92). We organized the included literature with respect to the technique used to represent human behaviour. We noticed a diversity of approaches in this respect, but primarily optimization techniques (28/92) and game theory (34/92). We noticed a substantial increase in publications using more highly structured models in the second 5-year interval. We attribute this to reduced technological barriers to developing more detailed models, and greater data availability. We discuss the realism of the models and their ability to capture real-world dynamics. Finally, we explore avenues for future research, and discuss unconventional routes such as online communities and artificial intelligence modelling to expand representation of human behaviour in CHES models.

4.2 Introduction

Ecosystem sustainability and human impact on ecosystem dynamics have been a focus of environmental research due to the importance of ecosystem services in various sectors such as agriculture, fisheries, and tourism, as well as support for natural ecosystem conservation. Ecosystems have undergone deterioration through various sources of disturbance. Damage caused by natural events, such as forest fires in fire-prone regions, can cause significant shifts in ecosystem dynamics if the burns become unnaturally large or frequent. In some cases ecosystems are sufficiently resilient to bounce back from low-impact natural disruptions. This is exemplified by the *Diadema antillarum* sea urchins consuming algal turfs to promote new coral establishment [2], or seed dispersal during the aforementioned fires to mitigate the damage and loss caused by the forest fires [184].

Humans can also have negative impacts on ecosystem services, causing a decline in resilience and often catastrophic disruptions. These disruptions can take many forms, such as eutrophication of lakes via pollution [85] or depletion of a natural resource via exploitation. These disruptions may not always be intentional. For instance, travelling individuals have unintentionally introduced pests or exotic species to forest ecosystems. This has occurred through individuals importing pests via infested firewood [17], or through exotic plant growth, which introduces competitive interactions into grassland dynamics [210]. The resulting regime shifts have often been characterized by a hysteretic feedback loop, wherein greater effort is required to reverse the catastrophic trajectory an ecosystem has taken, than what caused the catastrophic shift in the first place.

Human interventions are not always negative, however. Research has explored how conservationist strategies can emerge in response to disturbances to promote sustainability or recovery in affected systems [100, 197]. These efforts can range from the development of sanctuaries for protecting endangered species, or raising awareness of personal ecological footprints in a population[212]. These strategies, however, may not propagate through a population, if individuals are dissuaded from these strategies by incentives to act unsustainably. Therefore interventions seek ways to incentivize individuals to opt into acting in the interest of the community as a whole [80]. By promoting the development of social norms (peer influence) and social learning (fostering community and online interactions), individuals can be influenced to modify their strategies by changing their perceived utility in a way that benefits ecosystem integrity.

Environment system modelling has played a strong role in both developing and shaping the strategies required to promote ecological resilience and recovery. Classically, modelling techniques have incorporated fixed parameters to represent human input in ecological models (and vice versa)[181, 108]. However, human systems and ecosystems are rarely constant, and feedback between the systems, such as those mentioned above, can influence human and/or environmental behaviour. Such feedbacks have been observed in various scenarios, such as COVID-19's effects on social gatherings, or environmental activism sufficiently pressuring industries to adopt more ecologically sustainable alternative strategies. Thus, there is a need to develop models that capture the dynamic nature of human and environment interactions.

Coupled human-environment models incorporate a dynamic coupling between human and environment systems. These coupled human-environment systems (CHES) have been developed to incorporate a two-way feedback mechanism that integrates responses from both human and environment dynamics in a cyclical manner (Figure 4.1). As observed, this feedback loop represents the non-static nature of human behaviour, where strategies can

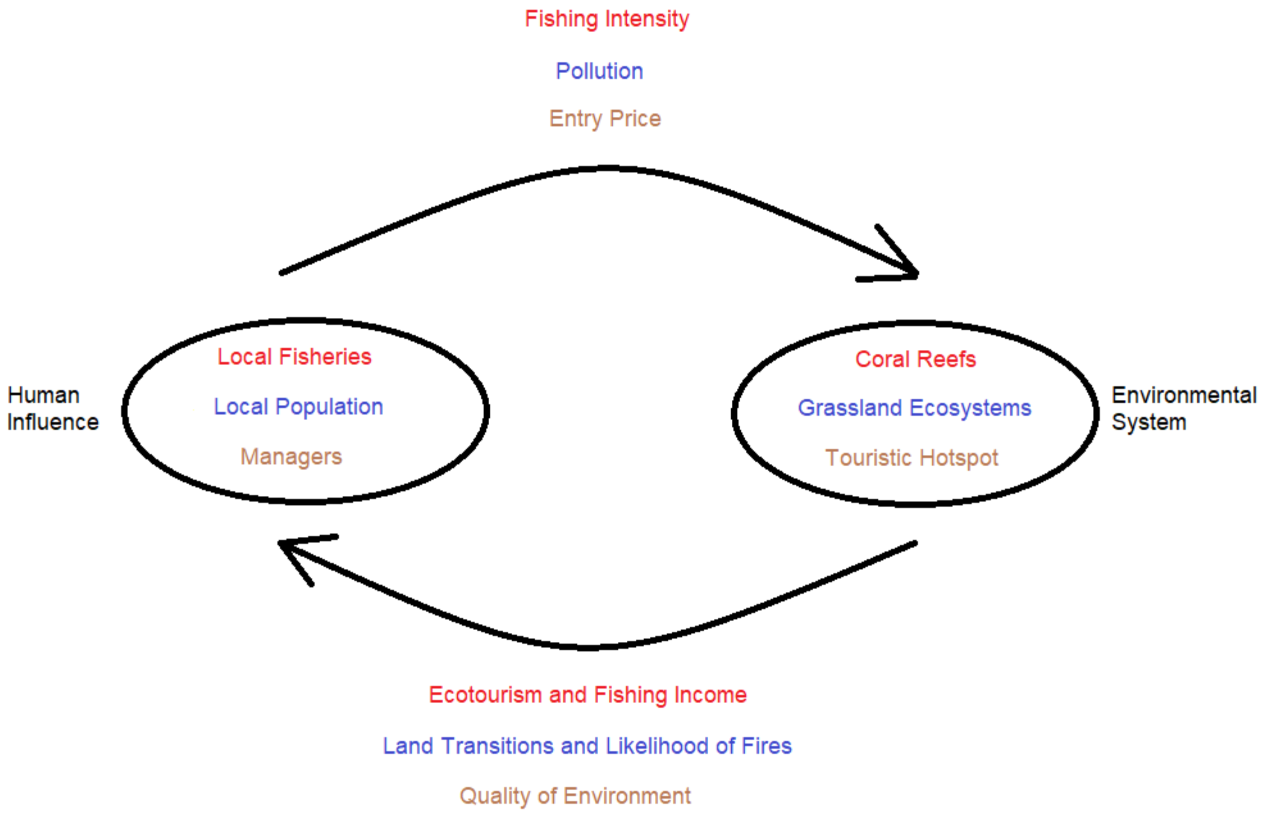

Figure 4.1: Cyclic nature of human behaviour to current state of an observed environmental system that is modelled using coupled human-environment systems.

be changed to optimize an individual's utility (i.e., subjective preferences). This methodology is often more realistic compared to static human parameter representations in classical environmental system models and has been utilized in a variety of ways in environmental systems research.

Numerous modelling methodologies have been developed that incorporate a dynamic link between human and environmental components and have ranged from extensions of classical modelling techniques (such as the Lotka-Volterra competition/fishery models) [181, 108] to more complex Cellular Automata-Markov chain models that investigate stochastically-driven land state transitions [220]. In addition, very complicated and detailed computational models and tools have also been developed [15, 12]. Typically, these modelling techniques require numerous input parameters for both environmental and human components, and as such can be computationally expensive. With technological improvements, computational models have become more feasible, enhancing the viability of these modelling techniques.

Human behaviour can be incorporated using a game-theoretic approach. This methodology assumes that individuals act to maximize their payoff (or utility). Individuals choose strategies from a strategy set, and their payoff for a given strategy depends on what strategies other players adopt [208]. As an example, we consider the two-player Prisoner's Dilemma [10]. The game supposes two individuals who have been caught under suspicion of committing a crime and are being interrogated in separate cells. A player may choose to cooperate with the other player (by not confessing), or defect against the other player (by confessing to the crime in the hope of a shortened prison sentence). If both players cooperate, they avoid a prison sentence. If both players defect, they suffer a shortened sentence. If one player cooperates and the other defects, the defector gets an even shorter prison sentence, while the cooperator gets a very long prison sentence. The prisoners would obtain the best outcome if they both cooperated, but game theory predicts that defection will be the strategy they both choose. This simple game illustrates the clash between what is socially optimal versus the individually optimal actions that individuals adopt in practice. This clash between socially and individually optimal outcomes occurs in many common pool resource problems in the environmental sciences. In more sophisticated games, payoff functions can be tailored to represent various strategies in a given ecological scenario. CHES in this context can be thought of as systems where individuals behave according to utility functions that depend on environmental states, which respond to the strategy choices of other members of the population, in turn.

To our knowledge, no one has performed a recent scoping review of CHES models of ecological and environmental systems. Here, we report a scoping review of the literature on CHES models over a ten year period from May 2009 to April 2019. Our aims are to assess the modelling methodologies, study systems, number of models published over time, and means of implementation of human-environment coupling. We performed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) methodology to synthesize and filter the literature. We end with a discussion of the future potential of these modelling techniques for capturing complex dynamics of human and environment interactions.

4.3 Methodology

4.3.1 Methods Overview

In the following sections, we outline the process used to perform our scoping review. Search-terms were developed to capture papers on coupled human-environment system models. Searches used both Web of Knowledge (WOK) and PUBMED databases to generate a collection literature organized by titles, abstracts and keywords over a ten-year period. These results were synthesized using the PRISMA process (detailed below) to identify modelling research that utilized coupled human-environment systems.

4.3.2 Necessary Criteria

Qualifying research literature were required to satisfy the following criteria:

1. *An Environmental or Ecological Foundation*: Collected literature was required to have a focus on environmental or ecological systems. These included topics of sustainability, ecological management, water allocation, tourism, etc. We included models that were not developed for a specific system but rather represented some general class of ecological or environmental systems (we refer to these as 'general system models').

2. *Mathematical Modelling Techniques*: We aimed to collect literature that utilized mathematical modelling, such as systems of differential equations. These can also include computational simulations. Models were required to exhibit coupling between human and environment systems. Examples ranged from land-use land change (LULC) models, to cellular automaton (CA)-Markov models. This condition also includes simulating population with artificial intelligence or machine learning techniques, and can include game-theoretic ecological modelling techniques.

4.3.3 Exclusions

To exclude irrelevant papers and limit the scope of the review, we developed a preliminary screening criteria for the PRISMA process which targeted and removed results from

TOPIC:	(((”social and ecological” OR ”ecological and social” OR ”human-environment” OR ”socioecological” OR ”human-and-natural” OR ”CHANS” OR ”human and environment” OR ”human-natural” OR ”socio-ecological” OR ”Natural-Human” OR ”environmental-Human” OR ”Environment-Human” OR ”social-ecological”) AND (”mathematical model*” OR ”differential equation*” OR ”simulation model*” OR ”dynamic model*” OR ”compartment model*” OR ”system dynamics” OR ”Markov Chain*” OR ”Generalized Modeling” OR ”Generalized Modelling” OR ”Decision Model” OR ”Theoretical Model” OR ”Decision-Making Model”)))
OR TOPIC:	((”human-environment system model” OR ”human-environment model” OR ”Human-environment dynamics” OR ”socio-ecological system model” OR ”socio-ecological model” OR ”socio-ecological dynamics” OR ”human-and-natural system model” OR ”human-and-natural system dynamics” OR ”CHANS model” OR ”ecological and social dynamics” OR ”social and ecological dynamics” OR ”environmental-human system*”))

Table 4.1: Search terms that were inputted into both Web of Knowledge, and PUBMED databases between May 2009 to April 2019

epidemiology (vaccinations, disease dynamics, etc.), urbanization, industrial ecology (work safety, worker-ecosystem, etc.), and other non-environmental related work.

4.3.4 Search Terms

The search terms are provided in Table 4.1.

4.3.5 PRISMA

To identify relevant literature for this review, we used PRISMA, a tool that has been established since 2018 useful for systematic scoping reviews. PRISMA uses a step-by-step methodology to identify the most relevant papers from any collection of research [147]. The process and the number of papers we identified at each step of the PRISMA method are:

Step 1: Papers were collected using the search terms in Table 4.1 using Web of Knowledge and PubMed. Search results were saved using containing title, author, abstract and keywords. 2188 papers were obtained in total.

Step 2: Papers were assessed manually, filtering out any duplicates that were obtained from both search engines. This decreased the number of relevant papers to 1922.

Step 3: Papers were further screened based on their relevance to the review topic after scanning the titles, keywords and abstracts. Models needed to pertain to environmental/ecological systems and needed to have some mention a related human component which impacts the modelled system dynamics. The number of relevant papers decreased further to 681.

Step 4: Papers were further screened after a more thorough reading of the obtained literature. During this process, original research were retained while reviews and papers unrelated to Ecology or Environmental Science were removed. A total of 92 papers remained upon the completion of PRISMA.

4.4 Results

4.4.1 Notable Highlights

Several temporal trends and patterns in the collected literature were clear. Nearly 33% of reviewed publications applied some form of real-world data (questionnaries, surveys, etc.) for use in model parameterization or calibration. Furthermore, a large subset of publications developed models for a generalized ecological system (19/92) rather than for a specific ecosystem type. Lastly, the largest subset of publications focused on agricultural settings (21/92), while the smallest subset focused on climate change dynamics (2/92).

4.4.2 Date of Publication

Results were organized based on publication date. The number of publications over the time window of the review showed variability from year to year, but overall they show an increasing trend (Figure 4.2). It should be noted that the endpoints do not accurately describe the total number of papers in those specific years since the review time window started in the month of May and ended in the month of April.

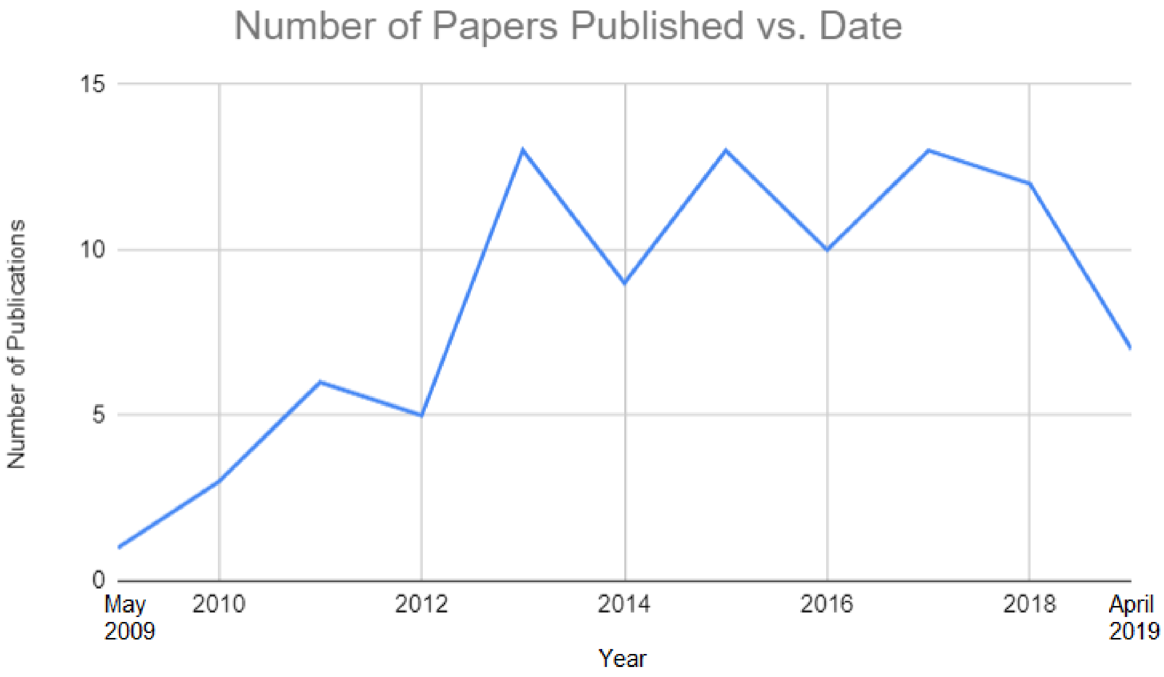

Figure 4.2: Literature organized by publication year. Papers were published between May 2009 and April 2019. Hence, the number of publications plotted for 2009 and 2019 only represent a subset of papers published in those calendar years.

4.4.3 Environmental System Topics

Results were also organized by the modelled system. Most papers focused on agricultural systems (41/92), and especially optimization of pastoral land-use benefits and land use transitions. We separated water allocation (4/92) from both land-use models and aquatic ecosystem management, since the topics of papers studying aquatic ecosystems (15/92) ranged from ecosystem well-being to optimization of fisherman benefits. Topics concerning tourism (5/92) were classified separately, since touristic CHES models were sufficiently numerous, regardless of the ecological setting they modelled. Forests and grassland models were combined under one classification (13/92), as were topics focusing solely on resilience

Region	Publications
Resilience/Sustainability	[213, 15, 12, 56, 21, 53, 13, 14, 195].
Water Allocation	[38, 221, 141, 3].
Agriculture/Land-Use	[117, 51, 90, 177, 116, 172, 98, 28, 119, 158, 76, 37, 136, 3, 123, 174, 29, 202, 173, 133, 120, 187, 56, 21, 131, 179, 44, 169, 129, 236, 20, 13, 140, 14, 201, 104, 137, 135, 219, 139, 146, 224].
Tourism	[165, 12, 149, 121, 113].
Aquatic Ecosystem Management	[84, 110, 161, 48, 209, 145, 235, 114, 121, 97, 107, 166, 190, 73, 138].
Forest and/or Grassland Dynamics	[122, 19, 180, 191, 90, 4, 17, 89, 99, 65, 177, 28, 162].
Theoretical/Generalizations	[16, 217, 78, 33, 32, 115, 200, 203, 205, 213, 228, 176, 95, 162, 150, 179, 104, 138, 224].

Table 4.2: Publications organized by study.

or sustainability (9/92). Finally, many CHES models were general system models, developed without reference to a particular study system (19/92). These models were included due to their applicability to different environmental topics that were usually mentioned in the paper's Discussion section. Results have been compiled in Table 4.2.

4.4.4 Model Type

Results were categorized by their model type to highlight the various methods of representing coupled human-environment systems. Models were placed into four different classifications - Differential equations (DEs), Agent (Individual)-Based Modelling (ABM/IBM), non-ABM stochastic models, and unspecified/other models, which are discussed in more detail below. Publications by model type are summarized in Table 4.3. We also plotted

Model Type	Publications
Difference/Differential Equations	[117, 122, 217, 161, 19, 78, 48, 33, 32, 180, 209, 191, 90, 145, 235, 4, 114, 17, 99, 115, 65, 116, 200, 213, 98, 76, 149, 136, 123, 29, 133, 121, 97, 95, 113, 107, 162, 53, 179, 140, 104, 190, 195, 138].
Agent(/Individual) - Based Modelling	[16, 110, 51, 165, 172, 205, 141, 119, 28, 158, 37, 11, 3, 174, 176, 202, 173, 120, 187, 150, 131, 236, 20, 201, 135, 219, 73, 146].
Stochastic Models	[89, 177, 203, 221, 228, 56, 169, 129, 224].
Other	[84, 38, 15, 12, 166, 21, 44, 13, 14, 137, 139].

Table 4.3: Publications organized by model type.

the number of each model type in each year. We noticed steady growth of DE models until 2016 following a decline, while the number of ABMs varied throughout the review time period. The number of stochastic models each year was roughly constant, while unspecified/other modelling techniques grew in the latter half of the review time period. The results were compiled and can be seen in Figure 4.3.

Differential Equations

Differential equations (DE) have provided the foundation for much mathematical modelling. Differential equations describe how system variables evolve dynamically in response to one another as a function of model parameters in continuous time. Differential equations can capture behaviour near equilibrium states, transient dynamics, and sudden transformations–regime shifts–in a natural way. In the case of classical mathematical modelling of environmental systems, these models represented human influence implicitly by considering the impact of humans on natural system parameters such as fecundity or flow rates, whereas human-environment models represent the human system explicitly–as a state variable–that itself is influenced by other parameters such as mitigation cost, for

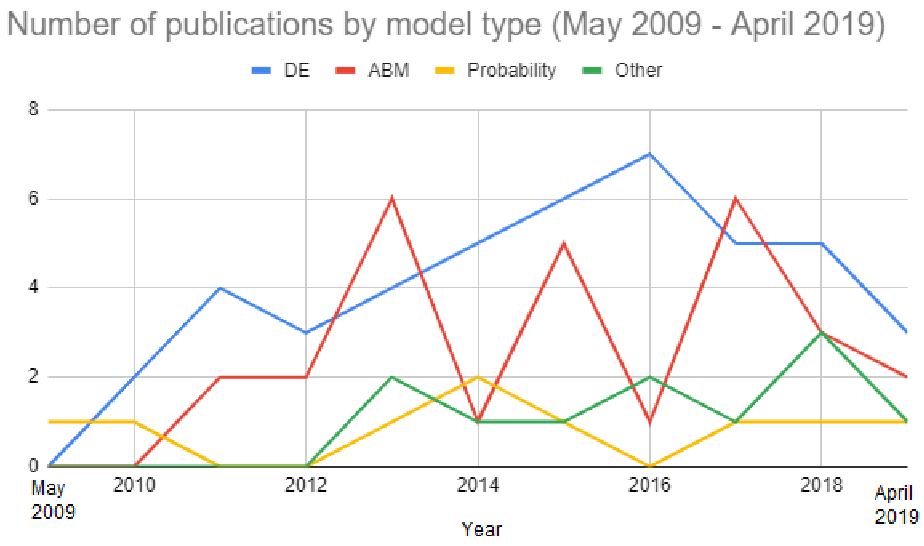

Figure 4.3: Number of publications using different model types between May 2009-April 2019. Because the start and end dates of our study fell partway through May 2009 and April 2019, the number of publications plotted for those years do not represent the entire calendar year.

instance.

Differential equation models of natural systems have been expanded into CHES models to explore a number of topics in human-affected ecosystems such as natural land depletion taxation [117], incentivization of fisherman behaviour [161], or conservationist opinion and behaviour propagation in populations through social processes [19].

Deterministic differential equations are a subset of DEs where the model trajectory is determined entirely by parameter values and initial conditions. Deterministic CHES DE models vary in complexity and implementation. In [99], Innes et al, conservation opinions regarding Brazilian forest-grassland mosaic model evolved dynamically according to ecosystem rarity. The perceived utility of individuals influenced land-use decision making. Horan et al [95] utilized decision dynamics in a modified Lotka-Volterra predator-prey model to investigate harvesting dynamics on crayfish and bass biomasses. In order to develop the human component of the model, fisherman harvesting choices were conditioned on the relative costs, benefits and regulation policies. In both models, behavioural components dynamically affected environmental system dynamics and *vice versa*.

An alternative DE methodology was developed to investigate the effects of mass tourism versus ecotourism by Monfared et al. [149]. The DE model was composed of a 4-dimensional dynamical system to investigate the ecological impact between mass tourists and ecotourists. In their model, two compartments were developed to represent different members of the population - mass tourists and eco-tourists, and another two compartments to asses changes in capital and ecosystem quality. Mass tourists exploit the ecosystem services regardless of its current status, whereas eco-tourists refrain from visiting these sites when environment system dynamics cannot adequately sustain visitors. Interactions between both tourists (similar to mass-action mixing components in disease models) would dissuade both populations of tourists from visiting. Coexistence of both different populations, albeit chaotic in nature, was proven possible through numerical analysis, and would lead to unsustainable (oscillatory) environmental quality.

Stochastic differential equations constitute another subset of DE models. These models incorporate stochasticity ('random noise') processes. An example of these models was developed by Ali et al [4] where a stochastic coupled human-environment system of pest invasions in provincial parks was developed. Imitation dynamics were observed to drive changes between strategies of buying firewood locally or transporting it. Social norms were incorporated to influence strategy switching under the concern of potential infestation. Another stochastic system developed by Lee et al [123], coupled a dynamic model of grassland dynamics to foraging decision-making. They used stochastic best-response dynamics, which is a modified technique of classic best-response dynamics where players choose the optimal outcome at the next time step, subject to a stochastic term that represents other influences on their decision-making process [72]. Bistability, where a system may end up either in one state or a different state, depending on initial conditions, was also observed. Furthermore, model dynamics admitted oscillatory behaviour between relative grass biomass and herder populations, where depletion of grasses causes herders to vacate the area. Given sufficient system resource resiliency, depleted grasses are able to recover over time and maintain the cyclic relationship between grass biomass availability .

Some papers used custom-built software to develop and analyze differential equation models. In Marin et al [133], a CHES DE model was developed with a mathematical modelling and simulation software package called STELLA, to investigate the impacts of social capital on scrubland dynamics. Another CHES model was developed by McClanahan et al. [145] in STELLA to investigate the dynamics of restrictions and regulations on coral reef fisheries. This software package uses compartmental diagrams to provide insight and aid in determining the appropriate linking elements in the model. Once all required elements of the model are defined, simulations can be generated and tested with empirical data [126].

Agent-Based/Individual-Based Modelling

Coupled human-environment systems can also be represented using agent-based modelling (ABM). These models employ autonomous agents to perform pre-defined actions that represent the role that they have been assigned [218]. Agents are capable of interacting with other agents, based on the design criteria of these models. These agents can also perform various decision-making processes based on the status of the system, sometimes in order achieve an optimal solution set, while taking into account factors such as demand and other predefined criteria. These can be visualized as pathway-based systems which performs actions upon performing an assessment of all collected possibilities and their overall payoffs [31].

An example of these models was used by Berfuss et al [16] who developed an ABM coupled human-environment system to explore policy making and its effects on economic growth with applications to climate change and fisheries. The model used Markov decision making processes, which processes decisions partially by choice and partially randomly, to characterize agent behaviour. Triggers were found to influence the adoption of both unsafe and unsustainable policy making strategies if agents blindly followed an economic optimization strategy. Another coupled human-environment system developed by Coutts et al [51] utilized an ABM to investigate agent behaviour in response to weed spread in pastoral regions. Agents relied on factors such as profit, invasion probability and social pressures when performing decision making processes. Weed prevalence was directly influenced via social pressure. This was also in part due to the effect of perceived benefits on how internal social norms influenced the severity of the weed prevalence.

Similar to DEs, software packages that allow users to develop and analyze ABMs have been used. Work by Synes et al [205] developed an ABM CHES to create a competitive scenario where social agents compete for land based on their ability to effectively use capital and ecosystem services. Modelling processes were simulated with the computational program CRAFTY, using ecosystem service levels to provide the basis for agent decision-making processes with respect to land-management. Results indicated a need to use agent-functional types of models to facilitate ABM application across a large spatial extent, and a potential loss of information by employing uncoupled modelling techniques. In addition, another CHES ABM model was developed Marohn et al [135] that coupled two software packages - LUCIA (soil, water and plant dynamics) and MP-MAS (farmland decision making, investment, production and income optimization). Their model assessed conservation strategies in a highland agricultural setting. They identified low-cost conservation strategies that could benefit soil quality, household income, and farmland productivity. In particular, changes in fertilizer prices can strongly influence agent decisions in choosing to adopt soil conservation practices, and can instead support the choice to maximize crop yield.

Stochastic Modelling

CHES models have also used stochastic modelling techniques such as Markov Chain modelling. Models in this category capture state transitions via a matrix where each element of the matrix represents the probability of a transition from one system state to another one. These can be used in tandem with other modelling techniques or also commonly with CA - cellular automata, which evolve based on both a set of predefined rules and the states or results of neighbouring strategies, or using system dynamics, which captures feedback loops and transitions based on predefined probabilities. Transition matrices are developed to illustrate the probability of an agent's decision and their impact on natural system states.

Henderson et al [89] illustrate this methodology with a Markov chain model of landowner decision-making based on preferences and land cover in each time step. Individuals may choose to clear a given patch of forest or have it harvested for lumber in each time step. Using utility-based decision making, it was determined that implementing certain conservation incentives did not support stable forest cover, and instead caused cyclical bouts of deforestation due to interactions between individual landowner decisions and total amount of forest cover and harvesting decisions in the whole population.

4.4.5 Human Component

The methods used to represent the human component of CHES varied widely in the included literature (Table 4.4). We explore these various approaches in the following paragraphs.

Optimization

Human behaviour was most commonly represented in coupled human-environment systems via the use of optimization techniques. In general, papers in this category optimized functional representations of individuals' personal interest in a natural system, and predicted the impact of optimized personal decision-making on natural system states. (This approach we treated as distinct from game theory, which will be discussed separately later, where individuals are assumed to optimize their payoff in a situation where their payoff is dependent on the actions of other individuals of the population.) Using a functional form to represent payoffs or utilities, members of the population can be modelled implementing strategy switching (imitation) to follow strategies with the greatest payoff value.

An example of representing human decision-making as optimization of an objective function is exhibited by Blanco-Gutierrez et al [29]. The authors develop an integrated economic-hydrologic CHES model where farmers aimed to maximize their income by assessing three different model scenarios: business-as-usual (BAU), EU-policy driven, and national policy driven scenarios. Results revealed farmers' behaviour when handling risk, causing the model to predict a tradeoff between risk-taking and overall profit obtained by farmers. Model dynamics revealed detrimental effects of BAU-scenarios, but showed management changes when both EU and national policy measures were implemented.

Human Representation	**Publications**
Optimization	[84, 16, 38, 165, 141, 76, 136, 11, 29, 176, 121, 97, 107, 187, 162, 150, 104, 140, 48, 235, 200, 213, 98, 37, 131, 201, 146, 138].
Phenomenological Fitting	[110, 15, 12, 202, 133, 166, 44, 169, 13, 14, 219].
Social Influence (Without Imitation Dynamics)	[84, 117, 209, 191, 165, 172, 205, 28, 158, 149, 3, 176, 113, 107, 166, 53, 129, 219, 65, 221, 121, 203].
Game Theoretical	[122, 217, 161, 19, 78, 48, 51, 32, 180, 209, 191, 90, 145, 235, 4, 114, 17, 89, 99, 115, 177, 116, 141, 119, 76, 228, 120, 162, 21, 131, 236, 73, 205, 37].
Other	[117, 65, 123, 95, 179, 20, 195, 3, 137, 174, 173, 56, 139, 224].

Table 4.4: Publications organized by the methods used to represent the human system.

In a fishery model by Hunt et al [97], a CHES model was developed using a "utility-theoretic" approach to model fisherman angler behaviour. In order to maximize utility, anglers considered a given set of lakes and chose a lake with the highest perceived utility. Model analysis revealed that low angler population sizes and high catch importance reduced the potential for anglers to overfish.

Phenomenological Modelling

Phenomenological models describe the observed dynamics of a system without articulating a mechanistic basis for the components of the model structure. In general, these models utilize empirical data from various sources to establish functional representations for their components. Additionally, in some cases where empirical data is insufficient, parameters can be calibrated based on historically observed trends or biologically plausible trajectories [4]. Examples of phenomenological fitting in the reviewed literature used surveys or other empirical data such as fisherman catch per unit effort (CPUE) or firewood transport costs in order to quantify model parameters governing phenomenologically-justified functions [107, 17].

Artificial Intelligence (AI) and Machine Learning (ML)

AI and ML models have also been developed to simulate the dynamics of human interactions with environmental systems [224]. These approaches are often used to represent human behaviour in a CHES model. But in other cases, investigators have hybridized the use of machine learning algorithms to inform land use modelling, with role-playing games involving real human participants. For instance, Washington-Ottombre et al. [224] use this approach to study land use decisions in a fictional land named Mageria, based on interactions between pastoralists, farmers, and a land commissioner. AI and ML methods were relatively unexplored by the CHES modelling literature, but do possess potential application to capture individual behaviour.

Game Theoretical Techniques

As mentioned previously, game theory can be used to model how humans behave in strategic decision-making where their payoff depends on the strategies choosen by both themselves and other individuals. These methods have also been used in CHES models. One such method employs replicator dynamics, in which individuals do not automatically switch to the highest-payoff strategy at some point in time but rather only switch after some kind of learning or imitation processs. For instance, in imitation dynamics, an individual samples other individuals in the population and, if the focal individual encounters someone playing a different strategy, the focal individual switches their strategy with a probability proportional to the perceived payoff gain for switching to that strategy. These methods are implemented using differential equations to develop representative utility/payoff functions that become incorporated into the overall model structure for dynamic human behaviour.

An example of replicator dynamics was observed in a CHES model developed by Henderson et al [90], investigating the effects of coupling human dynamics of land preference on the Brazilian forest-grassland mosaic. Imitation dynamics were developed to capture the preferences of the population when choosing whether to modify or keep land for either agricultural, forest or grassland uses. With modifications to the utilities for the protectionist strategy, the model predicted significant impacts on human-environment stability. Some examples of these effects include high conservation values tending to transform land away from agricultural purposes. Model predictions demonstrated a straightforward response to increasing conservation values of grasslands. Increasing forest conservation values instead caused model dynamics to stabilize to a state governed by forest-grassland limit cycles, or grassland stability. Additionally, with sufficiently high economic discount rates, compared to conservation discount rates, model dynamics tend to stabilize in either forest or grassland states (and conversely stabilize in an agricultural state for sufficiently low economic discount rates).

Lade et al [115] utilized a game-theoretic CHES model to analyze common-pool resource use dynamics. In their work, the human component followed replicator dynamics and payoff functions for defectors and cooperators were defined. Results revealed significant resource depletion driven by humans. In addition, with a constant inflow of a resource, the net benefit of the defection strategy would outweigh the value of a co-operative regulatory strategy, leading to a catastrophic collapse of resource. Given that regime shifts can occur unexpectedly in response to slowly changing external drivers, this work emphasizes the danger of exploiting environmental resources, especially under lack of proper monitoring. The authors emphasize that including human dynamics in their model revealed predictions that would not occur without the dynamic coupling between human and natural systems.

In a model by Rodrigues et al. [177], the impact of human behaviour was implemented in a 2-strategy, 2-person game CHES model of forestry dynamics. In their work, deforestation was utility-driven, with state transitions being described using Markov-chain transition probabilities. Results showed that deforestation would benefit the landowners, but would cause degradation of ecosystem services and value of neighbouring land, especially if forest recovery is sufficiently slow. Overall, forest regeneration would favour mutual cooperative strategies, but would also govern the rate of agricultural abandonment as the decision to conserve would be dependent on the choices of neighbouring landowners. Alternatively, if forest recovery is sufficiently fast, landowners would be more likely to choose to deforest, a similar scenario observed by Lade et al. [65] with resource exploitation. This prediction is an excellent example of the 'law of unintended consequences' and demonstrates the value of including feedback between human and natural systems via CHES models.

In a model developed by Mason et al [141], an agent-based evolutionary game model was developed to determine operator decision criteria with respect to water resource systems. In their model, operators (agents) undergo a negotiation process until a successful proposal is achieved. Agents aim to increase their own utility for personal benefit, which would be equivalent to a decrease in utility for unsuccessful agents. Knowledge of the current state would influence future decisions as well as proposals agents make under various climactic conditions. While new proposals cannot directly undermine other agents, new solutions would add to the agent's total set of proposals, and agents must grant a concession to another agent. Model dynamics were tested on synthetic flood control and water supply dynamics and were successfully able to capture operator behaviour under climatic conditions of extreme wet and dry scenarios.

Social Learning (Without Replicator Dynamics)

A number of CHES models represent social learning and other social processes without invoking replicator dynamics. In these models, in any given population the effects of social influence or interactions can influence individuals to modify their personal strategies in order to maximize their personal gain, without using the specific structure of the replicator equations. Rebaudo and Dangles [172] developed a CHES model with a human component that utilized information transferal mechanisms to investigate the role of social dynamics in pest dynamics. In their model, agents were capable of self-awareness to modify strategies based on their prior experiences. In addition to this, agents were capable of learning from other successful strategies, and were also capable of training others to increase knowledge of pest management. Despite the short-term costs incurred by implementing cooperative behaviour, model dynamics predicted decreased overall infestation levels over time.

Another example of this technique was utilized in a CHES model by Walsh et al. [219].

Using an ABM approach, a detailed model was developed to examine the relationship between an agricultural village population and their environment. Social modules were developed describing individual changes in social networks, population and assets, and land dynamics regardless of current climatic conditions.

4.5 Discussion

Our review shows that the number CHES models published each year has increased over the past decade. Moreover, there is a growing diversity in modelling techniques, including in the ways that human behaviour is represented. We found diverse methodologies in the construction of CHES models, including DEs (44/92), agent-based models (28/92) and stochastic models (9/92), with the remainder of the literature labelled as 'other' (11/92). With respect to modelling the human component, most papers used either optimization techniques (28/92) or modelled social influences with (34/92) or without (22/92) a game-theoretic foundation. Model complexity varied considerably. For instance, some papers using computational programs such as STELLA, or FSM [145, 12] calibrated their models using numerous parameter values generated from various data sources. In some cases, these models have also been able to successfully replicate historical trends [200].

We observed striking differences in the degree to which different environmental and ecological systems were represented in the literature: some types of natural systems were explored much more than other types. As observed in Table 4.2, CHES models have been implemented most commonly in agricultural settings, or in generic system models. Water allocation and tourism were the focus of the fewest papers. Furthermore, the impact of anthropogenic stress on the dynamics of terrestrial wildlife appeared to be relatively unexplored. Given that both marine and grassland systems are subject to invasive species and direct exploitation by humans, CHES modelling techniques could be applied to terrestrial wildlife dynamics more widely than they presently are. As an example, modelling techniques used to study overfishing of marine resources can be utilized as a template to build models for studying the dynamics of human-wildlife interactions with respect to hunting and poaching, especially with regard to restoration of critically endangered species. We speculate that the variation in how often different types of systems were studied over the past decade has more to do with 'leader effects' in the process of selecting research study systems, rather than inherent suitability or desirability of systems for CHES modelling.

Another topic that has not been explored in great detail is the effect of tourism on elements other than marine ecosystems. Touristic aggression on ecosystem dynamics have not been investigated in great detail in forest or grassland systems, despite the pervasiveness of tourism in those systems. As such, there is a great opportunity to study ecosystem interference and stress caused by tourism in a CHES framework.

As mentioned previously, the number of published CHES models increased significantly over the past decade. One possible reason for this increase could be diminishing computational barriers to developing complicated models, both with respect to computational power as well as making modelling accessible through specialized software like STELLA. As computational power has grown, it has become easier both to simulate complex models and parameterize them in increasingly sophisticated ways. Increasing complexity, on average reflects a general trend in model development in many fields, where models begin simple and over time become enhanced and increasingly complex [143]. Progression is due to the fact that simple models require less time to analyze, and provide insight on the opportunities to explore and enhance their explanatory power. In the context of CHES, these can take the form of newly recognized opportunities to expand existing ecological or environmental models to accommodate the increasing evidence of human impact and human inter-relatedness with natural systems. This does not imply that simple models are necessarily less accurate, but rather that they can provide the foundation for more complex future iterations based on the critical assumptions made during their initial development.

Misinformation is an important determinant of decision-making [204]. Most of the models we reviewed did not address misinformation explicitly. Many papers from outside our included literature are concerned with the spread of fake news and how to stop it, using a range of modelling techniques [206, 35, 86]. One paper employed approaches ranging from stochastic models to difference equations [35] to study the spread of fake news. Another example used game theory to investigate the Nash equilibrium strategy of a hypothetical 'digital' citizen who combats fake news regarding COVID-19 [86], while others have used a network model used to simulate the spread of hoaxes and their debunking [206]. However, some of the models included in our review studied imperfect information (which differs from misinformation in that the latter is deliberately falsified). In imitation dynamics models, for instance, it is often assumed that individuals respond to some proxy of ecosystem health (such as perceived forest cover or perceived climate events) rather than acting in full knowledge of current or future impacts on the natural system [17, 42].

Human interactions have evolved over the past few centuries from predominantly in-person interactions to communication at a distance through telephones and, more recently, online social media. With the introduction of online forums, groups and various outlets of social media, individuals can be exposed to different individuals with different beliefs, strategies and cultural norms [231, 6, 50]. Overall, these changes in the scale over which social forces operate will change individual relationships to natural systems. Moreover, we believe that the data provided by these sources will provide great insight into how individuals make decisions concerning natural systems, and how they are influenced by social forces.

Emerging data from new study systems suggests both new topics for behavioural modelling as well as new modelling techniques. For instance, the advent of online social media has led to the formation of social groups that are harmful to their own members, such as pro-anorexia groups [75]. The combination of changes to social conformity (e.g. peer pressure) and new digital means for socializing [58, 47, 229], mean that individuals can meet and interact with various others who share similar or different ideologies. Based on the guidelines of these groups, one must conform to a strict set of rules in order to be accepted. Thus, an individual using alternative strategies can be sufficiently influenced to adopt the beliefs set by the online group. In summary, the definition of one's community interactions is not limited to strictly interpersonal interactions, and as such mathematical models can be extended to accommodate online influence in social networks. Such situations can be approached using social network simulation models.

In conjunction with the growth of online communities, there also appear to be opportunities for using simulated environments to observe human interactions in response to various stresses. An example of this occurred in an accidental epidemic caused by Blizzard Entertainment in their MMORPG (massively multiplayer online role playing game) World of Warcraft, where their player-base reacted to a rampant in-game epidemic [130]. This represents a natural experiment that is not dissimilar to controlled experiments used in economic game theory, for instance [30, 223]. Using simulated systems such as these, alternative data for measuring complex psychological behaviour can be obtained. For study populations where insufficient empirical data are available, trends from simulated environments can be extrapolated into CHES models to achieve a data-driven representation of human-environment interactions and potential intervention scenarios that can be explored.

Coupled human-environment systems models can hasten the identification of the forces that most strongly impact natural systems in the Anthropocene Era, and improve the representation of natural systems mathematical models. The literature we collected represents diverse and numerous variations of CHES modelling with similar long-term goals of not only explaining empirical observations, but also achieving sustainable trajectories for ecosystem dynamics. Continuing improvements in computational power and accessibility of model development software, together with growing data on both natural and human systems in the era of widespread digital data, suggest CHES modelling will continue to grow as a field and become more useful for applications to finding pathways toward environmental sustainability.

Chapter 5

Conclusion

5.1 Summary of Findings

Two game-theoretic DE CHES models were developed to model dynamic human behaviour in two different environmental systems. The objective was to study recovery and sustainability in human-environment systems. The coupling of a human system to a natural system revealed new types of dynamics that have not been explored in great detail in literature on models of environmental systems in the absence of dynamic human feedback. Both systems exhibited bistability on account of CHES feedbacks pertaining to social norms. Similarly, changes to the social learning rate or population sensitivity to natural states caused a considerable change in the model solution trajectories in both models. If sufficiently strong, social norms can become can become an overwhelmingly powerful mechanism to favour either mitigation or non-mitigation, depending on the system's initial conditions. Because of their ability to incorporate behavioural feedbacks based on changes to parameters governing individual incentives and perception of ecosystems, CHES models show potential to inform effective policy implementations to promote and sustain natural ecosystems.

Human activities have led to considerable damage to many ecosystem goods and services, sometimes leading to collapsed states that are difficult to recover from, as evidenced by lake eutrophication[85]. We set out to investigate the changes in model predictions that occur when implementing a simple dynamic human component to replace the implied static human behaviour in most environmental and ecological models. Furthermore, we sought to determine biologically plausible conditions to achieve stable natural system states. Parameter regimes corresponding to natural system stability were achieved in both models through a mechanism whereby declining ecosystem health stimulated the human population to shift to a predominantly conservationist strategy that was subsequently entrenched by injunctive social norms. The models also predicted new system dynamics that have not been widely reported in the CHES modelling literature. For instance, it was possible for system dynamics to stabilize in a state completely governed by natural system dynamics without the need for intervention by human conservationists. In both models, this was achieved through an early transient phase of either sufficiently low levels of human exploitation or sufficiently high incentivization to protect. This initial phase wanes, leading to a desirable equilibrium state where the natural system can persist robustly despite the lack of conservationist effort. As a result of the shift from static to dynamic representation of human behaviour, our CHES models revealed new scenarios that can be used to inform and educate the population of the associated costs and benefits of harmful behaviour in various environmental systems. Furthermore, based on the simplicity of its implementation, this methodology can be adapted to various fields and disciplines to accommodate dynamic human behaviour in differential equation models.

The inclusion of social norms has not been explored in great detail in the CHES literature. In cases where it has been included, it is usually assumed that norms can only operate to sustain the natural state. However, individual choices can be based on a variety of factors such as economic status, social perceptions, and peer pressure. In this thesis, a simple model component was implemented to represent social support for one's strategy choice when developing the dialogues for each strategy–whether that strategy be mitigation or non-mitigation–in order to observe its effects on environmental system dynamics. Despite the simplicity of the representation of social norms, model simulations captured the behaviour of two competing strategies and their impact on the environmental trajectories. This effect was observed in results of the reef-ecosystem model, where strength of social norms promoted or suppressed conservationism. While this effect was not as evident in the grassland model, its influence nonetheless created oscillations in grass biomasses of both native and exotic grass species, where the local population could change their stance on conservation in response to the current biomass of exotic grasses. The inclusion of injunctive social norms in CHES models provides a unique approach to understanding the interplay between social influence and incentivization of sustainable behaviour.

The thesis also addressed how the various forms and uses of CHES modelling have evolved over the past decade. Results of our scoping review of CHES modelling revealed an increasing trend in the number of published models. We suggested that this represents the large number of under-explored opportunities in this field. Given the strong evidence of human impact on environmental systems, there is a great need to develop CHES models capturing the complex interactions and effects of human behaviour in various environmental settings. The literature revealed that these models most often employed DE or ABM techniques to accomplish their goals, but varied in complexity and implementation. In addition, the surveyed literature revealed most models focused on agricultural or land-use studies. Thus, there is a great opportunity to adapt or expand on existing methodologies in other environmental settings.

5.2 Future work

The simplicity of our models raises the question of how well simple models can accurately represent complex human-environment interactions. In general, theoretical modelling attempts to identify patterns from empirical data, while also assessing how the modelling techniques may influence predictions, and comparing the relevance of predictions to real-world dynamics. As such, this requires formulating model assumptions, such as whether stochastic or spatial dynamics are required, and which parameters and variables need to be included. Simple models have several advantages: they require less development time and analysis; they can provide the foundation for increasingly complicated extensions; they can provide clearer insight than complicated models; and their predictions are sometimes almost as reliable as those of more complicated models (and occasionally even more reliable, given that complicated models are more subject to over-fitting of data). In both models, we utilized deterministic DEs, similar to previous models, and coupled the dynamic human component to observe the effects of behavioural mechanisms on these environmental systems. In both systems, future work could add effects such as spatial structure to better represent population heterogeneity, or stochasticity to capture the influence of a multitude of other processes on decision-making. Despite their simplifying assumptions, the two models generated robust and qualitatively realistic predictions similar to predictions made by more complicated models.

The representation of many psychological aspects of behaviour should also be a target for future models. For instance, the imitation dynamic assumes that an individuals changes their strategy after they have sampled someone else with a positive probability that scales with the payoff difference. However, the assumption of a fixed probability that applies at each sampling is not consistent with some aspects of real-world psychology. A sudden shift in personal choices may be difficult and require time to perform. For instance, consider the difficulty of quitting addiction without the benefit of reinforcement. A simple solution would be for the individual to quit altogether once that individual realizes that the 'payoff' for sobriety is better, but these habitual changes require time, and in some cases require external support mechanisms to achieve their goals [227]. In some cases a waning period is required for individuals to ease off or into these habitual choices, such as gym consistency after a long pandemic. As such, the human component can be expanded to accommodate these slow changes in individual behaviour. One such method can incorporate a mass-action mixing of strategies from infectious disease transmission modelling [81] that could utilize sigmoidal functions to characterize the slow transition from one strategy to another. This would result in a multi-tiered modelling framework that could enhance existing imitation dynamic representations of human behaviour and provide a deeper understanding of the complex interactions between human and environmental dynamics. Another approach would be to treat psychological states like addiction as a form of behavioural hysteresis at the individual level.

The dynamics of both models could be compared to the dynamics of models for the same study system but represented with a different modelling methodology. From the review, we noted a large proportion of the collected literature utilized DEs to develop their CHES models. One effective comparison would be to develop an ABM as used in tourism modelling [165, 121], where agents employ entrance fees or purposefully divert attention away from protected sites as a way to promote localized conservationist strategies for an endangered species. This methodology could be adapted more easily to the reef-ecosystem model, where sanctuaries have already been established. In the case of the grassland model, an effective agent based defector-cooperator game as studied in [122] can be used to test the results for a local parcel of grasslands. In both cases, the model can be developed such that agents utilize prior information to determine which strategy provides a greater payoff. This effect can drastically change when implementing various levels of incentivization as agents can act in their best interest. Using this agent-based framework could reveal insights regarding the impacts of localized feedback on environmental system preservation and should be considered to suggest areas worth further study in terms of opportunities for different types of models.

Alternatively, future work can build on the imitation dynamic framework of the two models in this thesis to incorporate more complexity into social dynamics of their respective human-environment systems. Extensions of the coral reef model can incorporate the impacts of tourism on reef integrity. Work by [149, 113] utilized a DE CHES model to analyze the effects of eco-tourism vs mass tourism. Eco-tourism can be described using behavioural traits, where tourist visits to a particular site are considered based on the integrity of the site and the abundance of mass tourists already there. Alternatively, mass tourists visit the sites freely without considering the impact their presence has on the integrity of the ecosystem and are also also equally affected by a mass-action mixing presence of eco-tourists on the site. It is no surprise that coral reefs have qualities that attract tourists. As such, the model can be extended to incorporate a second human compartment determining the number of accessible sites for tourists, based on relative payoffs to exploit the features of the reef ecosystem.

The grassland model can also expanded and improved in several respects. It should be noted that several of the model parameters (plant-available nitrogen A, the half-saturation constant h, plant available nitrogen soil leaching rate k, and the biomass turnover rates m, μ) were chosen to give qualitatively plausible dynamics, based on correspondence with the original study author. Future work could improve the empirical basis for the model parameters. Furthermore, it is also well documented that Australia has imported various invasive species [214, 61]. As a first step in its expansion, the impact of case importation of invasive plant species can be investigated in order to replicate historical trends. Then, based on the results, and using geographic/topological data, the nitrogen deposition compartment can be adjusted accordingly to account for key contributors of nitrogen in the ecosystem, such as the division between local pollution and pastoral waste. By identifying the key components enabling invasive species population growth, the model can be enhanced to provide more realistic predictions, and provide insight into specific policy interventions to achieve sustainable native grasslands.

With the growth and development of technology, humans have been introduced to new platforms to interact with others, via messaging, forums, livestreams, and other forms of online social media. In our models, individuals can sample other individual strategies within their population (community). In future work, the definition of one's "community" can be broadened to distinguish geographically local versus online communities. To accommodate this change in our models, the game theoretic compartment can be expanded to represent the competition between local and online influence, alongside their respective social norms. Furthermore, continuing from the discussion of the relentless evolution of technology, human decision-making could be modelled using artificial intelligence (AI), such as exemplified by recent work where AI agents must make harvesting decisions in a common-pool resource problem [164]. In addition to AI, gamification has already been used to study several relevant and interesting human behaviour changes. In 2007, Blizzard Entertainment accidentally implemented a debilitating infectious disease in a software up-date that quickly spread throughout the server, infecting and causing disastrous outcomes for all players [130]. Interesting behaviour was also observed in the AI agents that the game uses, which resulted in numerous different dialogues for what individuals wanted and how decisions were made by the governing party. Many different player reactions were observed: some players chose terror-inflicting behaviours, while others chose pacifistic routes by staying offline to prevent further infection. Using AI or virtual (gamification) methodologies, new avenues of exploration for modelling human impact on environments can be established. Furthermore, virtual simulations can be more ethical, practical, and faster than running experiments with empirical human and environmental study systems, thereby revealing new pathways to more closely capture the intricacies behind human decisions in CHES modelling.

5.3 Concluding comments

This thesis has presented a game-theoretic approach to model dynamic interactions between human behaviour and two non-linear environmental system models. The methodology revealed new pathways to achieve sustainable natural ecosystem dynamics and has contributed to the discussion of system resilience and sustainability. The use of CHES models in environmental system modelling is relatively new and is slowly gaining traction. There is great urgency to develop CHES modelling methodologies to establish more effective policies and incentives to promote growth and recovery of endangered species and ecosystems. The results from our CHES models highlight valuable information that is not accessible without a social and environmental coupling represented in mathematical modelling. Future work will focus on improving the quality of their mathematical representation and providing guidance for changes to real-world policies, in order to promote sustainable environmental system growth and development.

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APPENDICES

Appendix A

Matlab Code for Making a PDF Plot

A.1 Using MATLAB to generate plots

MATLAB was used to generate time series and parameter planes for both models. The simulation codes used for the thesis can be found at https://github.com/vthampi/Thesis-code.git

Appendix B

Alternative Non-Baseline Time series Results of the Caribbean Reef-Ecosystem Model

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This section contains supplementary figures originally included in the paper : Thampi, Vivek A., Madhur Anand, and Chris T. Bauch. "Socio-ecological dynamics of Caribbean coral reef ecosystems and conservation opinion propagation." Scientific reports 8.1 (2018): 1-11.

In this section we provide additional figures which were generated by the reef-ecosystem CHES model.

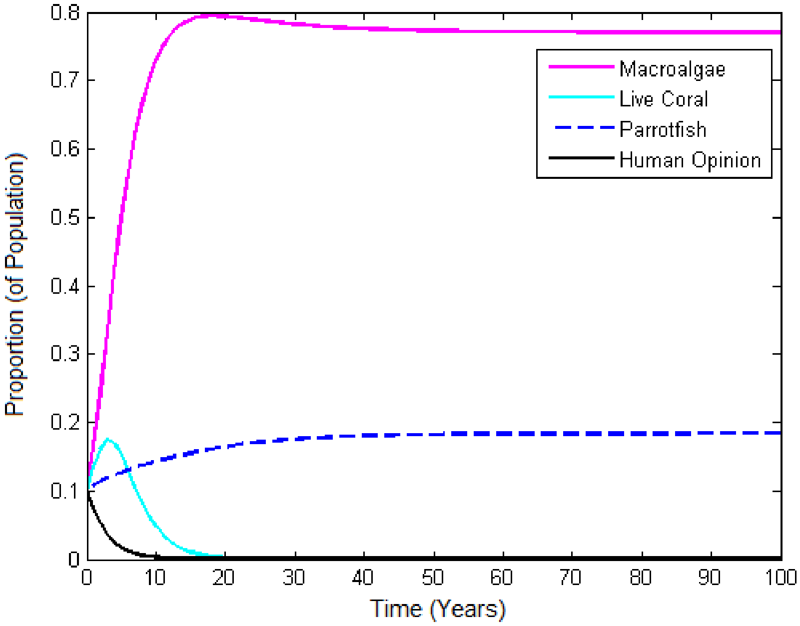

Figure B.1: Time series illustrating the behaviour corresponding to *Dead Corals (ii)* for $\sigma = 0.4$ yr^{-1} and $J = 1$ with corresponding initial conditions $M = 0.1$,$C = 0.1$,$P = 0.1$,$x = 0.1$ and all other parameters fixed baseline.

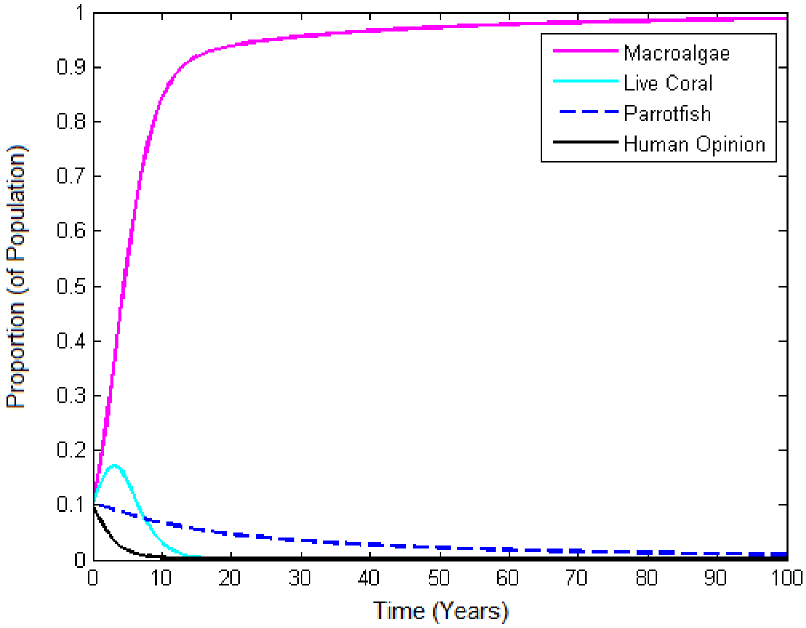

Figure B.2: Time series illustrating the behaviour corresponding to *Dead Corals (iii)* for $\sigma = 0.5$ yr^{-1} and $J = 1$ with corresponding initial conditions $M = 0.1$,$C = 0.1$,$P = 0.1$,$x = 0.1$ and all other parameters fixed baseline.

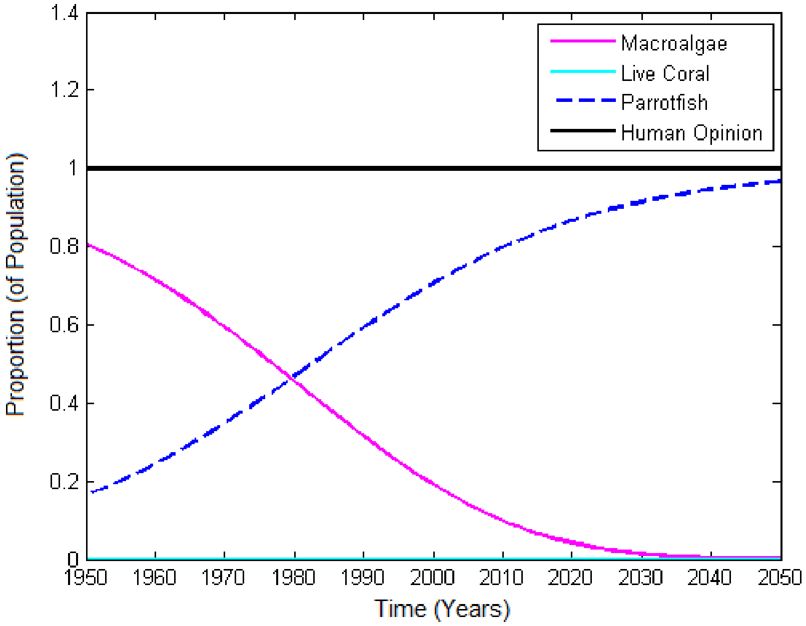

Figure B.3: Time series illustrating the behaviour corresponding to *Dead Corals (iv)* for $s = 0.4$ yr^{-1} and $\phi = 0.6$ with corresponding initial conditions $M = 0.1$,$C = 0.9$,$P = 0.7$,$x = 0.7$ and all other parameters fixed baseline.