Assessing the cascading impacts of rewilding using ecosystem models

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This thesis is submitted in partial fulfillment for the degree of DPhil at the University of Oxford

2023

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Abstract

The core question this thesis seeks to address is how to provide a firm theoretical basis for recovering the health of degraded ecosystems. Rewilding has been proposed as a solution for improving biodiversity and resilience, but concerns have also been raised about the challenges of predicting its outcomes, especially any potential ecological consequences resulting from species reintroductions. Currently, there is limited means of using quantitative methods to understand the potential impacts of rewilding. With the number of projects increasing, there is a clear opportunity for a framework or analytic approach that can forecast the outcomes of different management decisions and help strengthen the desired effects while minimising unintended consequences. The primary aim of this thesis is therefore to develop a new model that can inform decision-making by optimising interventions and assessing the impacts of rewilding on ecosystem composition and resilience. A secondary aim is to provide clarity on the level of model complexity needed to answer these questions, ensuring it is as simple as possible while also capturing key ecosystem components and processes.

Two new types of ecological network models are developed and presented: an ordinary differential equation (ODE) and a more complex, spatial agent-based model (ABM). Both are applied to a case study in regenerated English farmland in collaboration with the Knepp Wildland Project. The ODE represents the first use of this methodology to a moderately data constrained system, i.e., one which has some time-series abundance data and qualitative expert knowledge, to explore knock-on impacts of rewilding and management interventions on ecosystem dynamics and resilience. The ABM uses, for the first time in this context,

rejection sampling, and additional complexities such as space and heterogeneity of individuals to model rewilding outcomes. The models are shown to produce acceptable dynamics based on simple interaction networks, and they can be used to understand the ecosystem-wide impacts of species reintroductions, optimise management interventions, and assess the resilience of the system, providing practitioners with quantitative estimates about the range of possible future system states. Importantly, they can be flexibly and easily updated to incorporate both empirical data and qualitative expert opinion, giving them considerable potential for complementing the more subjective decision-making process used by most rewilding projects, providing valuable information and support while also facilitating ongoing collaboration and model improvement.

The models are demonstrated to have similar high-level insights, indicating the simpler ODE can adequately capture the system and may therefore be preferable for answering these questions. However, for case studies like Knepp which have a relatively high amount of data, further mechanisms may need to be added to the model to improve its calibration process and realism of some outputs. The ABM is used as an uncertainty analysis to guide further research and improvements to the ODE, with the goal of identifying a 'middle ground' wherein the benefits of the simpler ODE can be maintained while enhancing the ease of calibration, realism of its outputs and range of questions it can explore. Practical benefits and drawbacks to each model are discussed, such as model runtime, computational intensity, and the types of questions they are best suited to answering. This thesis therefore helps provide some clarity on which methodology may be most suitable for a given case study. Several possible model improvements are suggested, but despite these, the approaches are demonstrated to show

promise as predictive support tools for assessing species reintroductions before their implementation, informing management decisions, optimising resilience in the face of the biodiversity and climate crises, and constraining possible outcomes. They could therefore help increase the evidence-base of rewilding while addressing some of its key criticisms, particularly that more research is required into its potential as a policy and management technique.

Acknowledgements

First, I would like to express my enormous gratitude to my supervisors, Professor Richard Bailey and Dr. Ernesto Carrella, for their unending encouragement, support, and coding-related banter throughout this project. I think I've advanced along the Dunning-Kruger curve over these past five years, having acutely felt all the stages of 'Mount Stupid,' the 'Valley of Despair,' and eventually, I hope, the beginnings of the 'Slope of Enlightenment.' Reaching this final stage was in large part thanks to them.

Special thanks are also due to the CoHESys Lab for their knowledge and words of wisdom, and to the Knepp Estate, in particular Penny Green, for their support and for facilitating some excellent and inspirational field visits. Huge thanks to my examiners, and to those who have provided financial support over these years: National Geographic, the Born Free Foundation, and Worcester College.

To my friends and family, thank you for everything – the advice, encouragement, and for never (well, rarely) asking when this PhD will be finished. I would like to thank my husband, Nick, for taking extra shifts walking the dog and doing the dishes while I wrote code in a huff, and for helping keep everything in perspective, encouraging me to go sit outside with the birds and the butterflies – reminding me why I love rewilding and nature when I got bogged down in technicalities. Finally, a special shout-out to Baby for sitting tight in there, giving me (hopefully) just enough time to submit this before the next adventure begins.

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CHAPER 1

Introduction

1 Introduction

1.1 Thesis rationale

The United Nations General Assembly declared 2021-2030 the Decade of Ecosystem Restoration. Rewilding, a new conservation approach that aims to rebuild autonomous and resilient ecosystems through the restoration of natural processes and complete food webs, is a key theme within this agenda (Carver et al., 2021). Rewilding projects often have different priorities and approaches depending on the region; this thesis involves a collaboration with the Knepp Estate in the United Kingdom, and therefore focusses largely on the European context. European initiatives tend to focus on giving nature space via land abandonment and the removals of other human control (Morel et al., 2020), and reintroducing large-bodied species (Jones & Comfort, 2020; Schepers & Jepson, 2015). Many are inspired by Frans Vera's 'wood-pasture' hypothesis, which proposes the primaeval European landscape would have been a mix of grassland, scrubland and woodland, with dynamics driven by the behaviours of large grazers (Harding & Rose, 1986; Rose, 1993; Vera, 2000). Following global declines and losses of megafauna beginning in the late Pleistocene, and continuing more recently with the expansion of agriculture, these biomes were restructured with a subsequent loss of wood-pasture associated biodiversity (Kaplan et al., 2009; Vera, 2000). Today, rising levels of land abandonment across Europe are leading to areas becoming overgrown, and biodiversity associated with open habitats to decline (Johnson et al., 2018;

Navarro & Pereira, 2012). Many projects are therefore reintroducing large grazers to restore and maintain these habitats (Smit et al., 2015). Although the goal of rewilding is to restore fully autonomous ecosystems, many initiatives require a degree of ongoing management intervention, for example population control of reintroduced species (Tree, 2018).

Proponents of rewilding see it as means of reversing the damage done to ecosystems, reinstating species and their interactions, and benefiting human society and well-being (Noss, 2020; Perino & et al., 2019). Some have argued that it could be integrated into policy to help address many of the most pressing global issues, such as climate change and biodiversity loss (Ermgassen et al., 2018; Navarro & Pereira, 2012; Svenning et al., 2016; Wrigley & Driver, 2019). There is also evidence that it can enhance resilience (Morel et al., 2020; Sheehan et al., 2021; Svenning, 2020), which is an important area of research as climate change is expected to increase the frequency and magnitude of extreme events and can lead to irreversible changes in ecosystems (Malhi et al., 2020). However, concerns have been raised about a lack of empirical research on its outcomes, especially any potential ecological consequences resulting from species reintroductions (Nogués-Bravo et al., 2016; Svenning, 2020), and there is evidence that management decisions - such as the functional groups or number of individuals to reintroduce - can impact outcomes (Newton et al., 2013; Scheffer et al., 2001; Tuomi et al., 2019). To some, the return of an autonomous and unpredictable nature is a key aspect of rewilding: "the wonderful thing about rewilding," wrote George Monbiot following a review of his book, *Feral,* "is that you don't know where it's going to go... the way ecosystems evolve once missing species are introduced and we stop trying to control them is delightfully unpredictable" (Saunders, 2013). Others have called for a shift

towards a more systematic appraisal of rewilding's costs and benefits, citing concerns that its impacts are unknown and can be consequential, even potentially leading to the declines or extirpations of other species (Nogués-Bravo et al., 2016). Currently, there is limited means of using quantitative methods to understand the potential impacts of rewilding. With the number of projects increasing (Jepson, 2019), there is a clear opportunity for a framework or analytic approach that can forecast the outcomes of different management decisions, for example the effects of species reintroductions on ecosystem composition and resilience, and help to strengthen the desired effects while minimising unintended consequences.

Understanding the possible outcomes of rewilding interventions is a significant challenge. Ecosystems are usually complex, and the effects of changes such as species reintroductions can be counterintuitive and lead to 'ecological surprises' (Delibes-Mateos et al., 2019). Impacts are also context-dependent, varying according to the diversity and abundance of communities (Bakker et al., 2016), spatiotemporal factors (Olesen et al., 2008), and ecosystem types (Hillebrand et al., 2007). Uncertainties exist not only around the outcomes of species reintroductions, but also around practical management questions such as the number of individuals to reintroduce, functional groups, and – in the case of multispecies reintroductions – the order to reintroduce each species in, as these factors can affect outcomes (Newton et al., 2013; Scheffer et al., 2001; Tuomi et al., 2019). Determining the capacity of ecosystems to adapt to change, and increasing resilience where possible, is also a global concern: this often requires an assessment of the existence and boundaries of stable states, the factors conferring resilience within desired stable states, and the extent to which environmental changes erode resilience (Angeler & Allen, 2016; Scheffer et al., 2018).

Ecosystem models have been proposed as a means of providing insights into rewilding and ecosystem responses to species reintroductions (Delibes-Mateos et al., 2019; Pires, 2017; Seddon et al., 2007). Defined as models that represent the interactions between different ecosystem components, they have been widely used in sectors such as fisheries (Bailey & van der Grient, 2020; Smith et al., 2007) and terrestrial ecosystem management (Baker et al., 2018; Purves et al., 2013) to make predictions about specific species or the ecosystem as a whole (Fulton, 2010; Geary et al., 2020; Peters & Okin, 2017). Several methodologies have been developed, including qualitative modelling (Dambacher et al., 2003; Kristensen et al., 2019; Raymond et al., 2011), fuzzy cognitive maps (Baker et al., 2018; Dexter et al., 2012; Ramsey et al., 2012), and ensemble ecosystem modelling (Baker, Bode, et al., 2016; Baker et al., 2019; Bode et al., 2017; Peterson & Bode, 2021). These have been used to forecast the ecosystem-wide impacts of species reintroductions, such as predicting which species may increase or decrease following dingo reintroductions to an Australian national park, or wolves to Yellowstone National Park in the United States (Baker et al., 2016). Spatial agent-based models have also been applied to rewilding and ecosystems, for example to inform lynx reintroduction sites in Scotland (Philips, 2020), and analyse food web networks (Flores et al., 2019).

Developing ecosystem models involves trade-offs between complex approaches which faithfully reproduce idiosyncrasies of the studied system but are often less transferable to other systems, or simpler approaches which may miss out on key ecological processes in each of their applications. Many recommend developing “the simplest accurate model,” in

which the model is only as complex as the objective requires and the available information allows (Hunter-Ayad et al., 2020). However, choosing models is not always a straightforward process; direct comparisons are uncommon, and where they exist, outputs can be highly variable, in some cases having the same qualitative behaviour and dynamics (Colon et al., 2015), and in others, conflicting (Simpkins et al., 2018; Zeller et al., 2018). Careful consideration therefore needs to be given to the number of ecosystem components, interactions, and processes to include, and the spatiotemporal scales (Evans, 2012; Geary et al., 2020).

A new model is needed which can explore questions related to restoring damaged ecosystems via rewilding, such as optimising the number and functional traits of reintroduced species, improving ecosystem resilience, and informing how to achieve a given end goal or avoid unintended consequences. At the same time, clarity is needed on which model methodology is best suited to answering questions related to rewilding, ensuring it is as simple as possible while also capturing key ecosystem components and processes. A model that addresses the above points could act as a predictive management support tool, providing practitioners with a means of assessing species reintroductions before their implementation, informing management decisions, and constraining possible outcomes. If there is uncertainty included, sensitivity analyses can help determine where data collection should be focussed to get the most benefit per observation (LeBauer et al., 2013). This would have widespread applications not just to rewilding literature and practice, but also to the fields of invasive species, reintroductions, and ecosystem restoration. In these ways, the model can help practitioners make scientifically informed decisions while considering risks and uncertainties in a

systematic manner and, in turn, address some of the key criticisms of rewilding, particularly that a more robust appraisal is required of its potential as a policy and management technique (Pettorelli et al., 2018; Rubenstein & Rubenstein, 2016; Torres et al., 2018).

1.2 Aims and objectives

The core question this DPhil seeks to address is how to provide a firm theoretical basis for recovering the health and resilience of degraded ecosystems. This is further divided into the following aims and objectives:

Aim 1: Develop models that can inform rewilding decision-making at a case study in the UK by assessing the impacts of species reintroductions on ecosystem composition and resilience.

- **Objective 1:** Develop, test, and validate two types of ecological network models with varying levels of complexity, an ordinary differential equation (ODE) and a relatively more complex spatial agent-based model (ABM), in collaboration with the Knepp Estate rewilding project.
- **Objective 2:** Use the models to assess the impacts of large herbivore reintroductions on the ecosystem and forecast future changes.
- **Objective 3:** Work with collaborators to identify management end-goals (e.g., engineering the system towards a wood-pasture habitat), and use the models to predict how these can be optimally achieved, for example through further species reintroductions or changes in large herbivore numbers.

- **Objective 4:** Use the models to explore questions related to ecosystem resilience, such as the existence of multiple stable states at Knepp and possible transitions between them, over relevant future forcing scenarios.
- **Objective 5:** Compare resilience metrics under different interventions and assess how the system can be engineered towards a preferred stable state.

Aim 2: Analyse the significance of model complexity for answering questions related to rewilding and ecosystem resilience.

- **Objective 6:** Assess the benefits and drawbacks of the simpler ODE versus the more complex ABM for exploring these questions.
- **Objective 7:** Compare the outputs of the two models and identify under what conditions they were meaningfully different.

1.3 Thesis outline

This thesis follows the paper format. **Chapter 1** provides an overview of the research rationale, aims, and objectives of the project, as well as the case study and methodologies used. **Chapter 2** is a detailed literature review of the history, science, and practice of rewilding, focusing specifically on the impacts of species reintroductions on ecosystem structure, composition, and resilience. The challenges of forecasting complex systems are also explored, as are the availability and potential of different types of ecosystem models.

Chapter 3 {Paper 1, Objectives 1.1-1.3} presents a new ODE of the Knepp Estate which is designed to assess the ecosystem-wide impacts of rewilding and forecast the impacts of different management decisions. This includes details on model construction, calibration, and sensitivity tests, and a discussion of the model results, strengths and weaknesses of the methodology used, and opportunities for future research. **Chapter 4 {Paper 2, Objectives 1.1-1.3}** then presents a new spatial ABM of the Knepp Estate. The model provides quantitative predictions of the range of possible future system states, explores the potential impacts of future species reintroductions, and identifies indicators for whether mosaic wood-pasture ecosystems will be maintained in the long term.

Chapter 5 {Paper 3, Objectives 1.4-1.5, 2.6-2.7} applies both the ODE and ABM to questions about ecosystem resilience at the Knepp Estate. The rationale for assessing two types of models, and similarities and differences between the two methodologies, are outlined. Alternative stable states and possible transitions following forced perturbations of different magnitudes and frequencies are explored. Results of the two models are discussed, including under what conditions they are meaningfully different.

Chapter 6 brings the papers of the thesis together and identifies how the aims and objectives were addressed. The contributions of the individual papers to the literature are discussed, as are future research directions and opportunities.

CHAPER 2

Literature Review

2 Literature Review

2.1 Rewilding: history and definitions

Rewilding was first conceptualised in the 1980s by a group of American conservationists led by Dave Foreman, founder of the Wildlands Network and the Rewilding Institute (Noss, 1985). Originally, it called for the large-scale restoration of interconnected ecosystems to preserve focal species, most notably wolves, and their trophic relationships (Foreman, 1998; Noss, 1985; Power et al., 1996). Soulé & Noss (1998) then refined the science of rewilding in a landmark paper, envisaging it as the restoration of ecosystems based on the "3Cs": cores, corridors, and carnivores. 'Corridors' connect patches of wilderness or protected areas ('cores') to facilitate natural ecosystem functioning at a large-scale, while 'carnivores' play a crucial role in top-down ecological regulation.

Rewilding has since become popular worldwide, and the number of projects is increasing (Jepson, 2019). It has gained significant support from stakeholders, including the general public, practitioners, and policymakers: proponents see it as a bold new conservation approach which can reverse the damage done to ecosystems, reinstate species and their interactions, and benefit human society and well-being (Noss, 2020; Perino & et al., 2019), while also opening the possibility for new, nature-based enterprises and economies such as eco-tourism and the harvesting of natural products (Tree, 2018). Rewilding can also combat 'shifting baseline syndrome' - in which each successive generation becomes accustomed to

worsening environmental conditions and unknowingly accepts the declines and damages of the preceding generation - and reveal limitations in our understanding of the conditions nature needs to thrive (Jones et al., 2020). In contrast to the dominant environmental narrative of 'doom and gloom', it is framed as a hopeful new approach in which nature can recover on its own, without human management (Schepers & Jepson, 2015). Some have argued rewilding should be integrated into policy (Jepson & Schepers, 2016; Navarro & Pereira, 2015), and centralised in efforts to tackle the dual, interlinked challenges of the Anthropocene: climate change and biodiversity loss (Svenning et al., 2016). However, not all the attention has been positive (Jones & Comfort, 2020), and there are significant perceived risks around human-wildlife conflict (O'Rourke, 2019), compatibility with rural livelihoods (Mikołajczak et al., 2022), unintended consequences resulting from species reintroductions (Nogués-Bravo et al., 2016), and erasure of human communities and their cultural activities from natural areas (Jørgensen, 2015).

Another concern is the lack of consensus on its definition and goals, which has prompted extensive debate (Hayward et al., 2019; Lorimer et al., 2015; Pettorelli et al., 2018; Prior & Ward, 2016). Since the 1980s, the term has evolved and diversified to encompass several concepts which have considerable overlap but vary in ecological baselines, spatiotemporal scales, conservation activities, and levels of direct intervention and ongoing management. There are five main framings of rewilding in the literature: Pleistocene, trophic, passive, ecological, and translocation (Nogués-Bravo et al., 2016; Pettorelli et al., 2019). Pleistocene rewilding promotes the reintroduction of proxy species to fill the niches and ecosystem functions of megafauna lost during the Pleistocene extinctions, for example

African or Asian elephants in place of the American mastodon, highlighting the idea that the loss of species and their interactions can have profound effects throughout the ecosystem (Donlan et al., 2006). Trophic rewilding does not focus on this reference time-period, but is otherwise conceptually similar in that it seeks to reinstate large areas and megafauna-rich ecosystems, particularly top-down trophic interactions, to restore ecosystem health and function (Bakker & Svenning, 2018; Svenning et al., 2016). Passive rewilding refers to nature being given space via land abandonment or other removals of human control (Morel et al., 2020). Ecological rewilding seeks to limit ongoing management and interventions to facilitate natural processes (Law et al., 2017; Pettorelli et al., 2019). Finally, translocation rewilding focusses on 'refaunation', or reintroducing species to restore missing or dysfunctional ecosystem processes (Nogués-Bravo et al., 2016).

Mirroring the many different framings found in the literature, rewilding projects have different priorities and approaches depending on the regional context. European projects tend to focus on passive rewilding of abandoned farmland and reintroducing large grazing species (Jones & Comfort, 2020; Schepers & Jepson, 2015), whereas those in North America prioritise establishing large, interconnected systems of wilderness to support top predators and their prey (Corlett, 2016b). Initiatives tend to focus on North America and Europe (Svenning et al., 2016), however, examples are emerging elsewhere in the world. Australian rewilding projects, for example, emphasise the restoration of apex predator and small mammal populations alongside invasive mesopredator control (Sweeney et al., 2019). In South America and Africa, although organisations do not always use the term 'rewilding', large-scale efforts to reintroduce megaherbivores and top carnivores (Gordon et al., 2023;

Hayward et al., 2019; Root-Bernstein et al., 2017), and to increase habitat connectivity (Bhatasara et al., 2013), fall under its umbrella.

In some cases, the different definitions and approaches of rewilding have limited its practical application and hampered policy integration efforts (Pettorelli et al., 2018). In response to this, the International Union for Conservation of Nature Commission (IUCN) on Ecosystem Management's Rewilding Thematic Group published a unifying definition and guiding principles (Table 2.1): it defines rewilding as the process of rebuilding an ecosystem via the restoration of natural processes and food webs, with the ultimate goal of restoring functional native ecosystems which contain species at all trophic levels, and which are, where possible, self-sustaining (i.e., where biodiversity and ecological functions can be sustained via natural processes, without the need for human management) (Carver et al., 2021).

Table 2.1: *A summary of the ten guiding principles of rewilding (adapted from Carver et al., 2021)*

Principle 1	**Principle 2**	**Principle 3**	**Principle 4**	**Principle 5**
Rewilding restores trophic interactions, considering the roles of large herbivores, apex predators, keystone species, and ecosystem engineers.	Rewilding functions on the landscape-scale and considers core areas, connectivity, and co-existence.	Rewilding aims to restore self-sustaining and resilient ecosystems through the recovery of ecological processes and interactions.	Rewilding recognises - and is responsive to - the dynamic nature of ecosystems.	Rewilding anticipates and, where possible, mitigates the impacts of climate change.
Principle 6	**Principle 7**	**Principle 8**	**Principle 9**	**Principle 10**
Rewilding actively engages with stakeholders, utilising participatory approaches to encourage public understanding and address concerns.	Rewilding is informed by a range of sources, including science, traditional ecological knowledge, and other local knowledge.	Rewilding relies on monitoring and feedback.	Rewilding recognises the intrinsic value of species and ecosystems, embracing the values of compassion and coexistence.	Rewilding requires a paradigm shift in the relationship between humans and nature, promoting a greater awareness of the importance of ecosystems.

This definition is widely accepted and unifies the different rewilding framings outlined above; however, some ambiguity remains for projects where fully self-sustaining ecosystems are not possible and a degree of ongoing intervention is therefore necessary. In densely populated countries, very few - if any - rewilding initiatives can fully adhere to the IUCN principles, as the possibility of having large-scale wilderness areas with all trophic levels is very unlikely. Oostvaardersplassen in the Netherlands and the Knepp Estate in the UK, for example, are both well-known and self-described rewilding projects; however, they are relatively small, enclosed areas and do not have the space to reintroduce large carnivores. To adhere to animal welfare standards and allow sufficient forage and vegetation regeneration, ongoing management is required via the removal of herbivores (in some cases culling for meat) (Tree, 2018; Weston, 2022). Although still described as rewilding projects in the literature (see Dempsey, 2021; Gamborg et al., 2022; Schulte to Bühne et al., 2022) there is some debate over whether projects like these are better described as ecological restoration (Anderson et al., 2019), or regenerative agriculture (Cusworth et al., 2022). Others have wondered whether rewilding should reject a single, fixed definition and instead view it as a journey towards becoming more dynamic and self-sustaining, with a spectrum of scales and degrees of management (Tree, 2018).

Furthermore, the IUCN definition assumes that given an initial boost, natural processes will eventually be capable of pushing ecosystems towards healthy equilibriums. This may be possible, but the transition could take some time, during which the system could be fragile to shocks. Given the unprecedented environmental changes the world is currently

undergoing, disturbances such as extreme weather events, changes in average conditions due to climate change, and other anthropogenic stressors could become more intense and frequent. These threats could lead the system to quickly collapse into an unhelpful state, such as a homogeneous ecosystem unable to support high levels of biodiversity (Glynn, 1993; Jones et al., 2004). If there is some sense of the equilibrium nature is pulling towards, actively helping it on its way via continued management could, in some situations, be a better alternative to leaving it be and hoping it can get there on its own.

2.2 Ecological and scientific background

2.2.1 Cascading impacts of species reintroductions

A major scientific underpinning of rewilding is that complete food webs, containing all trophic levels, are crucial for self-regulating ecosystems. Many rewilding projects are reintroducing relatively large-bodied animals (also known as megafauna) to reinstate top-down interactions and associated domino-effects on the ecosystem. Megafauna are focused upon for two reasons: 1) Human-driven extinctions have been strongly size-selective and many megafauna species have been wiped out; once roaming across all habitable continents, today they are largely confined to parts of Africa and Asia (Smith et al., 2018), and; 2) Megafauna have large and often unique effects in their ecosystems (Dirzo et al., 2014; Estes et al., 2011). Many have been identified as keystone species, which have disproportionately large effects on their ecosystems (Mills et al., 1993; Paine, 1966), or

ecosystem engineers, which significantly create or modify their habitat (Jones et al., 1994). These two points will be discussed in further detail below.

Diverse faunas of large-bodied species were once typical worldwide, but massive losses began in the Pleistocene, particularly in the Americas (Estes et al., 2011; Malhi et al., 2016; Smith et al., 2018). The disappearance of species such as giant sloths, peccaries, mammoth, mastodons, horses, and camels coincides with the spread of *Homo sapiens* around the planet; many therefore consider the human "overkill" hypothesis to be the most likely explanation of the pattern and timing of extinctions (Sandom et al., 2014), although climate change may have also played a role (Koch & Barnosky, 2006). Habitat restructuring and the extinctions of large and smaller-bodied species continued into more recent centuries due to overhunting, industrialisation, and the expansion of agriculture. Today, the few remaining megafaunal species are often functionally declining through range contractions and population reductions, and in many places, the largest living terrestrial animal is akin to a medium-sized deer. This marks a significant 'trophic downgrading' relative to the settings in which most of our present biodiversity evolved (Stegner & Holmes, 2013). These megafaunal extinctions had long-lasting, global consequences, leading to shifts in ecosystem trophic structure and biogeochemistry, and changes in plant diversity and community composition due to the loss of long-distance seed dispersal. Many locations experienced an increase in fire activity from the loss of large grazers, as well as co-extinctions of megafauna-dependent species, such as dung beetles and scavenging birds (Galetti et al., 2018; Malhi et al., 2016; Pires et al., 2018; Zimov et al., 1995). Today, ecosystem downgrading continues to accelerate and the Living Planet Index shows a 69% decline in wildlife populations since 1970 (Almond et al., 2022).

By reintroducing large species, rewilding projects aim to boost biodiversity and allow trophic interactions to regulate and steer the trajectory of the ecosystem, thus reducing the need for human management.

Apex predators are common candidates for reintroduction due to their ability to regulate the impacts of herbivores and mesopredators (Dirzo et al., 2014; Estes et al., 2011; Ripple et al., 2014). A famous example is the reintroduction of wolves *Canis lupus* to Yellowstone National Park in 1995. Their return resulted in trophic cascades, or the propagation of a species' effects down the food web to affect multiple trophic levels, with impacts on ecosystem processes, structure, and complexity (Figure 2.1) (Estes et al., 2011; Paine, 1980; Ripple et al., 2001): wolves predated on the American elk *Cervus Elaphus*, reducing their numbers and creating a 'landscape of fear', in which elk changed their behaviour and foraging patterns to avoid areas where they lacked clear sight or opportunity to avoid predators (Brown et al., 1999). This allowed aspen and willow tree regeneration in areas of high wolf use (White et al., 1998), and had a series of indirect effects on other species such as beavers, riparian songbirds, fish (Ripple et al., 2001), and even the course of a river (Foreman, 2004). An increase in elk kills likewise benefitted a range of scavengers, including bears, cougars, wolverines, and ravens. Similar trophic cascades were observed following the extirpation of grizzly bears and wolves from Grand Teton National Park in the USA, which led to an increase in herbivory on willow by moose and decreased avian diversity (Berger et al., 2001).

Counterintuitively, the loss of wolves from Yellowstone coincided with a precipitous decline in pronghorn antelope. This was due to a phenomenon known as 'mesopredator release' (Prugh et al., 2009; Soulé et al., 1988), in which populations of a secondary carnivore - coyotes - increased in the absence of larger predators and significantly impacted fawn survival rates (Berger et al., 2008). Mesopredator release may also be a factor in the decline of ground-nesting birds in North America (Rogers & Caro, 1998). Reintroducing apex predators can therefore boost biodiversity by controlling mesopredator populations and facilitating an increase in their prey, which then provides more food for species like eagles and osprey. Predation can also enhance the coexistence of competing prey species by reducing abundant competitors (Ishii & Shimada, 2012; Paine, 1966).

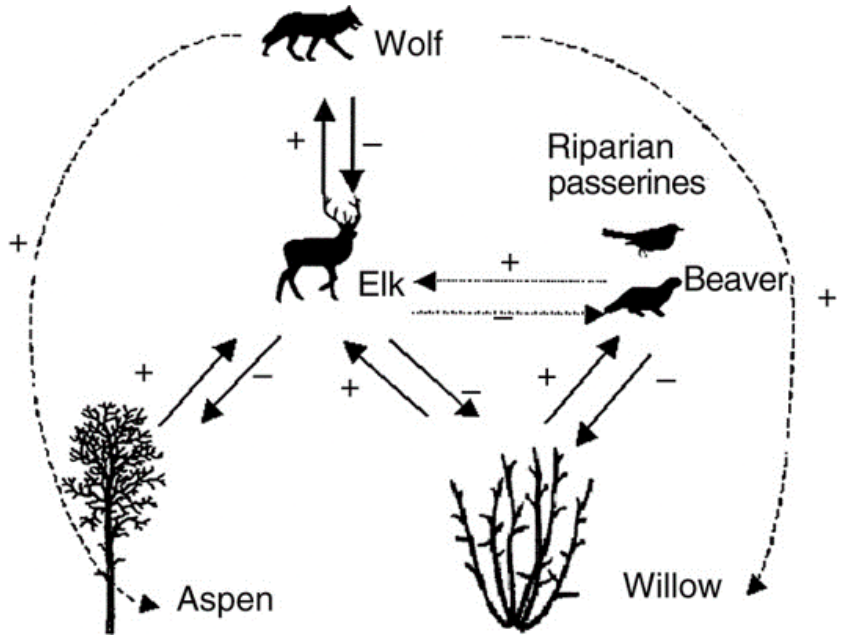


Figure 2.1: *Cascading impacts resulting from wolf reintroductions (from Hebblewhite et al. (2005)). Solid lines depict direct trophic interactions which can be either positive or negative (e.g., predation, herbivory). Dashed lines show indirect interactions, such as wolf displacement due to human activities, and competition between herbivores.*

Large herbivores are another common candidate for reintroduction due to their strong effects on vegetation structure and composition (Bakker et al., 2016; Vandegehuchte et al., 2017). Grazing pressure can be a driver of habitat composition; for example, megaherbivores have been proposed as the driving force for the maintenance of "mammoth steppe" ecosystems in Siberia, primarily via their suppression of woody vegetation and stimulation of grass growth, which reduce waterlogged areas (Zimov et al., 1995). Mammoth steppes once supported high levels of megafauna, including mammoths, woolly rhinoceroses, bison, musk oxen, and horses, but following the loss of these species, the steppes were replaced by wet, boggy ecosystems dominated by low-diversity shrubs, mosses, and forest (Zimov et al., 1995). The presence of large herbivores can also enhance nutrient cycling (Bakker et al., 2016; Doughty et al., 2013), facilitate long-distance seed dispersal (Guimarães et al., 2008), and alter fire regimes by reducing fuel loads (Rouet-Leduc et al., 2021). They can profoundly influence soils and their biota via trampling, compaction, defecation, and by altering plant allocation patterns through herbivory (York, 2012; Zimov et al., 1995). More complex impacts have also been documented, for example, beavers create and dramatically alter riparian landscapes via dam building (Law et al., 2017; Wright et al., 2002).

Large herbivores boost biodiversity in several ways. Grazing can foster environmental heterogeneity, which strongly correlates with species richness (Bakker et al., 2016; Stein et al., 2014). Spatiotemporal variation in herbivory facilitates increased diversity in vegetation species and structure, providing habitat niches for many different types of organisms, such as invertebrates (Andersen et al., 2023) and birds (Hovick et al., 2014). At the Knepp Estate, UK, an increase in vegetation cover and complexity arising from reduced management and

the reintroduction of large grazers likely contributed to rises in invertebrate, bird, and small mammal diversity, including the return of rare species such as nightingales, turtle doves, and purple emperor (**Figure 2.2**) (Schulte to Bühne et al., 2022; Tree, 2018). Grazing, trampling, and wallowing behaviours also diversify vegetation and physical substrate, creating habitats for other species.

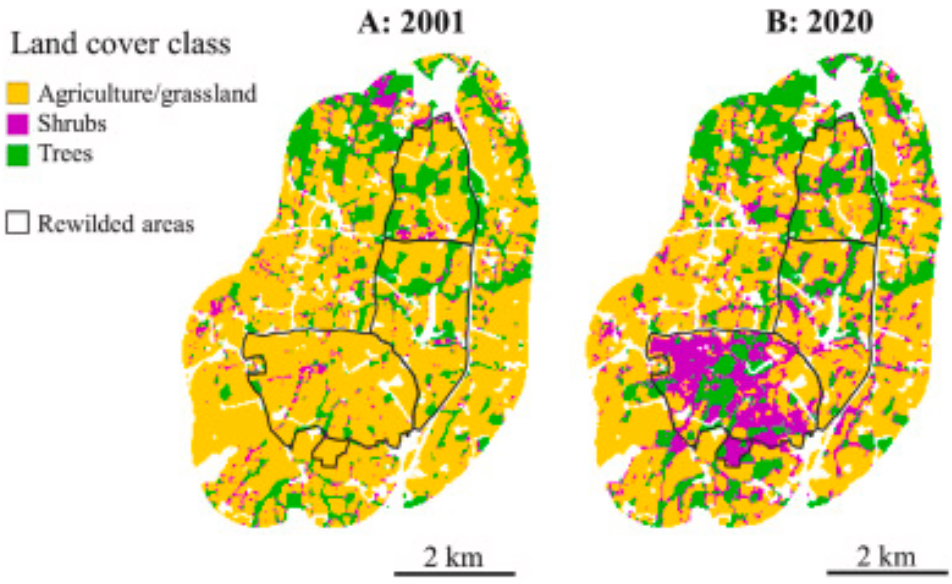


Figure 2.2 *Land cover classification maps at Knepp between 2001 and 2020. Boundaries of the estate are outlined in black. From Schulte to Bühne et al., (2022).*

Where megafauna species have gone extinct, reintroducing functionally analogous species have been proposed as a means of reinstating some of these processes and tackling environmental challenges. In Europe, many projects have used old breeds of domestic livestock as proxies for either 1) extinct native grazers, i.e., the aurochs and the tarpan (Eurasian wild ox and horse, respectively, both of which were hunted to extinction by the seventeenth century), or 2) native living species which are unavailable or considered too dangerous for close proximity with the public, such as wild boar; this is common for projects

in areas of high human density (Gordon et al., 2021; Tree, 2018). In Australia, elephants have been proposed as a way to fill the vacant role of extinct giant marsupials, controlling wild grasses and reducing wildfire risk (Bowman, 2012). In Mauritius, the non-native Aldabra giant tortoise was successfully reintroduced as a proxy species for an endemic giant tortoise, whose extinction led to ecosystem dysfunction and declines in native wildlife (Griffiths et al., 2011). However, concerns have been raised that rewilding with exotic species could have unintended consequences, fail to restore the historical baseline (Rubenstein et al., 2006), and remove focus from preserving wildlife in their native ecosystems (Rubenstein & Rubenstein, 2016).

2.2.2 Wood-pasture hypothesis

As briefly discussed in Chapter 1, many rewilding initiatives – particularly in Europe - are centred on reassembling large herbivore guilds to restore dynamic mosaic landscapes of wood pasture (Carver et al., 2021). The openness of Europe's primaeval landscape, and the historical role of large herbivores in shaping these landscapes, are under debate (Birks, 2005; Svenning, 2002). The traditional view is that before the significant alteration of the environment by humans, Europe would have been largely closed canopy forest (Iversen, 1960; Peterken, 1996). The 'closed canopy' theory was challenged by Dutch scientist Frans Vera, who, in his book *Grazing Ecology and Forest History* (2000), hypothesised that the role of large free-roaming herbivores in creating habitats and driving natural processes has been overlooked. In his 'wood-pasture' theory, he describes how primaeval Europe would have been a shifting mosaic of grassland, scrubland, and woodland similar to the Serengeti,

capable of supporting high levels of biodiversity and whose dynamics were driven primarily by the browsing, grazing, and trampling of large herbivores (Vera, 2000). In this theory, vegetation is on a continuous cycle of change. Glades are formed in closed-canopy woodland by falling trees, which allows space and light for saplings and grasses to regenerate. Herbivores are attracted to the new undergrowth, and their presence expands the glades to eventually create open grassy areas that attract a range of grazing species. In these grazer-maintained grasslands, spatial association with unpalatable plants (e.g., thorny scrub) enables palatable saplings to regenerate. As the saplings grow, they outshade the species that facilitated them and form groves, leading to cyclical turnover and a shift back towards closed-canopy woodland (Figure 2.3) (Olff et al., 1999).

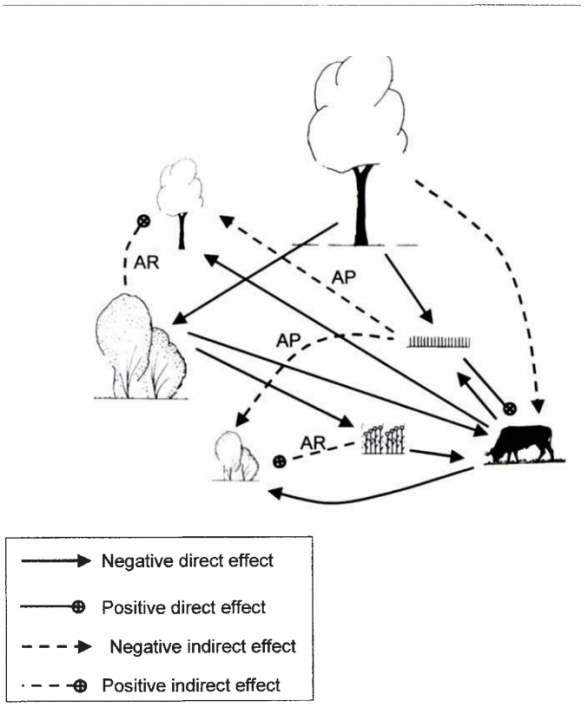


Figure 2.3: *An overview of the wood-pasture hypothesis. This network shows the interactions between plant functional types and a large grazing species. Indirect interactions are either associational resistance (AR) or associational palatability (AP). From Olff et al. (1999).*

However, global declines and losses of megafauna led to the restructuring of these biomes, and a loss of grassland and wood-pasture associated biodiversity (Kaplan et al., 2009). There is therefore growing recognition that some of Europe's treasured woodlands may be the result of large herbivore extinctions, rather than evidence of a once ubiquitous primaeval forest. Today, increasing levels of rural depopulation are resulting in the abandonment of traditional agriculture, and as areas become overgrown, biodiversity associated with open habitats declines, and in dryer regions the risk of wildfires increases (Johnson et al., 2018; Navarro & Pereira, 2012). To solve this problem, and inspired by the wood-pasture theory, many rewilding projects in Europe are focused on reintroducing large grazers to maintain these habitats.

The wood-pasture theory is supported by studies showing grazers can halt vegetation succession and maintain open habitats (Kowalczyk et al., 2021), and that high herbivore density in interglacial periods is associated with vegetation diversity (Sandom et al., 2014). Beetle species associated with grasslands and open areas were also shown to be present throughout the European Holocene (Whitehouse & Smith, 2010). However, pollen records from Europe and the eastern USA generally reject the wood-pasture theory, instead lending support for the closed canopy theory (Mitchell, 2005; Roberts et al., 2018). The use of pollen may not be a reliable indicator of past vegetation composition though, as grass pollen is more fragile than other woody plants and may not persist to the same extent (Jepson & Blythe, 2020). Disturbance factors other than herbivory, such as fires and storms, may have also been integral in creating open landscapes (Bradshaw et al., 2003).

2.3 Rewilding and ecosystem resilience

2.3.1 Concepts and definitions

Anthropogenic stressors such as climate change, habitat loss, and biodiversity declines are threatening natural processes and systems. Ecosystems have limited ability to adapt to these disturbances, and may eventually undergo phase-shifts to alternate community compositions and functions (Hughes et al., 2013). The outcomes of these shifts are uncertain but can have significant implications for human health and welfare (McMichael et al., 2008), as well as conservation and other sectors, for example leading to undesirable changes in terrestrial vegetation (Dublin et al., 1990), collapse of fisheries (Jackson et al., 2001), and loss of biodiversity from coral reefs (Schmitt et al., 2019). Consequently, determining the capacity of ecosystems to adapt to change, and increasing resilience where possible, has become a global concern.

The concept of resilience was created fifty years ago by Holling (1973) and, like rewilding, has been defined and conceptualised in a variety of ways. Broadly, it is defined as the ability of a system to maintain its function and structure when subjected to a disturbance. There are two main definitions in the literature for investigating relevant metrics and details: ecological and engineering resilience. Ecological resilience is a measurement of the amount of shock a system can absorb without shifting to an alternative stable state (i.e., its robustness), for example, the size of a wildfire an ecosystem can successfully recover from without switching to a new state (Holling, 1973). This definition therefore assumes a system can have multiple

alternative stable states. Engineering resilience, on the other hand, refers to the recovery rate, or the rate of return to equilibrium following a disturbance, within a single stability regime (Pimm, 1992). Determining the potential existence of alternative stable states has significant implications for conservation and management: if only one exists, the system will eventually reassemble into its original condition, but if multiple exist, a sufficiently severe disturbance could shift the system to a new state.

The 'ball-in-basin' analogy is a useful way to visualise these concepts (Figure 2.4): the state of an ecosystem is represented by a ball, and its movement can be anticipated from the topography - the peaks and valleys - of the landscape, where the valleys (or 'basins') represent stable states. If perturbed, the ball may roll back towards the centre of the basin (i.e., it reaches equilibrium) or it could be forced into a new one. The steepness of the basin is analogous to the resilience of the system: deeper basins result in a faster recovery to the original stable state (i.e., higher engineering resilience) and require larger disturbances to force the ball into neighbouring basins (i.e., higher ecological resilience). Ecosystems faced with multiple, repeated perturbations within a shallow basin, for example, will have a slower rate of return following a disturbance, and subsequent disturbances may therefore have a higher chance of moving the ball from the basin entirely.

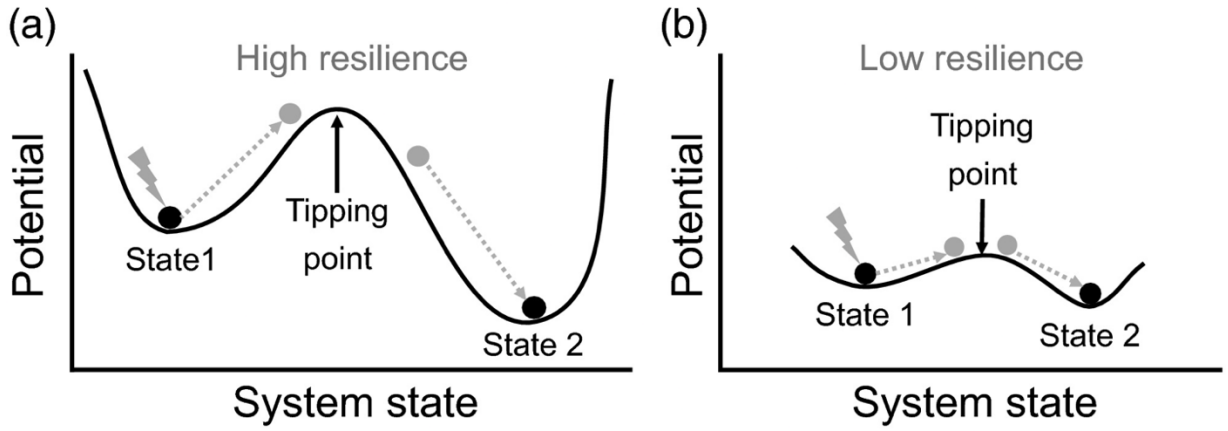


Figure 2.4: *The 'ball-in-basin' analogy representing the resilience of an ecosystem. The black ball represents the ecosystem at equilibrium (i.e., within a basin) and the grey balls illustrate potential trajectories. Lightning symbols are disturbances which can shift the ecosystem to a new alternative stable state. The width and depths of basins are important characteristics for resilience: a ball within a deep and wide basin (a) will be more resilient than one in a flat and narrow basin (b). From Capdevila et al., (2021).*

Structural changes such as species reintroductions, extinctions, or decreases in woodland due to forest fires, change the position of the ball and cause a reconfiguration of the ecosystem, in which it can either absorb and adapt to the new conditions and maintain its original structure, or shift to a new stable state if one exists. The landscape topology can be altered by shifts in the parameters governing the ecosystem, such as increases in vegetation growth rates due to shifting precipitation and temperatures under climate change. In some cases, these shifts create new stable states, or they can make shifts to new states easier or more difficult. Identifying the factors which affect the 'resilience landscape' is particularly important for ecosystem managers: environmental conditions often shift gradually and may not have noticeable effects on the ecosystem state, but nevertheless can lead to a loss of resilience by reducing the depth of the basin, making the system more susceptible to tipping into a new stable state. Furthermore, under conditions of environmental change, interplays between the landscape topology and position of the ball (i.e., the state variables) can produce cascading effects. Long-term decreases in precipitation in a woodland ecosystem, for

example, can lead to increased wildfires, fewer trees and pollinators, and reduced vegetation growth rates, resulting in the system reaching a tipping point and reorganizing into a new stable grassland state. In some cases, it may be difficult for ecosystems to reverse a shift to an alternative stable state, or the return trajectory to the original equilibrium may differ from the outgoing trajectory; this is a phenomenon known as 'hysteresis' (Angeler & Allen, 2016; Beisner et al., 2003). To illustrate this concept, and continuing the woodland example used above: following decreases in precipitation and a subsequent phase-shift from woodland to grassland, precipitation may subsequently increase to its previous levels, but the ecosystem is resilient to this change and does not return to its original state.

2.3.2 Effects of rewilding on resilience

Rewilding has been proposed as a means of building resilience into natural systems (Morel et al., 2020; Sheehan et al., 2021; Svenning, 2020). Rewilding seeks to encourage natural processes and dynamism, and it is therefore important to emphasise that resilience is not equivalent to stasis, i.e., encouraging resilience does not necessarily require systems to be held in certain optimal states. Instead, many of the guiding principles for increasing resilience involve increasing adaptive capacity, or the ability of an ecosystem to adjust its characteristics to expand its ability to cope with a stressor, maintaining its functions even if in a reconfigured state (Brooks & Adger, 2005). In other words, adaptive capacity is about focussing on what the system is doing, rather than its exact structure (Angeler et al., 2019).

Enhancing resilience can be achieved through several means, such as increasing biodiversity, promoting migration through the creation of corridors, identifying positive and negative feedbacks, and focusing on managing ecosystem services (Bailey, 2020; Brooks & Adger, 2005); rewilding addresses these in several ways. As discussed in section 1.2.1, the restoration of native species and interactions can contribute to a rise in biodiversity, which plays a substantial role in resilience (Peterson et al., 1998). A diverse array of species within functional groups buffers against declines and losses of individual species, ensuring the continuity of vital ecosystem services and functions – this is also known as functional redundancy (**Figure 2.5**) (Elmqvist et al., 2003; Truchy et al., 2015). Without high functional diversity, key ecosystem processes may not be carried out at all if a specialist or keystone species is lost, for example decomposition or pollination (Oliver et al., 2015), or the dispersal of particular fruits (Pires et al., 2018). Species richness also confers higher response diversity as different species have varying tolerances to stressors, which is critical for ecosystem reorganisation following a disturbance (Elmqvist et al., 2003).

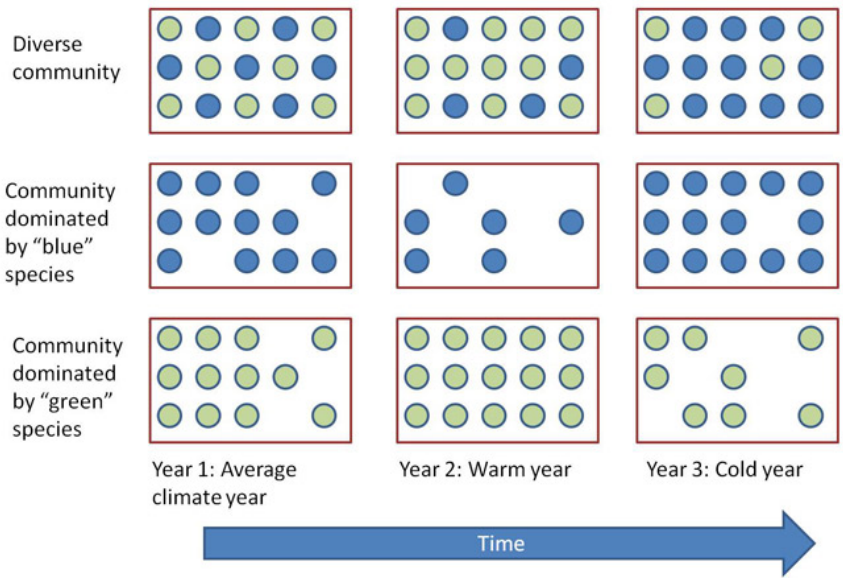


***Figure 2.5**: A conceptual diagram showing how biodiversity can affect ecosystem resilience. In this case, an ecosystem contains two species (blue or green) which fulfil the same ecosystem function (i.e., pollination). Green species increase in abundance in warm years, whereas blue species increase in cold years, leading to fluctuations in their abundances and functions when there is climatic variability. Conversely, in an ecosystem containing both blue and green species, decreases in one species is compensated for by increases in the other, therefore creating stability and ensuring the continuation of ecosystem services. From Cleland (2011).*

Reintroductions of megafauna may also reduce the risk of high-magnitude flooding and wildfire (Johnson et al., 2018), confer resistance to invasive species (Pardi & Smith, 2016), and provide increased resilience to climate extremes (Isbell et al., 2015; Svenning et al., 2016). For example, a study on the reintroduction of bison in the US found that compared to domesticated cattle, bison doubled plant diversity and led to an increase in drought-resilient species (Ratajczak et al., 2022). One of the key principles of rewilding is functioning on a landscape scale; in doing so, initiatives can increase resilience by facilitating species' range shifts to areas with more suitable climate (Perino & et al., 2019; Svenning, 2020), and allowing ample space for natural disturbances such as fire and flooding, as well as stabilising feedbacks, to occur (Carroll & Noss, 2021).

In the same vein, there is a large body of literature exploring the relationship between stability and complexity (e.g., species richness, connectivity, interaction-type diversity) in ecological networks (Feng & Bailey, 2018; Landi et al., 2018; May, 1972). In this context, stability is typically an umbrella term referring to the ability of a system to maintain its state despite changing conditions, and encompassing properties such as ecological and engineering resilience, resistance, and recovery (Van Meerbeek et al., 2021). Ecologists in the mid-twentieth century believed diverse assemblages of species and interactions enhanced stability, a belief largely based on real-world observations of more extreme fluctuations in population abundances in simplified terrestrial community than diverse ones (Elton, 2000;

MacArthur, 1955). However, May (1972) challenged this assumption: using randomly-constructed community matrices and linear stability analyses, he demonstrated that network stability decreases with increasing complexity. Significant work has been done in the decades since, and most recent advancements suggest the inclusion of more processes and realism in models, for example, considering non-random properties related to ecosystem interactions and structure (Jacquet et al., 2016), multiple interaction types (Fontaine et al., 2011), and spatial dynamics (Gravel et al., 2016) can lend more support for a positive complexity-stability relationship. However, the fundamental relationship between the two remains debated (Landi et al., 2018).

2.4 Challenges of predicting ecological outcomes

Alongside the growing interest in rewilding have come concerns regarding the lack of empirical research and challenges of predicting its outcomes, especially any potential ecological consequences (Nogués-Bravo et al., 2016; Svenning et al., 2016). A common concern is that rewilding initiatives can result in major unintended consequences. Species introductions can have unexpected detrimental outcomes, including the declines or extirpations of other species (Lovari et al., 2014; Pace et al., 1999a), or significant alterations in species composition (Johnson & Cushman, 2007). Vegetation regeneration resulting from, for example, passive rewilding following land abandonment, can increase fire risk (Mantero et al., 2020), reduce water availability (Beguería et al., 2003), and in some cases lead to habitat homogeneity and species losses (Delibes-Mateos et al., 2019;

Torres et al., 2018). There could also be risks for the general public; for example, apex predator reintroductions can inadvertently increase the risk of zoonotic disease by controlling mesopredators, which may increase the abundance of their prey - disease-carrying rodent populations (Ostfeld & Holt, 2004). A lack of research on rewilding's potential impacts (Nogués-Bravo et al., 2016), and limited scientific support for facilitating sound decision-making (Pettorelli et al., 2018), have led to calls for a more systematic appraisal of its costs and benefits (Nogués-Bravo et al., 2016; Svenning et al., 2016).

Practitioners face several key challenges when predicting the ecosystem-wide impacts of rewilding. The first is that community webs are usually complex, and the interactions of newly reintroduced species can be highly uncertain. "Rewilding is a process involving the complex interaction of different elements within an ecosystem," states Jones & Comfort (2020), "and it is thus difficult to predict the results with any great accuracy." Put another way, management is a "wicked problem" with limited solutions for foreseeing all possible outcomes of interventions (DeFries & Nagendra, 2017). Studies assessing ecological interactions and the impacts of species reintroductions are limited (Hale & Koprowski, 2018; Nogués-Bravo et al., 2016), with ad hoc and fragmented empirical evidence of outcomes (Seddon et al., 2007). Even where assessments do exist, rewilding - by definition - creates novel ecosystems and unexpected, emergent properties can arise. For example, peregrine falcons - a species known for nesting on cliffs - are nesting in oak trees at the Knepp Estate in the UK, suggesting the dynamics we see today are not the 'ideal' but instead the result of falcons having lost their preferred interactions (Tree & Burrell, 2023).

Even the dynamics of seemingly simple systems can be complicated and involve several trophic levels (Krebs et al., 2001), and impacts can be context-dependent. For example, the effects of herbivores on vegetation structure is dependent on the diversity and abundance of large herbivore communities (Bakker et al., 2016), and varies according to spatiotemporal factors (Olesen et al., 2008) and ecosystem types (Hillebrand et al., 2007). While low grazing pressure can increase biodiversity (Bakker et al., 2016), too much can have negative effects on vegetation complexity and soil nutrients (Mills et al., 2020), and an overabundance of a single herbivore species can lead to homogenisation of the environment, lowering species diversity (Beguin et al., 2022; Côté et al., 2004; Iida et al., 2016). The magnitude of cascading impacts from predator reintroductions can also be highly variable and may not always restore top-down control (Shurin et al., 2002).

Predictions of reintroduction outcomes are often based on highly simplified behavioural expectations or other ecological assumptions, such as the importance of bottom-up or top-down trophic interactions (Doak et al., 2008). These may oversimplify or even entirely miss out on key dynamics: for example, although carnivores can lessen herbivore populations and their impacts, it would be an oversimplification to say this is always the case; the presence of apex predators has minimal impact on Serengeti herbivores such as elephants, hippopotamus, and rhinoceros, for example, as these large-bodied species are rarely predated upon (Sinclair et al., 2003). In a more extreme case, following the loss of lobsters (*Jasus lalandii)* off the western coast of South Africa, their prey species, predatory whelk, substantially increased in number. Upon their reintroduction and in a surprising case of predator-prey reversal, lobsters were immediately overwhelmed and predated upon by the

whelks. Within a week, no live lobsters could be found in the area (Barkai & McQuaid, 1988; Doak et al., 2008). In another example, the reintroduction of red deer to national parks in Italy led to an unexpected decrease in threatened Apennine chamois due to direct interspecific competition for food sources (Lovari et al., 2014). Reintroduced species can likewise have variable impacts on invasive species, in some cases suppressing their populations and slowing down invasions, and in others, not (Derham et al., 2018). Given the extensive and complex ways species interact with each other, 'ecological surprises' like these may be unavoidable (Delibes-Mateos et al., 2019).

Another key challenge is anticipating the effects that shifting environmental conditions will have on ecological communities. Species interactions can alter due to changes in the physical environment such as extreme weather events or shifts in average conditions (Doak et al., 2008). This introduces uncertainty around, for example, the extent to which a reintroduced species will fulfil its old ecological functions, as there could have been changes in context such as increases in human-modified landscapes, shifts in community composition, or a new ecosystem equilibrium reached after the loss of the species (Smith, 2005). For example, coyotes may be filling part of the niche once occupied by now-extirpated wolves in the north-eastern United States (Gompper, 2002). Changing climatic conditions will create new environmental gradients as species shift northwards (Roberts et al., 2019), and change the timing of events such as migration, flowering, and spring leaf unfolding, all of which can have significant effects on ecosystem composition and functioning. Climate change and increases in extreme weather events can affect the extent to which reintroduced species can survive in their new locations, and result in population

declines and extirpations, with cascading effects (Maxwell et al., 2019). It is important to take these uncertainties into account, as they will likely increase with future environmental changes driven by climate and land use change, and biodiversity loss (Corlett, 2016b).

Rewilding practitioners not only face uncertainties around the outcomes of species reintroductions, but also around several practical management questions. The number of individuals, the choice species to reintroduce, and - in the case of multispecies reintroductions, which are becoming increasingly common (Tree, 2018; Zamboni et al., 2017) - the order to reintroduce each species in, are all challenging decisions that can affect ecosystem outcomes (Newton et al., 2013; Putman, 1986; Tuomi et al., 2019). There are uncertainties around whether, for example, it is best to reintroduce one species at a time, or all at once, to achieve optimal ecosystem results (Jepson & Blythe, 2020). Another question is which functional groups are best to reintroduce to achieve a balanced, self-sustaining ecosystem. For example, herbivores have different foraging preferences and therefore variable impacts on wood-pasture formation; one study found that cattle have an effect on invading scrub, whereas ponies can maintain grassland habitats but have no impact on scrub development (Lamoot et al., 2005). Interactions between different species can lead to profoundly different ecosystem impacts. Differences in feeding strategy between herbivores in multi-grazer systems, for example, can change the way that herbivory impacts plants (Odadi et al., 2011; Putman, 1986), and plant productivity (Vickery, 1972). These multispecies interactions can be critical for maintaining community structure and composition following reintroduction (Hooper et al., 2005; Malone et al., 2018). The number to reintroduce can also have implications for ecosystem composition and resilience;

in one case, the combined effects of climatic events and overgrazing by cattle likely led to phase-shifts from perennial vegetation to desert in the Sahel region (Charney, 1975; Scheffer et al., 2001).

A final challenge is understanding the resilience of an ecosystem. Resilience is multidimensional, encompassing several properties, disturbance types, and spatiotemporal scales, and the mechanisms underlying it are often poorly understood (Egli et al., 2019). Measuring resilience in real-world systems often relies on a combination of qualitative (e.g., via stakeholder engagement) and quantitative approaches (e.g., drawing from empirical data), but are often highly location or time-dependent, or face challenges related to obtaining sufficiently long and high enough resolution time-series data (Bailey, 2020). There are also uncertainties around what factors affect resilience; for example, biodiversity can enhance a system's resilience, but perturbations can still lead to the creation of novel states or catastrophic shifts towards undesirable states (Carroll & Noss, 2021). A famous example is the bleaching of coral habitats and precipitous decline in biodiversity in response to rising ocean temperatures (Glynn, 1993). Predicting regime shifts like this is notoriously difficult: gradual changes in underlying drivers typically have little perceived impact until a tipping point is reached, and therefore go unnoticed until it is too late. When a system is close to this threshold, a shock that previously had little consequence can trigger the shift to a new state (Scheffer et al., 2001). Furthermore, multiple disturbances can interact and compound one another (Côté et al., 2004; Orr et al., 2020): in one case, loss of predators was found to exacerbate the impacts of extreme climatic events on marine tropicalization in Western Australia (Nowicki et al., 2021).

Defining the existence and boundaries of stable states, assessing which factors confer resilience within desired stable states, and gaining an understanding of how environmental changes erode resilience, can help avoid undesirable changes while increasing awareness of the shifts that may occur with ongoing anthropogenic stressors (Beisner et al., 2003). In terms of active management, this could inform which species to reintroduce to increase functional and response diversity and the overall adaptive capacity of the ecosystem (Angeler & Allen, 2016). If there is sufficient monitoring, leading indicators could be used within the management approach. These act as 'early warning signals' and assess whether conditions are present for a potential ecosystem regime shift (Scheffer et al., 2009); examples include slower return rates after disturbances, wider swings in the dynamics of key ecosystem elements (Carpenter et al., 2007), and increased spatial variance (Donangelo et al., 2010). Long-term monitoring and field tests are needed to evaluate these, but by the time the signal is noticeable, the system may already be poised to change (Carpenter et al., 2007; Donangelo et al., 2010).

Accurately predicting the outcomes of complex systems often requires significant amounts of data or the use of tools such as computational models. However, a 2004 study found that only 2.4% of conservation management actions are related to the primary literature, with the vast majority of managers basing their decisions on 'common sense', which oftentimes was not consistent with empirical evidence (Sutherland et al., 2004). To some, a degree of uncertainty is the point of rewilding, in that nature leads the way and there is no set 'end goal' (Carver et al., 2021). Others have called for "rewilding science… to keep up with

rewilding practice" (Corlett, 2016a), with a shift towards empirical analysis and a better understanding of the impacts of species reintroductions on biodiversity and ecosystem function (Bakker & Svenning, 2018; Nogués-Bravo et al., 2016; Svenning et al., 2016).

2.5 Ecosystem models

2.5.1 Definitions and examples

Ecosystem models have been proposed as a means of providing insights into rewilding and the system responses to species reintroductions (Delibes-Mateos et al., 2019; Pires, 2017; Seddon et al., 2007). Defined as models that represent the interactions (i.e., predation, facilitation, competition) between different ecosystem elements (i.e., species, habitat types, or functional groups), they are typically used to make assessments or predictions about specific components or the ecosystem as a whole (Fulton, 2010; Geary et al., 2020; Peters & Okin, 2017). They can be parameterised using empirical field-collected or experimental data, qualitative expert knowledge, or a mixture of both, and are typically visualised as diagrammatic networks, with nodes representing ecosystem elements, and arrows representing their interactions (Figure 2.6).

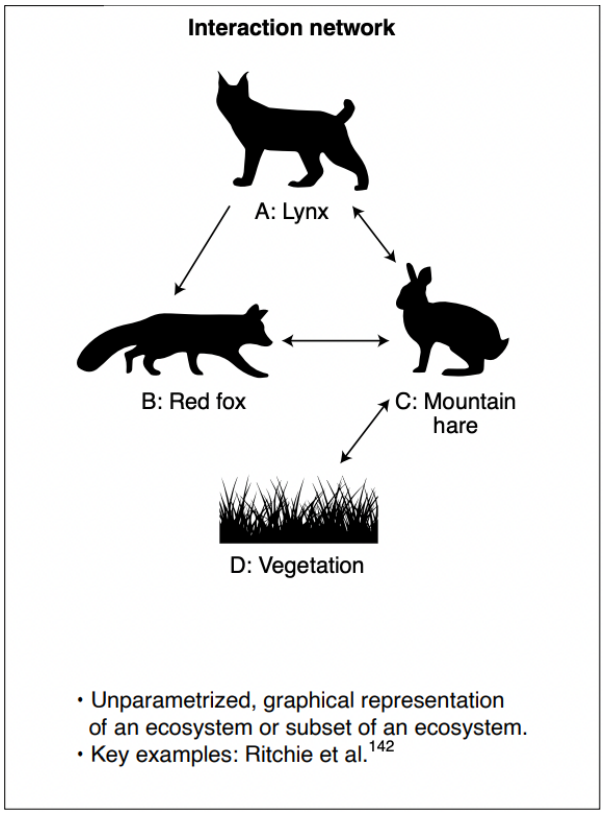


Figure 2.6*: An interaction network representing the interactions between ecosystem elements in a Central European landscape, containing an apex predator (Eurasian lynx), mesopredator (red fox), herbivore (mountain hare), and vegetation. These illustrations are the foundations for more complex ecosystem models. From Geary et al. (2020)*

Ecosystem models were originally developed to assist with predicting ecosystem dynamics and disentangling the complex relationships between elements (Evans, 2012; Peters & Okin, 2017). Historically, they were difficult to implement due to lack of information on ecosystem elements, for example time-series data on species' abundances, types and strengths of interactions, feedback loops, and spatiotemporal dynamics. Recent decades have seen an increase in data availability and an associated increase in demand for these models; they have been used extensively in fisheries (Bailey & van der Grient, 2020; Smith et al., 2007) as well as terrestrial ecosystem prediction and management (Baker et al., 2018; Purves et al., 2013), including to answer questions related to rewilding and species reintroductions (Baker, Bode, et al., 2016; Baker et al., 2019; Philips, 2020). They can be valuable tools for ecological

predictions and experimentation, as it can be difficult and costly to manipulate species and environmental effects experimentally (D'Antonio & Corbin, 2003; Laurenroth et al., 2003). For example, Philips (2020) developed a model to predict lynx dispersal following a hypothetical reintroduction to Scotland, and found that road crossings could result in high mortality and hinder effective dispersal; suitable candidate release sites were then identified based on dispersal with and without road mortality effects. Through sensitivity analyses, ecosystem models can also reveal which processes or variables have the most influence on results, helping practitioners prioritise their data gathering efforts and guiding future research (Freckleton, 1999; Jackson et al., 2000).

There are a wide range of ecosystem modelling approaches available; Geary et al. (2020) summarise their properties into four categories: 1) the objective of model development, and the represented 2) spatiotemporal patterns, 3) components, and 4) processes (Figure 2.7). These are discussed in more detail below.

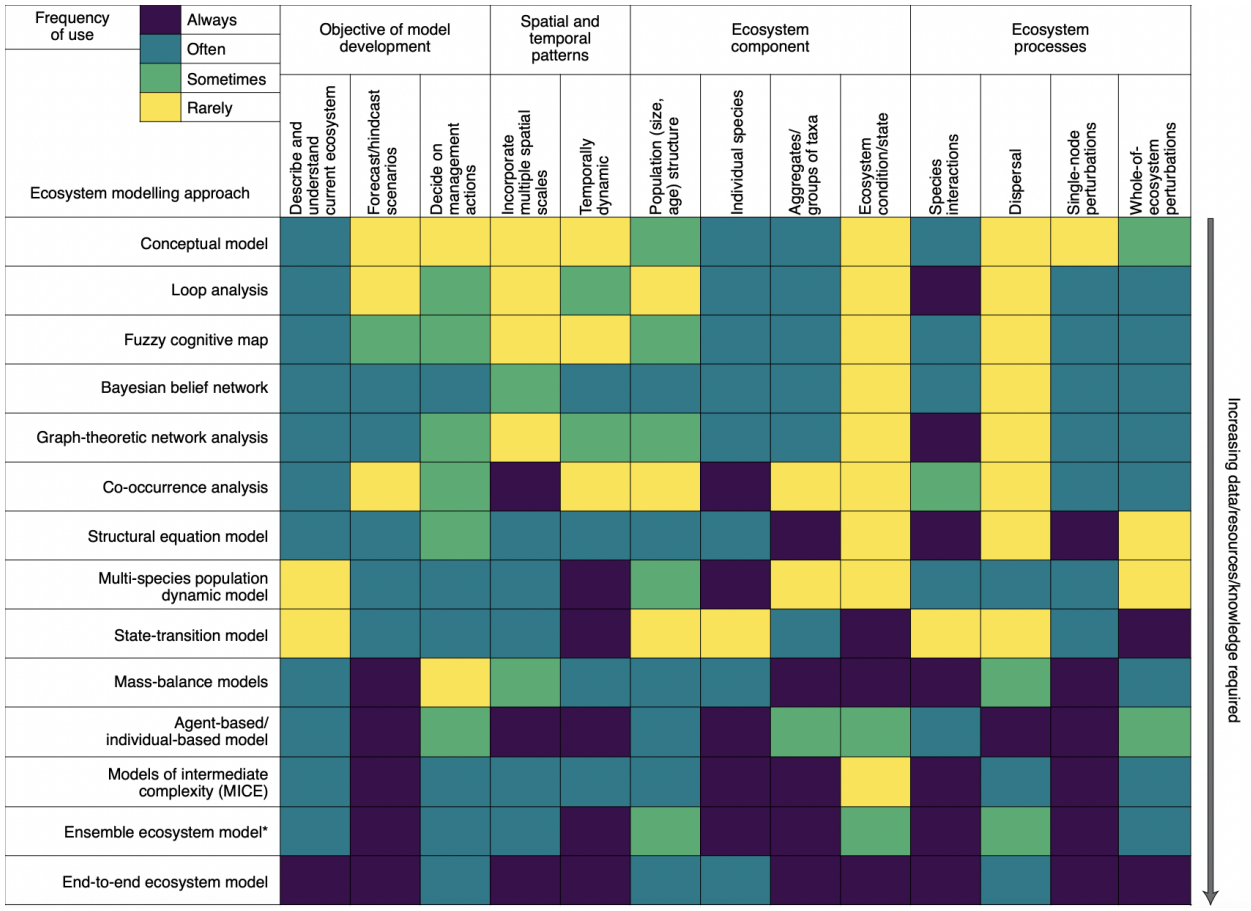


Figure 2.7*: Ecosystem modelling methodologies (rows) and their frequency of use (columns), with more complex approaches shown towards the bottom of the figure. From Geary et al. (2020). This thesis focusses particularly on two methodologies: 1) agent-based models and 2) ordinary differential equation models following the ensemble ecosystem modelling approach.*

1. The objectives of model development

A key objective of most ecosystem models is to describe the system: this can be enabled via simplistic models showing cause-and-effect relationships between different elements, or by more qualitative assessments which may assign positive or negative interactions between elements (Dambacher et al., 2003) or use Boolean analyses to describe relationships (Kristensen et al., 2019). Fuzzy cognitive maps go a step further by providing semi-quantitative assessments of the knock-on impacts of changes to an ecosystem element,

describing the impacts of one element on another as high, medium, or low (Baker et al., 2018; Dexter et al., 2012; Ramsey et al., 2012). When empirical data and/or qualitative expert knowledge are available, quantitative assessments of the interactions between elements can be provided. These can be relatively simplistic, using techniques such as Bayesian belief networks or network analyses to predict the propagation of species' impacts across the food web, or they can be complex, such as end-to-end ecosystem models which attempt to represent the entire system with as many elements and processes as possible (Fulton, 2010), or the Madingley model which uses an agent-based approach to capture global dynamics of both terrestrial and marine biodiversity (Purves et al., 2013). Network models can depict all relationships between ecosystem components, making processes and interaction assumptions open and explicit. Since all interactions are contained within the model, indirect effects are much harder to miss, such as the trophic cascades resulting from mesopredator release discussed in section 2.2.1.

A second objective of ecosystem model development is to back-cast or forecast scenarios. Forecasting has been widely used in ecology, for example to predict the effects of ocean fisheries policy interventions on socio-economic-environmental responses (Bailey et al., 2019), the relationship between biodiversity and ecosystem stability (Thébault & Loreau, 2005), and the biomass of ocean animals under different climate change scenarios (Lotze et al., 2019). Ordinary differential equation (ODE) models, for example Lotka-Volterra based ensemble ecosystem models (EEMs) have been proposed as a means of predicting rewilding outcomes (Delibes-Mateos et al., 2019) as they have been widely used to forecast the impacts of species reintroductions, such as which ecosystem elements may increase or

decrease following dingo reintroductions to an Australian national park, and wolves to Yellowstone National Park in the United States (Baker, Bode, et al., 2016), or the ecosystem-wide impacts of eastern quoll and long-nosed potoroo reintroductions at Booderee National Park, Australia (Baker et al., 2019). In the case of rewilding, there is no 'reliable template' to point the system towards (based on, for example, paleoecology or pristine ecosystem examples, as discussed in section 2.2). This means the system can only be dynamically managed towards a potentially non-analogous future state rather than looking to the past, and for this, models are needed.

Finally, a third objective is to assist with decision-making around management interventions. This often has considerable overlap with the second objective. Relatively simple models of interacting elements, such as Lotka-Volterra based EEMs, can guide management decisions (Lurgi et al., 2018), for example to identify the most important species to manage for the preservation of other important elements (Bode et al., 2017). More complex agent-based models (ABMs) have been used to predict recolonisation patterns of large carnivores in Scandinavia (Recio et al., 2020), analyse food web networks (Flores et al., 2019), and assess ecosystem responses to interventions or stressors (Bartlett et al., 2016; Flores et al., 2019). Models can be especially useful for assessing multidimensional problems where gathering empirical evidence can be challenging, such as resilience, which encompasses properties such as recovery, resistance, and adaptive capacity (Egli et al., 2019). They can also capture emergent properties relevant to management decision-making, for example ABMs have the potential to produce emergent

structures and behaviours, including the emergence of resilience arising from individual interactions across an ecosystem (Egli et al., 2019).

When forecasting different scenarios, there are usually significant uncertainties related to model parameters (Baker et al., 2019). Models face a trade-off between generality, realism, and accuracy and precision (i.e., the level of uncertainty) (Levins, 1966). Uncertainty is inevitable in complex ecosystems, and limited information can make the prediction of ecosystem dynamics difficult or impossible. Explicit communication of parametric uncertainties is therefore required to avoid misinterpretation. Failure to do so could have significant consequences: for example, overestimation of future northern cod stocks in Newfoundland, Canada, led to significant overfishing and collapse of the fishery (Walters & Maguire, 1996). Structural uncertainty (i.e., assumptions and choices made related to the model design) can also have significant impacts on results (Wildermuth et al., 2018). Techniques such as model skill assessments, in which ecosystem model predictions are compared against field data, and ensemble modelling, which can explicitly assess both parametric and structural uncertainty, are strategies for acknowledging and navigating uncertainty (Geary et al., 2020).

2. Spatiotemporal patterns, components, and processes

Except for the simplest conceptual models, ecosystem models incorporate temporal patterns to depict the interactions of components over time. Time can be coarsely represented, such as via non-descript time steps as seen in fuzzy cognitive mapping (Baker et al., 2018) and

continuous-time EEM models (Baker, Bode, et al., 2016), or they can incorporate much finer resolutions such as discrete hours, days, or months (Kramer-Schadt et al., 2004). Likewise, ecosystem models can depict components at a range of resolutions, for example taxonomic or functional groups, species, or individuals. Spatially explicit ecosystem models are less common (but see Kramer-Schadt et al., 2004; Recio et al., 2020), but spatial heterogeneity and spatially-dependent interactions may be important characteristics to consider. Some processes are inherently patchy, and if these are averaged over space, the overall behaviour of the system can be affected (Dieckmann et al., 2000). In the case of the wood-pasture hypothesis, for example, areas of thorny scrubland could lessen the interaction between neighbouring woodland and herbivory, whereas grassland could have the opposite effect by leaving tree saplings exposed to consumers (Van Uytvanck et al., 2008). 'Landscapes of fear' or differences in consumer habitat preferences can also affect species' spatial concentrations. If patchiness affects model behaviour, space must be included, but if not, methodologies such as ODEs, which assume a 'mean field', are appropriate.

Models incorporate a range of ecological processes that impact ecosystem structure and composition, particularly trophic (e.g., predation) and/or non-trophic (e.g., competition, facilitation) interactions between ecosystem components, dispersal, disturbances that impact individual components (e.g.., management interventions such as culling), and disturbances that affect the entire ecosystem (e.g.., extreme weather events, changes in climatic conditions). Models that combine interactions with other environmental or anthropogenic components are especially important for improving the management of ecosystems under changing climatic, biodiversity, and land use conditions. Such models are not common,

although examples exist (Pachzelt et al., 2013). Models that predict ecosystem resilience to perturbations have also been developed to identify important species for amplifying or mitigating the effects of disturbances (Griffith et al., 2019), and assess the response of plant-pollinator and plant-herbivore networks to species loss (Maia et al., 2021). However, models that capture the ecosystem-wide impacts of rewilding, including on composition, structure, and overall resilience, have not yet been developed. A new holistic model is therefore needed to explore questions related to restoring damaged ecosystems via rewilding, such as optimising management interventions and informing how to achieve a given end goal or avoid unintended consequences.

2.5.2 The choice of model complexity

As discussed in section 2.5.1, developing ecosystem models involves trade-offs between complex approaches which are not easily transferable to other systems, or simpler approaches which may miss out on key ecological processes. Many consider simpler models to be the 'gold standard' for ecological modelling as they typically have a smaller parameter space and require less data and computational power, yet can answer many research questions just as well as complex models (Evans, 2012; Harrison et al., 2011). The primary drivers of uncertainty in ecosystem models are parametric and structural (i.e., the ecosystem elements and their interactions included in the model), meaning that as structural complexity increases, so too does uncertainty in model predictions (Evans, 2012). Complex models can therefore come at the cost of increased uncertainty, reduced analytical tractability and insights, and decreased precision due to stochastic effects (Evans, 2012; Schoener, 1986).

However, it is possible that the relative simplicity of a model could abstract or exclude important mechanisms, and restrict the applicability of the results when applied to some situations (D. DeAngelis, 1988; Parunak et al., 1998). Doak et al. (2008) notes, for example, that while reductions may be necessary for model manageability, "it drastically curtails the full range of species complexities" and could miss out on key ecological processes. Management and policy questions may also be very specific and difficult to answer using general models. Contrasting the results of different models has provided insights into such mechanisms that simpler models may overlook, such as heterogeneity (Hastings, 1990), localised interactions, and spatiotemporal complexity (Donalson & Nisbet, 1999). If these simplifications are expected to affect model results and applicability, a different strategy is required, such as ABMs which can be made more complex and are arguably the best candidates for 'realistic' modelling.

Careful consideration therefore needs to be given to the number of ecosystem components, interactions, and processes to include, and the spatiotemporal scales (Evans, 2012; Geary et al., 2020). To construct decision-useful ecosystem models, many recommend using "the simplest accurate model," in which the model being developed is only as complex as the objective requires and the available information allows (Hunter-Ayad et al., 2020). However, choosing between model options is not always a straightforward process. Direct comparisons between model methods are uncommon, but where they exist, outputs can be highly variable, in some cases having the same qualitative behaviour and dynamics (Colon et al., 2015; Thierry et al., 2015), and in others, conflicting (Simpkins et al., 2018; Zeller et al., 2018).

Clarification on which model methodology is best suited to answering questions about rewilding and resilience is therefore needed. This need could be addressed by developing two models on either end of the complexity scale, such as ODEs and spatial agent-based models; fitting the models to the same data and exploring the same questions would allow for a comparison of their outputs.

Summary

Predicting the ecosystem-wide impacts of rewilding

Rewilding aims to rebuild self-sustaining ecosystems via the restoration of natural processes and complete (or near complete) trophic webs. It shows promise for enhancing biodiversity and ecosystem resilience, but concerns have been raised about the lack of empirical research and challenges of predicting its outcomes, especially any potential ecological consequences. There are also practical management uncertainties, for example to what extent different interventions can build resilience into a system or achieve a given end goal. Models have been proposed as a means of predicting the impacts of rewilding on ecosystems. Many methodologies are available and have been applied to make predictions about ecosystems, forecast scenarios, and assist with decision-making. However, none have yet captured the ecosystem-wide impacts of rewilding, for example on composition, structure, and resilience.

A new model is therefore needed to explore questions related to restoring damaged ecosystems, such as optimising management interventions and informing how to attain a desired end state or avoid unintended consequences. When developing this new model, careful consideration needs to be given to the number of ecosystem components, interactions, and processes to include, as model complexity can affect the utility and

applicability of results. Development of this model can allow practitioners to make scientifically informed decisions while considering risks and uncertainties and address the need for "rewilding science… to keep up with rewilding practice" (Corlett, 2016) and shift towards more empirical analyses.

CHAPER 3

3 Assessing the cascading impacts of rewilding at the Knepp Estate, UK, using ensemble ecosystem models

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Abstract

Rewilding is a conservation approach that aims to rebuild autonomous and resilient ecosystems through the restoration of natural processes and complete food webs. A growing body of evidence supports rewilding's benefits, but concerns have also been raised about its potential risks, as species reintroductions can have widespread and unexpected knock-on effects, such as the declines or extirpations of other species. In this paper, an ensemble ecosystem model (EEM) is developed to assess the ecosystem-wide impacts of species reintroductions at the Knepp Estate rewilding project in the UK. The model is used to answer questions such as: a) how have species reintroductions impacted habitat composition? and b) how can managers engineer the system towards an end goal, such as a mosaic wood pasture habitat? This is the first application of EEMs to a moderately data-limited system (i.e., with time-series abundance data available in addition to expert knowledge). Simple 'reality check' constraints can be used to narrow the parameter space and identify simulations that are not fundamentally theoretically sound despite replicating the time-series data. Updating the EEM framework to explicitly include these constraints could improve the accuracy of results while also simplifying the calibration process. Despite this, a trade-off emerges, where adding abundance data and constraints may make the model more realistic and the distribution of accepted parameters less wide, but they also

make the EEM process more difficult because many more runs get rejected; including further model complexity could be a valuable next step. Overall, the model produced acceptable results, and could potentially serve as a predictive management support tool to provide managers with a means of assessing species reintroductions and other management decisions before implementation. This could, in turn, address some of the key criticisms of rewilding, particularly that more evidence is required of its potential as a policy and management technique.

3.1 Introduction

Rewilding is a conservation approach that aims to restore natural processes and food webs at all trophic levels, thereby promoting autonomous and resilient ecosystems (Carver et al., 2021). In Europe, rewilding initiatives are often inspired by the wood-pasture hypothesis (Carver et al., 2021), which proposes that the primaeval European landscape would have been wood pasture, characterised by a shifting mosaic of grassland, scrubland and woodland, with dynamics driven by the grazing, browsing, and trampling of large herbivores (Harding & Rose, 1986; Rose, 1993; Vera, 2000). In this theory, spatial association with unpalatable plants (e.g., thorny scrubs) enables palatable plants (e.g., tree saplings) to regenerate in grasslands maintained by large grazers. The palatable plants then outshade the species that facilitated them, leading to cyclical turnover (Olff et al., 1999). As agriculture and pasture expanded, these biomes were restructured (Kaplan et al., 2009; Vera, 2000). Today, rising levels of land abandonment across Europe are resulting in the abandonment of herding, and as areas become overgrown, biodiversity associated with open habitats declines, and in dryer regions the risk of wildfires increases (Johnson et al., 2018; Navarro & Pereira, 2012). To

solve this problem, many initiatives are introducing large herbivores to maintain dynamic wood pasture habitats (Smit et al., 2015). Although the goal of rewilding is to promote fully self-sustaining ecosystems, many projects, such as those operating within relatively small, enclosed areas, may require a degree of ongoing intervention, for example population control of reintroduced species (Tree, 2018).

A growing body of evidence supports the benefits of rewilding, and some have argued that it could be integrated into policy and included as a global sustainable development agenda to help solve global issues such as climate change and biodiversity loss (Ermgassen et al., 2018; Navarro & Pereira, 2012; Svenning, 2020). However, concerns have also been raised about the lack of empirical research and challenges of predicting its outcomes, especially any potential ecological consequences (Nogués-Bravo et al., 2016; Svenning et al., 2016). Ecosystems are usually complex, and perturbations can have widespread and unexpected knock-on effects, potentially producing major unintended consequences. Species reintroductions, for example, can lead to the declines or extirpations of other species, (Lovari et al., 2014; Pace et al., 1999a), or significant alterations in species composition (Johnson & Cushman, 2007), and the effects can be dependent on management decisions such as the functional groups or number of individuals to reintroduce (Newton et al., 2013; Scheffer et al., 2001; Tuomi et al., 2019). Vegetation regeneration following land abandonment (i.e., passive rewilding) can increase fire risk (Mantero et al., 2020) and reduce water availability (Beguería et al., 2003). With the number of rewilding projects increasing (Jepson, 2019), there is a clear need for a framework or analytic approach that can forecast the outcomes of

different management interventions, for example the cascading effects of species reintroductions or changes in stocking densities.

Predicting the outcomes of rewilding is a significant challenge not only due to the complexity of ecosystems, but also due to the often limited time-series data on species' abundances, and the sign and strengths of interactions between species; the latter is oftentimes only available as expert knowledge. Structural and parametric uncertainty regarding the number, combinations, and potential time-dependency of interactions can also impact the accuracy of predictions (Dexter et al., 2012; Levins, 1974). In this paper, a model following the ensemble ecosystem modelling (EEM) framework is developed in Python and applied to the Knepp Wildland Project in the UK. The EEM approach is conceptually similar to Approximate Bayesian Computation (ABC) with rejection sampling (Pritchard et al., 1999) in that it randomly samples parameter values, returning those that generate feasible, stable ecosystems (Baker et al., 2019). It was designed to assess the ecosystem-wide impacts of decisions made under uncertainty (Bode et al., 2017) and has been used in previous studies to forecast the ecosystem-wide impacts of species reintroductions (Baker et al., 2019; Baker, Gordon, et al., 2016; Bode et al., 2017), and the effects of assisted migrations on recipient ecosystems (K. Peterson & Bode, 2021). EEMs typically represent ecosystems as feasible and stable, but these idealistic representations, particularly in the face of novel environmental conditions such as climate change, have been questioned (Vollert et al., 2024). To the authors' knowledge, this paper represents the first time an EEM is applied to a moderately data-constrained system. The ecosystem is not assumed to be stable or feasible but can instead be represented by abundance data and expert knowledge.

In this study, the model is used to explore questions related to rewilding management strategies, such as optimising stocking densities and informing which new species should be reintroduced to achieve a given end goal. The aim is that it acts as a predictive management support tool, providing practitioners with a means of assessing species reintroductions before their implementation, and informing how a given end goal can be achieved. This could help practitioners make scientifically informed decisions while considering risks and uncertainties in a systematic manner and, in turn, address some of the key criticisms of rewilding, particularly that we must move towards a more robust appraisal of its potential as a policy and management technique (Pettorelli et al., 2018; Rubenstein & Rubenstein, 2016; Torres et al., 2018).

3.2 Methods

a. The Knepp Estate

Knepp is a 3,500-acre estate in West Sussex, England (Tree, 2018). Once a high-intensity arable and dairy farm, in 2001 the land was devoted to a pioneering project inspired by rewilding principles and the wood-pasture hypothesis. The aims of the project are to produce a dynamic, functional ecosystem and increase biodiversity through the reintroduction of grazing animals (Tree, 2018). The area is divided into three blocks: Northern, Middle, and Southern, each of which varies in management strategy, herbivore assemblage and density, and the year in which rewilding began. This paper focuses

specifically on the 4.45 square-kilometre Southern Block, which has relatively more time-series data as well as the full suite of species reintroduced at Knepp.

In 2009, Exmoor ponies, Old English longhorn cattle, and Tamworth pigs were reintroduced to the Southern Block to act as domesticated proxy species for the tarpan, aurochs, and wild boar, respectively. Fallow deer were then reintroduced in 2010, and red deer in 2013. Roe deer were already naturally occurring at the site in low numbers. Consumers are free roaming within the blocks of the estate and maintained at low densities relative to conventional farms and conservation grazing (Barkham, 2018; Natural England, 2018). This is done via culling (harvesting for meat) or the removal of breeding males, to allow for vegetation regeneration. There are no large carnivores present at Knepp, and the culling regime is primarily guided by: 1) animal welfare issues, i.e., reducing the population to a level that can survive long, harsh winters given fodder availability, and 2) a desire for a wood-pasture habitat (Tree, 2018). Knepp is self-described and widely recognised as a rewilding project and is referred to as such in this paper; however, some have argued that projects with ongoing human intervention and desired end goals may be better described as ecological restoration (Anderson et al., 2019) or in some cases, regenerative agriculture (Cusworth et al., 2022).

Since the project began at Knepp, there have been significant changes in habitat composition, particularly in the Southern Block; its fields were removed from production at different times over an eight-year period and then left fallow, which facilitated natural colonisation and habitat complexity prior to species reintroductions (Tree, 2018). As a result, the Southern Block changed from arable fields and grassland to a complex mosaic of predominantly scrub and woodland between 2001 and 2020 (Schulte to Bühne et al., 2022).

This increase in vegetation cover has likely had impacts on ecosystem services such as carbon sequestration and flood mitigation, and facilitated increases in invertebrate, bird, and small mammal diversity, including the return of rare species such as nightingales (*Luscinia megarhynchos*), turtle doves (*Streptopelia turtur*), and purple emperor butterflies (*Apatura iris*) (Kurwald, 2017; Tree, 2018).

Knepp was chosen as a case study for several reasons. It is a well-known rewilding project with similar goals to other sites across Europe: reintroduce grazing animals and reduce human impacts to create dynamic, self-regulating wood-pasture ecosystems. The results of the models could therefore be applicable to other rewilding projects more broadly. They have an on-site ecologist who can provide expert knowledge, as well as time-series data: a baseline survey of species and habitat types at Knepp was undertaken in 2005 before species reintroductions took place (Greenaway, 2006), and time-series data on each reintroduced species' stocking density is available on a yearly basis between 2009-2015, or monthly between 2015-2021. Data are also available on habitat composition from various studies conducted between 2001-2020.

b. The ecosystem network

The purpose of the model is to simulate the population dynamics of interacting species at Knepp. The model is based on a network of consumers and primary producers which was informed by the wood-pasture hypothesis, and constructed based on quantitative data from Knepp and similar sites, as well as qualitative expert opinion from the resident ecologist (Kirby, 2004; Olff et al., 1999; Putman, 1986; Penny Green, *pers comm.* 2020). There are

five nodes representing herbivores: Old English longhorn cattle, Exmoor ponies, fallow deer, red deer, and roe deer; one omnivore: Tamworth pigs; and three habitat components: grassland, woodland, and thorny scrub.

Interactions can be trophic (predator-prey, or in the context of Knepp, herbivory) or non-trophic (e.g., competition, facilitation) (Figure 3.1). Consumers are assumed to negatively impact, and be positively impacted by, habitat types via herbivory. Larger habitat types are assumed to negatively impact smaller types via competition for light, for example woodland is assumed to outcompete grassland and thorny scrub (Olff et al., 1999). As per the wood-pasture hypothesis, thorny scrub is assumed to positively impact woodland by protecting saplings from herbivory and facilitating regeneration (Smit et al., 2006; Smit & Ruifrok, 2011; Vera, 2000). Although other elements could be important for the system, such as the soil microbiome and nutrient cycling, they are not added primarily since they are outside the focus of the wood-pasture hypothesis, but also due to lack of data.

	Exmoor pony	Fallow deer	Grassland	Longhorn cattle	Red deer	Roe deer	Tamworth pig	Thorny Scrub	Woodland
Exmoor pony	0	0	1	0	0	0	0	1	1
Fallow deer	0	0	1	0	0	0	0	1	1
Grassland	-1	-1	-1	-1	-1	-1	-1	-1	-1
Longhorn cattle	0	0	1	0	0	0	0	1	1
Red deer	0	0	1	0	0	0	0	1	1
Roe deer	0	0	1	0	0	0	0	1	1
Tamworth pig	0	0	1	0	0	0	0	1	1
Thorny Scrub	-1	-1	0	-1	-1	-1	-1	-1	-1
Woodland	-1	-1	0	-1	-1	-1	-1	1	-1

Figure 3.1: *Signs of the interactions between ecosystem elements. Consumers are assumed to negatively impact, and be positively impacted by, each of the three habitat types. Habitats can negatively impact each other via competition for light. Thorny scrub positively impacts woodland by protecting saplings from herbivory. Habitats are assumed to be self-limiting with a negative diagonal, whereas consumers are assumed to have a negative r and diagonals of 0. This is to ensure their populations decline in the absence of primary producers.*

c. Model Construction

The model is based on the generalised Lotka-Volterra equations (Equation 3.1; Lotka, 1925; Volterra, 1926):

$$\frac{dn_i}{dt} = r_i n_i + \sum_{j=1}^{N} \alpha_{i,j} n_i n_j \qquad \text{(Eqn. 3.1)}$$

Where n_i is the total amount of ecosystem element i (relative population size, i.e., relative number of individuals or percentage habitat type), r_i is the growth rate (growth of the relative population per year), $\alpha_{i,j}$ is the strength of the interaction between nodes i and j (number of individuals^{-1}year^{-1}), and N is the total number of ecosystem elements. Initial population sizes for each node (e.g., the initial percentages of each habitat type or number of roe deer in 2005, and the initial number of each consumer upon its reintroduction) are rescaled to 1 so that the model tracks relative changes over time.

Primary producers have positive r_i values between 0 and 1 and are assumed to be self-limiting, i.e., with diagonals of the α matrix between -1 and 0 (Baker et al., 2019; Baker, Gordon, et al., 2016; Bode et al., 2017). Consumer species are assumed to have negative r_i values and diagonals equal to zero. This differs from other EEM models in the literature, which generally have positive intrinsic growth rates and negative diagonals of the α matrix for all ecosystem elements. The reason for this difference is that, in this model, it is important for consumer populations to collapse in the absence of primary producers. With positive intrinsic growth rates, consumer populations can survive without any inputs (i.e., food sources) for several years; while this is a standard assumption made in many EEM

papers, it was considered too unrealistic for this case. Bounds for interaction strengths are assumed to be between -1 and 5 depending on the sign of the interaction. The models cover three time-periods: the years before large herbivores were reintroduced (2005-2009), the years after large herbivores were reintroduced (2009-2020), and future projections (2021-2120). Splitting the model in this way allows for the assessment of what may have occurred if species reintroductions had not taken place.

The aim is to generate an ensemble of parameter sets that replicate the empirical data while also passing several simple constraints. Other EEMs have used constraints to exclude models that do not replicate the data or expected dynamics (Baker, Gordon, et al., 2016; Raymond et al., 2011). These are flexible and can be used not only to filter out empirical irregularities, but also to incorporate basic theoretical knowledge. In this paper, constraints are focussed on simple 'reality checks' to ensure the model is fundamentally theoretically sound, in addition to replicating the data. Four are explored in total (outlined below). Constraint 1 is passed by setting fixed parameters. Constraints 2-4 rely on additional filters, as they are not parameter-specific but instead dependent on model outputs and interactions between the parameters (i.e., they could not be accommodated by changing the priors alone).

1. Constraint 1: If all primary producers are removed, consumers should rapidly decline within one year. This is based on simple physiological needs of the animals and can be enforced by assuming the population must go to ≈0 within one year; this is achieved by setting consumers' r_i equal to $log(\frac{1}{100*n_i})$ given our initial assumption of consumer diagonals being equal to zero.

2. Constraint 2: If the model is run for 100 years with no herbivory, thorny scrubland should increase at the onset, but then eventually be outcompeted by woodland. This is based on expert knowledge and empirical evidence from other rewilding projects in England which found that agricultural fields can become shrubland-dominant after approximately 15 years, and closed-canopy woodland after 40-50 years (Broughton et al., 2021). The constraint gives some flexibility around these time-frames and assumes thorny scrub should be greater than woodland and grassland at 20 years, and woodland should be greater than thorny scrub and grassland at year 100.
3. Constraint 3: If a fixed number of herbivores is artificially maintained within the system for a long period of time, all habitat types should decline towards zero. This is based on studies in the UK which show excessive grazing can reduce structural complexity and species richness, and suppress tree regeneration (Anderson & Radford, 1994; Kinnaird, 1974; Pollock et al., 2005). To simulate this constraint, reintroduced species are added at twice their 2020 stocking densities. Consumers' positive interactions with grassland are set to the maximum of 5 and *r* values set to 0 to ensure their populations grow or stay constant. This could theoretically represent a scenario in which consumers are given supplemental feeding just for the purpose of keeping them in the area.
4. Constraint 4: In the absence of consumers or habitat competition, woodland, grassland, and scrubland should each level out at 100%, with any habitat types they negatively affect falling to 0% (e.g., in a habitat with only scrubland and grassland, scrub levels out at 100% with 0% grassland). Empirical data for habitat types are

available as percentages, but as these are rescaled to 1 in the model, it is theoretically possible that output values could be far above or below 100% without this constraint.

The inclusion of these constraints makes filtering too demanding to pass a simple accept/reject scheme. Therefore, optimisation using genetic algorithms is necessary to explore the space (46 parameters) and identify a parameter set that produces outputs closely matching the empirical data from Knepp while also passing the constraints. Genetic Algorithms (GAs) are search methods based on the principle of evolution via natural selection: the 'fittest' candidates - i.e., those parameter sets that closely fit the data - are selected to produce the next generation. Offspring have 'genes' which are similar to the parents' but can be subjected to mutation. Over successive generations, the community evolves towards an optimal solution (Bremermann, 1958; Fraser, 1957; Holland, 1975). GAs have been applied to a wide range of optimisation problems (Ross & Corne, 1994), including ecological ones (Hamblin, 2013; Ruxton & Beauchamp, 2008) and are favoured here over other optimisation approaches because they are able to search large parameter spaces to find global optimal solutions, with a smaller risk of becoming trapped in local minima (Massart et al., 1998). The objective function focuses on minimising the value a to achieve output values (x) which replicate the middle of each empirical filtering condition (y, with N being the total number of filtering conditions) (Equation 3.2), while also passing constraint 4, as this targets maximum values for nodes rather than more general ecosystem dynamics, and is therefore assumed to be the most difficult to pass:

$$a = \sum_{i=1}^{N} \frac{(x_i - y_i)}{y_i} \qquad \text{(Eqn 3.2)}$$

The GA output is then used to build a prior, on which to run ABC with rejection sampling (Pritchard et al., 1999) for identifying additional suitable parameters and model outputs. A wide uniform posterior is generated around the GA output, and 1 million simulations are run by randomly drawing all parameter values from these distributions. Rejection sampling is then used with a $\boldsymbol{\delta}$ of 1% and passing all habitat conditions. The second requirement exists because reintroduced consumer species are continuously observed and have many more filters to pass through, so it is possible that the top 1% of runs are skewed towards correctly fitting these species. A key aspect of the model is to understand the effect of grazing animals on habitat composition, and a usable model must therefore be able to correctly replicate habitat dynamics. The posterior joint distribution of parameters is then built using only the accepted simulations.

The final states in the accepted pre- and post-reintroduction simulations are used as the initial conditions in the post-reintroduction and forecasting simulations, respectively. Simulated years begin in March, which is when the annual livestock count takes place. At the beginning of each simulated year between 2009 and 2020 (post-species reintroductions), the average population value for each reintroduced species per year is forced into the model. From 2015, data on consumer populations are available on a monthly basis. At the end of each year from 2015, simulations pass through filtering conditions of the maximum population value per year, to ensure they are growing at realistic rates. Growth filters for fallow and red deer are calculated differently, as their populations are

only counted once per year at Knepp, but the number culled is recorded monthly. Therefore, these species' filters are equal to the number of deer at the beginning of the year, plus the number culled over the course of the year (i.e., their approximate net growth rate, excluding human impacts). Further information on forcings and filtering conditions is provided in the Supporting Information.

Simulations that produce consumer values within the following bounds around the known values are assumed to have passed the filter; these are assumed to be wide enough to allow sufficient numbers of simulations to pass, while narrow enough to produce realistic results:

- Exmoor pony: ±1 individual
- Fallow deer: ±25 individuals
- Longhorn cattle: ±25 individuals
- Red deer: ±5 individuals
- Tamworth pigs: ±10 individuals

Accepted simulations are used to forecast the range of potential future dynamics of the ecosystem in the long-term, and to explore questions such as: how have species reintroductions impacted the ecosystem, and how might they continue to impact it in the future? What characteristics would a new species need to have, or what changes in current stocking densities would need to occur, to engineer the system towards a particular end goal?

3.3 Results

a. Accepted simulations

One hundred separate GAs were run, with parameters given wide bounds of -1 to 5 as applicable, to identify a range of acceptable parameter sets. However, none of the outputs passed all constraints, and habitat filtering conditions were consistently failed, indicating model outputs may not be usable for understanding the impacts of grazing animals on vegetation (Supporting Information). Constraint 2 was the most difficult to pass with zero accepted runs, possibly due to the limited time-series data available for each habitat node (Supporting Information). Numerical optimization is greatly improved, especially when the number of parameters is large, by manually reducing the area over which the numerical optimization takes place. This is done here as a next step, by removing, before feeding to the optimizer, large parts of the parameter space which would obviously result in unrealistic population dynamics. Given enough time and computational resources, one would expect a genetic algorithm (or any other optimization algorithm) to discover this property of the parameter space independently, but by manually removing nonsensical options from the parameter space (nonsensical given our understanding of the ecosystem which GAs lack) we can greatly speed up the calibration process. The following adjustments were made:

1. Woodland *r* is assumed to be <= 0.15, and the positive interaction with thorny scrub <= 0.01, to prevent it from becoming 100% of the system in < 45 years; this would be considered unrealistically high growth (Broughton et al., 2021). The negative diagonal is assumed to be >= -0.025 to allow woodland to level out near 100% in the absence of herbivory (Constraint 4.3).

2. Thorny scrub *r* is assumed to be <= 0.5 to prevent it from becoming 100% of the system in < 15 years; this would be considered unrealistically high growth (Broughton et al., 2021). The negative diagonal is assumed to be >= -0.025 to allow scrubland to level out near 100% in the absence of habitat competition and herbivory (Constraint 4.2).
3. Grassland is assumed to have high growth rates (>= 0.5) so they can increase towards 100% in a year, in the absence of habitat competition and herbivory. The negative diagonal is bounded at -1 to -0.4 to allow grassland to level out near 100% in the absence of habitat competition and herbivory (Constraint 4.1).
4. To prevent grassland, thorny scrub, and woodland from falling towards zero by the 2020 filtering conditions, herbivory and habitat competition are assumed to have negative impacts of <= 0.05 each.
5. Consumers are assumed to benefit 0-0.5 from woodland and thorny scrubland (as opposed to 0-5); this is to prevent their populations from experiencing unrealistically rapid growth as these habitat nodes increase. To prevent their populations from collapsing in grassland-dominant environments, consumers are assumed to benefit >= 2.5 from grassland.

After manual adjustments and an additional 100 GAs, one parameter set was identified which satisfies constraints 1-4 and optimises Equation 2, passing 94% of the data filters (Supporting Information). The neighbourhood of the parameter set returned by the optimisation is explored to find additional suitable parameters and model outputs. This is done so by assuming, for each parameter, a uniform prior ranging ±10% of the value

returned by the genetic algorithm. This range was chosen as it allows for a high percentage of runs to pass the filtering conditions while also showing the range of potential outputs (Supporting Information). Of the 1 million runs, 637,020 passed the first set of filtering conditions in 2009, and 204,509 passed the final roe deer and habitat filters in 2020. Taking the top 1% left a total of 2,045 accepted simulations (Figure 3.2).

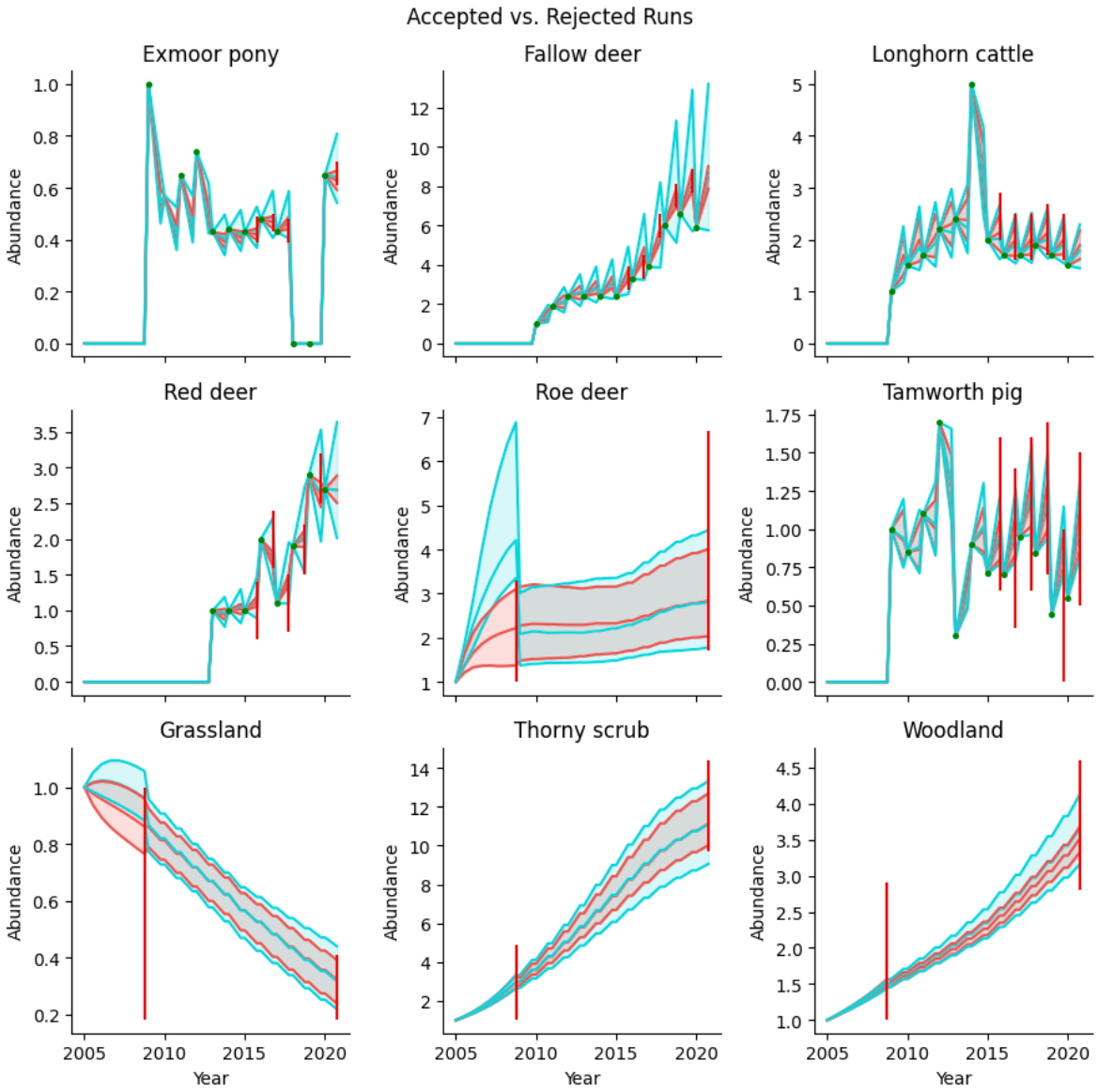


***Figure 3.2**: Time-series of accepted (blue) vs. rejected (red) runs for each ecosystem element. Each graph shows the median and the 95th percentiles (shaded areas) of the model outcomes. Red vertical lines indicate the filtering conditions*

each run passed through. Dots represent external forcings applied to the models (e.g., the number of consumers culled in a given time-step).

Each filtering condition was passed by at least 15.1% of runs. The two hardest filters to pass were fallow deer populations in 2018 (16.8%), and 2019 (15.1%). A one-at-a-time sensitivity analysis (ten Broeke et al., 2016) was undertaken to assess how changes in parameters affect the number of filters passed. Each parameter in the optimiser output was varied ±50, ±10, ±5, or ±1% around its values. The model was run with the new value, and the number of filters passed recorded. Eight parameters had a gradient with an absolute value of >= 0.46 (i.e., small changes in these eight parameters had the highest impact on the number of passed filters) (Figure 3.3).

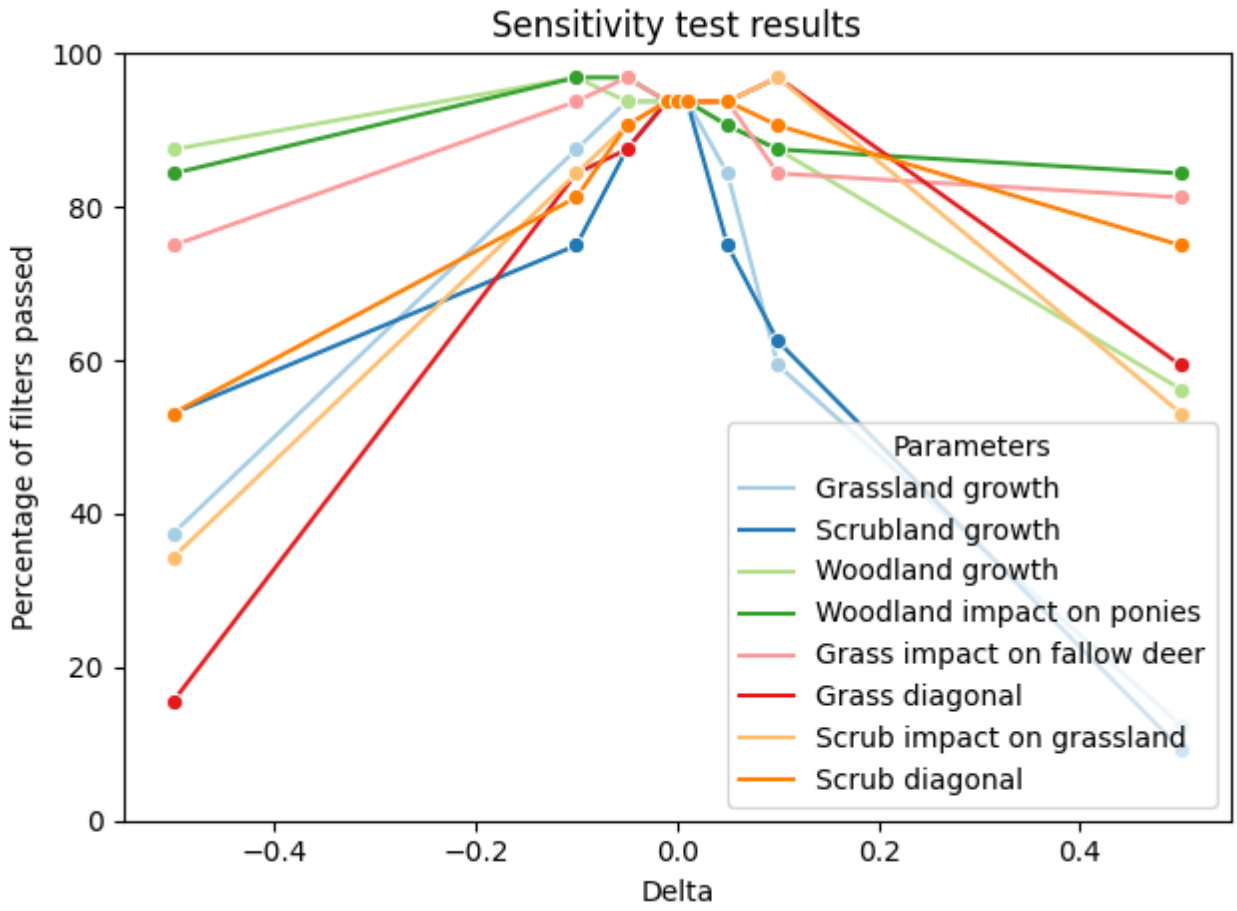


Figure 3.3: *Outputs of a one-at-a-time sensitivity analysis, in which non-uniform parameters were varied ±50, ±10, ±5, or ±1% (delta) around their values and the percentage of filters passed recorded. This figure shows the top eight model parameters which had the highest impact on the number of passed filters.*

d. Experiments

The model is used to replicate the ecosystem dynamics from 2005-2021 and project 100 years into the future, and to assess what may have occurred if species reintroductions had not taken place. At the beginning of each year when forecasting, reintroduced species' populations are forced to their 2020 populations, as Knepp seeks to maintain this stocking density in future (Penny Green, *pers comm.* 2020). Results suggest that with current

stocking densities, the system will become primarily (60%) woodland in the next 50 years, with scrubland being maintained at about 25% and grassland at approximately 10% (Figure 3.4). Had species reintroductions not occurred (i.e., the counterfactual), the ecosystem would have become almost exclusively (90%) woodland, with scrubland and grassland each declining to <5%. Roe deer numbers in the counterfactual are about twice as high compared to current dynamics. This aligns with expert opinion, as roe deer are a browsing species and adapted to woodland environments (Hewison et al., 1998).

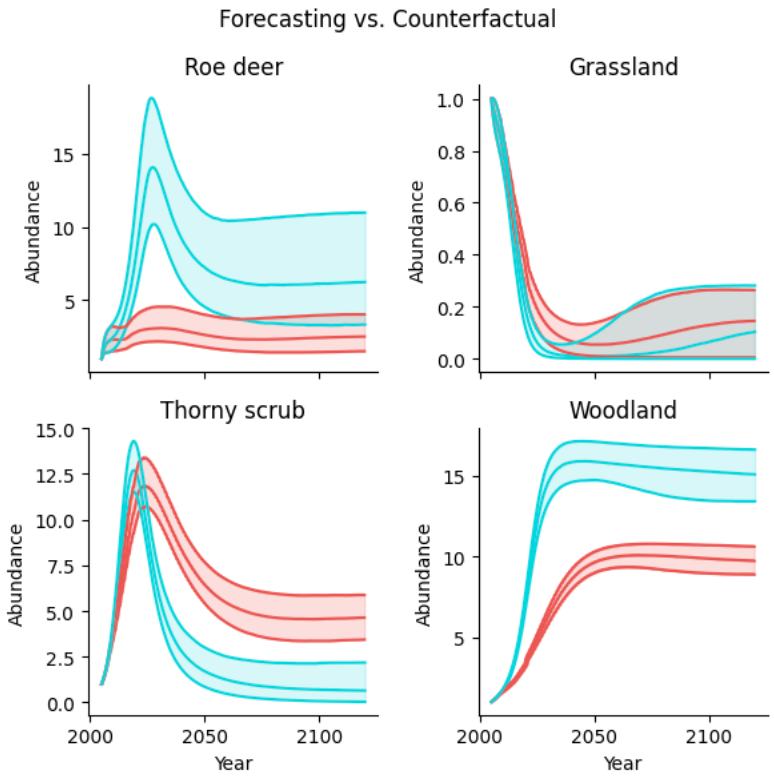


Figure 3.4: *A time-series of the Knepp ecosystem forecasted 100 years in the future. Red areas show the outcomes of current dynamics with the assumption that the 2020 stocking densities will continue to be used each year into the future, whereas blue areas show what may have occurred if reintroductions had not taken place. Each graph shows the median and 95th percentile (shaded areas) of the four nodes which have no ongoing management (e.g., culling).*

Next, experiments are run to assess how management can engineer the ecosystem towards a given end goal. First, the model is run 100 years into the future and stocking densities of the five reintroduced species are varied from 0 to 1,000% around their current levels. Second, a hypothetical new species is reintroduced, and the new species' parameters regarding the impacts it has on grassland, scrubland, and woodland (with bounds of -1 to 0), and the amount it gains from grassland, scrubland, and woodland (bounds of 0 to 5) are varied. It is assumed that the new species' populations are tightly controlled as per the other reintroduced species, so its numbers are forced back to 1, assumed to be equivalent to 50 individuals, at the beginning of each year. The hypothetical goals for both experiments are reducing woodland regeneration from 60% in 100 years to target values of either 50%, 45%, or 25%. Genetic algorithms are re-run for these targets, with the objective function equal to Equation 3.2.

Results suggest that all stocking densities would need to increase to reduce woodland regeneration (Figure 3.5). Outputs are within +150% of current stocking densities when engineering towards 50 or 45% woodland, with larger increases of 220-450% required when targeting 25% woodland. If each species' stocking density is varied one at a time, longhorn cattle, red, and fallow deer can feasibly achieve 50 or 45% woodland, however, it is not possible to realistically achieve 25% woodland by only varying a single species (Supporting Information).

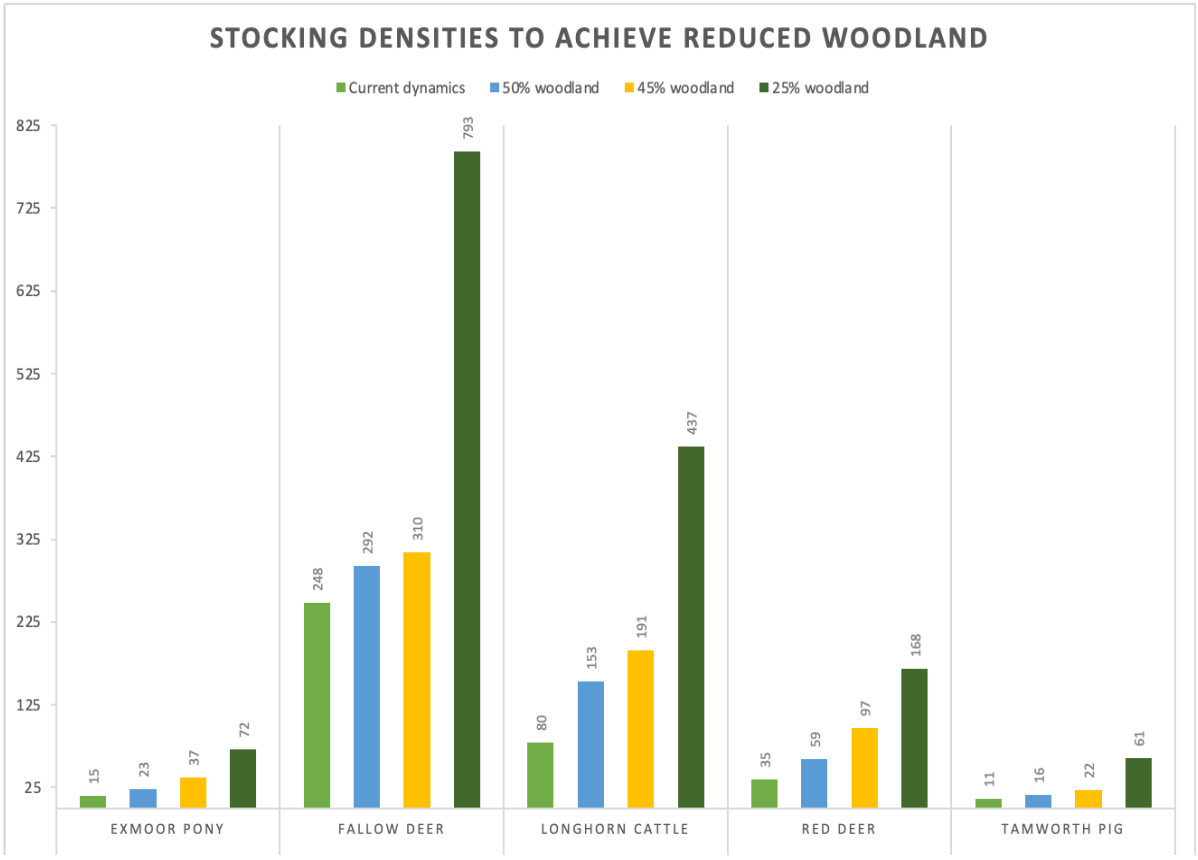


Figure 3.5: *A bar graph showing the collective change in stocking densities (i.e., number of individuals per species) required to achieve a given percentage reduction in woodland area, compared to the stocking densities used in 2020.*

If a new species is introduced to reduce woodland regeneration, optimiser outputs suggest it would have much higher impacts on scrub than the other consumers (Figure 3.6). Currently at Knepp, red deer, a large intermediate feeder, has the highest per capita impact on scrub. A large browsing or intermediate feeding species, such as elk or European bison, could therefore be a potential candidate.

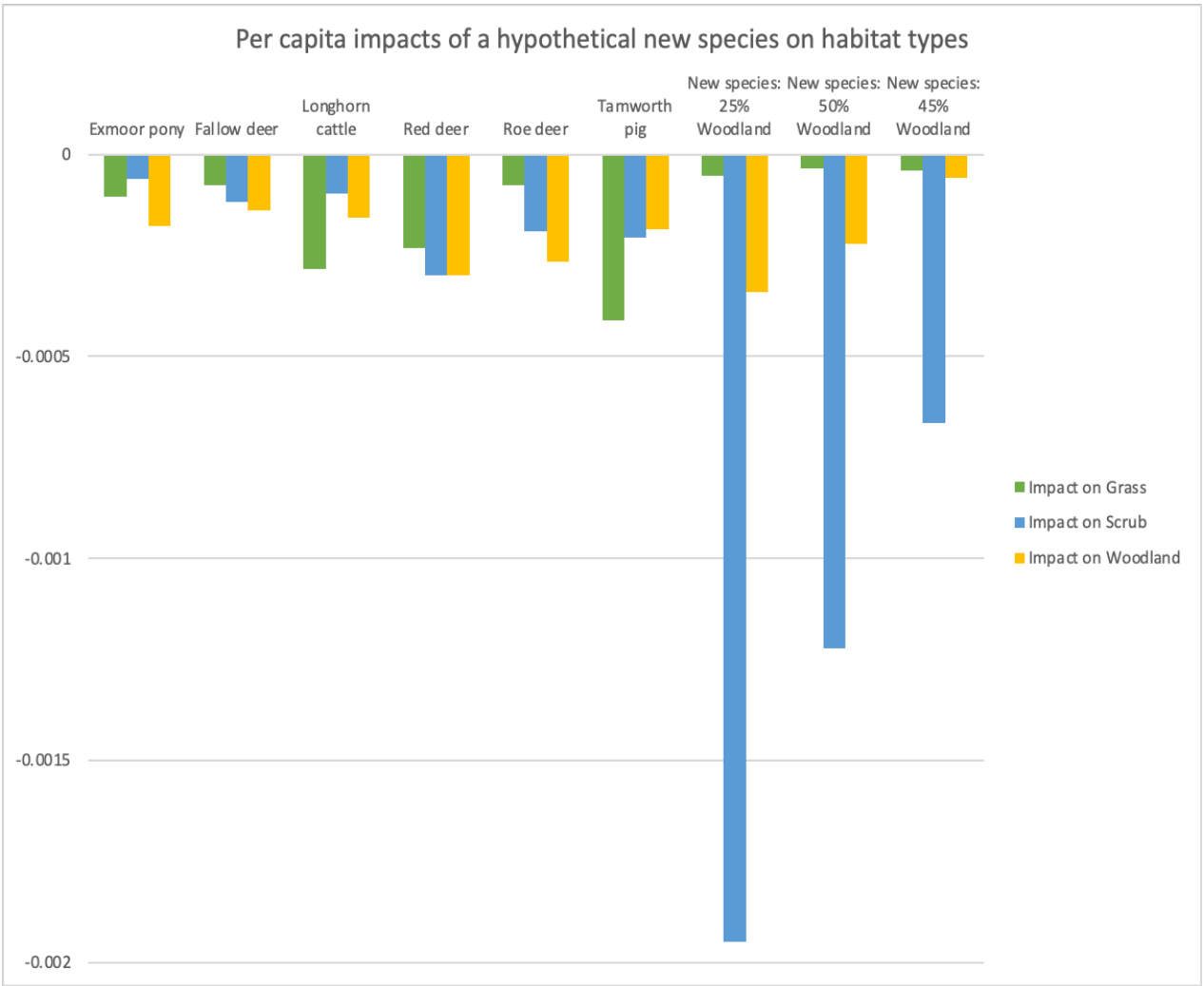


Figure 3.6: *A bar graph depicting the per capita impacts of each reintroduced species, including a hypothetical new species, on each of the three habitat types. To achieve a reduced woodland area in future, the hypothetical new species would need to have significantly higher impacts on both scrubland and woodland than the other species currently present.*

3.4 Discussion

In this paper, a new EEM model of a moderately data-limited system is developed to predict the ecosystem-wide impacts of species reintroductions and inform future rewilding decision-making. Results support the idea that naturalistic grazing with large herbivores can drive the formation of mosaic habitats. In all models, the reintroduction of large consumers is the

driving factor in maintaining a grassland-scrubland-woodland ecosystem; without them, all simulations indicate that the ecosystem would become woodland-dominant within fifty years. This then has knock-on impacts on roe deer, a browser naturally present at the site; in all simulations, roe deer populations increase with increasing woodland. Overall, the model produced reasonable and intuitive results, and could act as a predictive management support tool, providing managers with a means of assessing species reintroductions and other management decisions before their implementation.

The stocking density experiments suggest that all consumer populations would need to increase to reduce woodland in the long-term; this aligns with studies in the UK which show increases in grazing can suppress tree regeneration (Kinnaird, 1974; Pollock et al., 2005). The output values are one of potentially many stocking density combinations that could achieve this end goal, and optimiser bounds can be adjusted if management is interested in particular stocking ranges. In the reintroduction experiment, the hypothetical new species is predicted to have significantly higher impacts on scrubland than the other species currently present. This could be because scrubland is assumed to have a positive relationship with woodland via facilitation. Therefore, stocking densities may need to be high enough to push down both woodland and scrubland to achieve reduced woodland regeneration. An advantage of this methodology is that the model can be updated to incorporate more data and qualitative expert opinion, so future work could therefore revisit these assumptions to explore this result further; for example, assessing whether the inclusion of added complexity to the relationship between woodland and scrub impacts results. Multiple ecosystem structures could also be considered, e.g., Peterson & Bode (2021) randomly varied both the magnitude and signs of

the interactions in their EEM, meaning there was no predefined structure. The model can also be used to identify data gaps and uncertainties, for example, the model is sensitive primarily to habitat growth rates and diagonals, indicating these parameters are key to understand.

The paper builds upon the EEM literature by demonstrating how simple 'reality check' constraints (Bailey & van der Grient, 2020) can be helpful for further narrowing down the range of accepted parameters by augmenting the usual EEM approach - that is removing parameters that do not fit the data -, by also removing parameter sets that may fit any available data but are inconsistent with our understanding of ecosystem constraints. Updating the EEM framework to explicitly include these could improve the accuracy of results, while also simplifying the calibration process: consumer diagonals and negative growth rates (amounting to twelve parameters in this model) could be set through logic via fixed parameters, rather than varied during optimisation.

Despite this, a trade-off emerges, where adding abundance data and constraints may make the model more realistic and the distribution of accepted parameters less wide, but they also make the EEM process more difficult because many more runs get rejected. Constraints increased the number of filters, which had the benefit of narrowing down the uncertainty of predictions. However, as the number of filters increased, the number of acceptances reduced until rejection sampling on its own was no longer effective. Genetic algorithms are used to explore the parameter space, and fitting the model to the data using this methodology was relatively straightforward, but finding a parameter set that also passed the constraints was challenging. This has two implications: first, it suggests that without these simple constraints,

EEM models could produce results which appear to be reasonable but actually have unrealistic underlying dynamics. It is possible that this could significantly affect and reduce the trustworthiness of the results, especially when predicting unknown future states such as the outcomes of perturbations. Second, it points to a potential difficulty in identifying suitable parameter sets when a system is not sufficiently data-limited for a simple random search with rejection, but not so data intensive that system identification can be made based solely on the genetic algorithm output, as is the case at Knepp. In this paper, this meant that optimisers could assist with narrowing the search within the parameter space, but ultimately manual searching was also necessary.

There are other approaches to calibration in the EEM literature, for example Baker et al. (2019) iteratively changed the priors until a number of parameter sets were accepted; this method is beneficial in that it can identify different models (as opposed to many similar models). Likewise, running the genetic algorithm multiple times could lead to a diversity of solutions and prevent collapse on a single local minimum (see Williams et al., 2020). The calibration process used in this paper means that it is possible that only one local maximum was found; the accepted and rejected runs having similar trajectories (Figure 3.2) suggests this could be the case. However, this methodology was chosen due to the challenges discussed with finding even a single solution that could both replicate the data and pass the constraints. Even if using only a single GA output, future work could widen the prior bounds to potentially avoid only sampling around a single maximum and explore how this impacts the trajectories and divergence of accepted versus rejected runs, although this would come with a higher rejection rate.

In systems with relatively good data availability, like Knepp, the current Lotka-Volterra based approach may be too simplistic to fit the data while also passing all the constraints. The addition of noise (as per Baker et al., 2019), discrete time, or more complex interactions could lead to the identification of more parameter sets. For example, interactions between species are currently represented as linear relationships, but nonlinear relationships such as Type II functional responses may be more realistic and have been frequently observed in herbivores (Gross et al., 1993). Spatially-dependent interactions could be important to consider: areas of thorny scrubland could lessen the interaction between neighbouring woodland and herbivory, whereas grassland could have the opposite effect by leaving tree saplings exposed to consumers (Van Uytvanck et al., 2008), and consumers have different habitat preferences which could affect their spatial concentrations. Management actions at Knepp (i.e., culling) occur on a discrete-time basis, and decisions on how to handle culls and forcings in this continuous-time model may not have adequately captured these dynamics. A more granular model that includes these elements may have more success replicating the data while also passing the constraints.

In this paper, the five simple constraints were chosen to help ensure ecosystem dynamics were acceptable. Many other potential constraints exist and could be included in future, for example ensuring vegetation consumption rates are within reasonable bounds (see estimations by Pedersen et al., 2023), or perhaps that herbivore impacts on vegetation can increase with body size (Enquist et al., 2020), although these would come with the trade-off of a higher rejection rate. If further constraints and complexities are added to the model,

improving computational efficiency, for example by using a sequential Monte Carlo sampling approach for ensemble generation (Vollert et al., 2024), would be a valuable next step.

Finally, exploring alternative model structures could be an interesting avenue for future research. This model was based on the wood-pasture hypothesis, but alternatives exist; for example, the traditional view is that primeval Europe would have been largely closed canopy forest (Iversen, 1960; Peterken, 1996), and other researchers have pointed out that disturbance factors, such as fires and storms, may have also been integral in creating open landscapes and allowing sapling regeneration (Bradshaw et al., 2003). Irrespective of these possible improvements, it is clear that the approach outlined here has potential to both capture the underlying dynamics of ecosystems such as that at Knepp, to inform on future system states based on current trajectories, and to advise on new interventions aimed at achieving desired future system states.

Summary: Paper 1

Paper 1 focusses on developing a Lotka-Volterra ordinary differential equation (ODE) model using the ensemble ecosystem model (EEM) methodology to explore the ecosystem-wide impacts of species reintroductions at the Knepp Estate. It shows that grazing with large herbivores can maintain mosaic habitats and prevent the system from becoming woodland-dominant. To achieve a hypothetical end-goal of reducing woodland regeneration, varying the stocking densities of either longhorn cattle, red, and fallow deer could feasibly achieve reductions of 10-15% woodland in 100 years. Alternatively, a new species with high impacts on thorny scrub could be reintroduced to achieve this goal; a

large browsing or intermediate feeding species, such as elk or European bison, may be suitable candidates.

This study represents an important addition to the EEM literature and it is the first time the methodology is applied to a moderately data-limited system. Overall, the model produced acceptable results, and could be used by managers to assess species reintroductions and other management decisions before their implementation. Simple 'reality check' constraints were used to narrow the parameter space and identify simulations that are not fundamentally theoretically sound despite replicating the time-series data; updating the EEM framework to include these constraints could improve the accuracy of results while also simplifying the calibration process. However, a trade-off was identified where adding abundance data and constraints made the model more realistic and reduced the distribution of accepted parameters, but made the EEM process more difficult, as many more runs were rejected. One possible explanation for the difficult calibration process is the model is too simplistic to fit all the available data while passing the constraints. The addition of noise, space, or more complex interactions could lead to the identification of more parameter sets. Agent-based models, which are driven by 'if-then' statements rather than equations, could provide the necessary flexibility to explore the dynamics of this system. Paper 2 therefore develops an ABM of the Knepp Estate to explore this further.

3.5 Supporting Information

1. Ecosystem structure and time-series data

In the model, there are five herbivores: Old English longhorn cattle, Exmoor ponies, fallow deer, red deer, and roe deer; one omnivore: Tamworth pigs; and three habitat types: grassland, woodland, and thorny scrub.

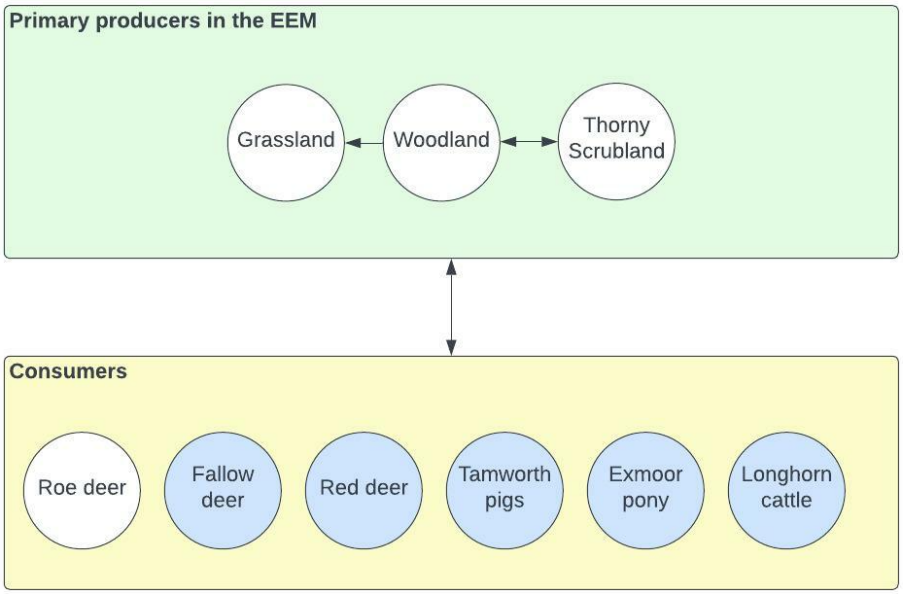


Figure A3.1 An ecological network of the Knepp Estate. Blue circles are species that were reintroduced to Knepp and whose numbers are continually managed. White circles were already present at Knepp and their populations are un-managed. Consumers are assumed to negatively impact, and be positively impacted by, each of the three habitat types. Habitats can negatively impact each other via competition for light. Thorny scrubland is assumed to positively impact woodland via facilitation of saplings.

Data on each reintroduced species' stocking density is available from Knepp on a yearly basis between 2009-2015, and monthly between 2015-2020 (Table A3.1).

Table A3.1: Reintroduced species' populations at Knepp (number of individuals)

Month	**Year**	**Longhorn cattle**	**Exmoor pony**	**Fallow deer**	**Red deer**	**Tamworth pig**
March	**2015**	107	10	100	13	18
April		115	10	100	13	22

May		129	10	100	13	14
June		129	10	100	13	14
July		129	10	100	13	14
Aug		129	10	98	13	14
Sept		130	10	96	13	14
Oct		91	10	93	13	14
Nov		91	10	86	13	13
Dec		86	10	80	13	13
Jan		86	10	73	13	10
Feb		86	10	63	13	8
March	**2016**	86	11	140	26	9
April		103	11	140	26	9
May		108	11	140	26	17
June		89	11	140	26	17
July		87	11	140	26	17
Aug		87	11	135	26	17
Sept		97	11	135	26	17
Oct		97	11	135	26	17
Nov		92	11	132	26	17
Dec		79	11	123	26	13
Jan		79	11	123	26	9
Feb		79	11	115	26	7
March	**2017**	79	10	165	14	7
April		100	10	165	14	22
May		109	10	165	14	22
June		94	10	165	14	22

July		94	10	165	14	22
Aug		94	10	149	14	22
Sept		90	10	144	14	22
Oct		88	10	140	14	22
Nov		88	10	138	14	22
Dec		88	10	92	13	18
Jan		88	10	92	13	11
Feb		88	10	78	12	16
March	**2018**	88	9	251	24	16
April		101	9	251	24	16
May		117	9	251	24	23
June		103	9	251	24	23
July		103	9	251	23	22
Aug		102	0	236	22	22
Sept		106	0	217	22	22
Oct		101	0	213	22	21
Nov		93	0	213	22	9
Dec		89	0	194	21	9
Jan		89	0	194	21	9
Feb		87	0	194	21	10
March	**2019**	87	0	278	37	9
April		101	0	278	37	8
May		110	0	278	37	8
June		89	0	278	37	8
July		91	0	278	37	9
Aug		91	0	278	37	9
Sept		93	0	263	37	9
Oct		88	0	263	37	9
Nov		87	0	256	34	9
Dec		80	0	244	30	10

Jan		80	0	220	30	10
Feb		79	0	208	28	8
March	**2020**	81	15	247	35	7
April		81	15	247	35	7
May		81	15	247	35	19

2. Filtering conditions and forcings

During the Approximate Bayesian Computation process, model runs pass through 'filters' (based on empirical data and expert knowledge) to ensure they are replicating observed dynamics. The filters used are outlined in Table A3.2 for the nodes present upon model initialisation, and Table A3.3 for reintroduced species (these have relatively more filters since their populations are controlled e.g., via culling).

Table A3.2: Prior ranges & justifications for n_i, and their filtering conditions. Initially, roe deer are the only large herbivores present in the system: Exmoor pony, fallow deer, red deer, Longhorn cattle, and Tamworth pig are all initialised at zero. Initial numbers for each node are re-scaled to 1 in the model.

Ecosystem element	**Filtering conditions (2009)**	**Filtering conditions (2020)**	**Comments & References**
Roe deer	1-3.3	1.7-6.7	**Initial condition:** Approx. 12 roe deer at Knepp in 2005 (Greenaway, 2006) **2009:** 12-40 individuals (wide bounds given as no data available) **2020:** 20-80 individuals (Penny Green, *pers comm*)
Grassland & Parkland	0.18-1	0.18-0.41	**Initial condition:** Approximately 89.9% of the Southern Block was grassland in 2001 (Schulte to Bühne et al., 2022), the number was assumed to be similar in 2005 **2009:** Wide bounds between the initial condition and lowest value in 2020 were used, as no further data were available. **2020:** 26.8 +-10% (Schulte to Bühne et al., 2022)

Thorny scrubland	1-4.9	9.7-14.4	**Initial condition:** Approximately 4.3% of the Southern Block (Schulte to Bühne et al., 2022) was thorny scrubland in 2001, the number was assumed to be similar in 2005 **2009**: Closest available data was 4.3% in 2005 (Schulte to Bühne et al., 2022) and 21% in 2012 (Thomson Ecology, 2016). **2020:** 51.8 +- 10% (Schulte to Bühne et al., 2022)
Woodland	1-2.9	3.3-3.7	**Initial condition:** Approximately 5.8% of the Southern Block was woodland in 2001 (Schulte to Bühne et al., 2022), the number was assumed to be similar in 2005 **2009:** Wide bounds between the initial condition of 5.8% (Schulte to Bühne et al., 2022) and 17% (Müller, 2019) was used **2020:** 21.5% +- 5% (Schulte to Bühne et al., 2022; Wheldon, 2019) was used.

Table A3.3: Forced culling values per reintroduced species at the beginning of each year, and filtering conditions at the end of each year.

	2009	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
Exmoor pony												
Forcing	1	0.57	0.65	0.74	0.43	0.44	0.43	0.48	0.43	0	0	0.65
Filter	-	-	-	-	-	-	0.39-0.49	0.43-0.5	0.39-0.48	0	0	0.61-0.7
Fallow deer												
Forcing	0	1	1.9	2.4	2.4	2.4	2.4	3.3	3.9	6.0	6.6	5.9
Filter	-	-	-	-	-	-	2.7-3.9	3.3-4.5	5.4-6.6	6.9-8.1	7.7-8.9	-
Red deer												
Forcing	0	0	0	0	1	1	1	2	1.1	1.9	2.9	2.7
Filter	-	-	-	-	-	-	0.6-1.4	1.6-2.4	0.7-1.5	1.5-2.2	2.5-3.2	-
Longhorn cattle												
Forcing	1	1.5	1.7	2.2	2.4	5.0	2.0	1.7	1.7	1.9	1.7	1.5
Filter	-	-	-	-	-	-	2-2.9	1.6-2.5	1.6-2.5	1.7-2.7	1.6-2.5	-
Tamworth pig												
Forcing	1	0.85	1.1	1.7	0.3	0.9	0.71	0.69	0.95	0.84	0.44	0.55
Filter	-	-	-	-	-	-	0.6-1.6	0.35-1.4	0.6-1.6	0.7-1.7	0-1	0.5-1.5

3. Genetic algorithm process

Initially, many separate GAs were run with the goal of identifying a range of acceptable outputs. After 100 runs with wide bounds between -1 and 5 (as applicable), no outputs were found that passed all the constraints, and none were able to pass each of the two filtering conditions per habitat component (Figure A3.2).

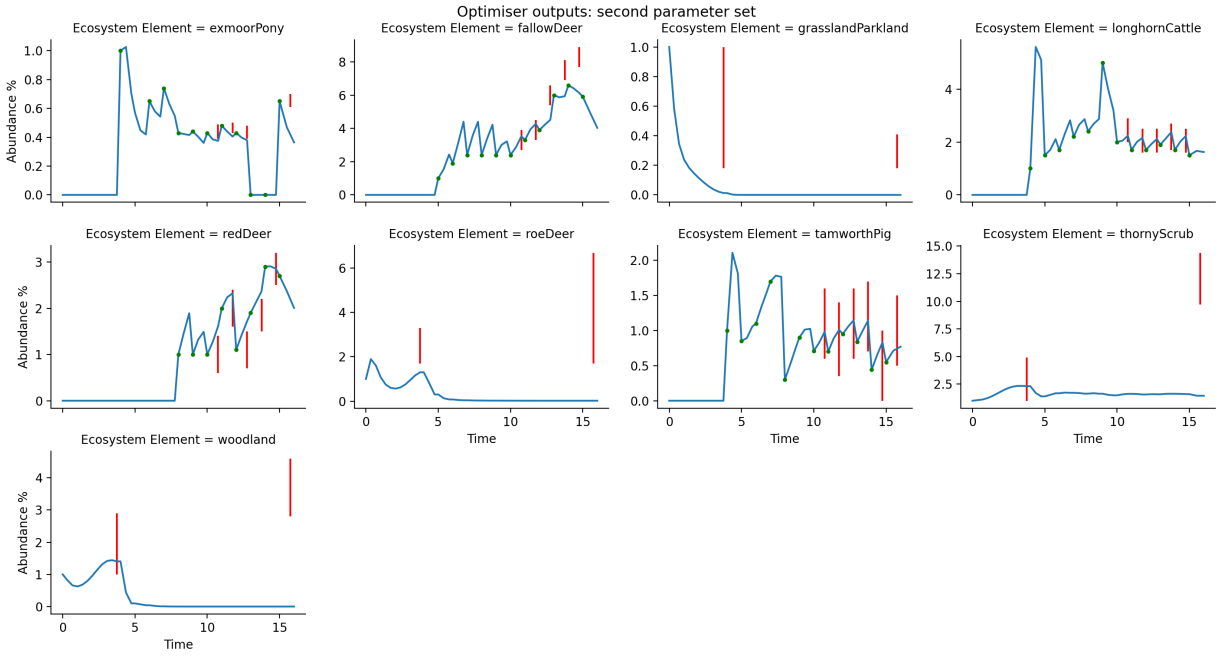


Figure A3.2 An example genetic algorithm time-series output (fit = 8.3). Filtering conditions are shown by red vertical lines. Most filtering conditions for habitats, roe deer, and fallow deer were failed.

As a next step, we explored manual adjustments of the bounds to reduce the parameter space. After running the GA an additional 100 times, a single output was found that passed all criteria (fit = 2.6) (Table A3.4). To save time and computational power, this parameter set was used (Figure A3.3).

Table A3.4: The number of runs that passed each constraint, and the range of fits outputted during the GA process.

	100 GAs with wide (-1 to 5) bounds	100 GAs with manually adjusted bounds
Range of fits	7.3-14.8	2.6-4.8
Number that passed Constraint 1: Consumers decline to ≈0 in one year without primary producers	100%	100%
Number that passed Constraint 2: Without any herbivory, thorny scrub should be > woodland and grassland at 20 years, and at 100 years, woodland should be > thorny scrub and grassland	0%	63%
Number that passed Constraint 3: After 100 years of high herbivory, all habitats should be ≈0	100%	100%
Number that passed Constraint 4.1: With no herbivory or habitat competition, after 100 years grassland should be equal to 100% (relative to its starting condition, this value is 1.1; ± 10% was acceptable)	19%	27%
Number that passed Constraint 4.2: With no herbivory or habitat competition, after 100 years thorny scrub should = 100% (relative to its starting condition, this value is 23.3; ± 10% was acceptable) and grassland 0%	4%	32%
Number that passed Constraint 4.3: With no herbivory or habitat competition, after 100 years woodland should = 100% (relative to its starting condition, this value is 17.2; ± 10% was acceptable) and grassland and scrubland 0%	5%	12%
Number that passed all constraints	0%	1%

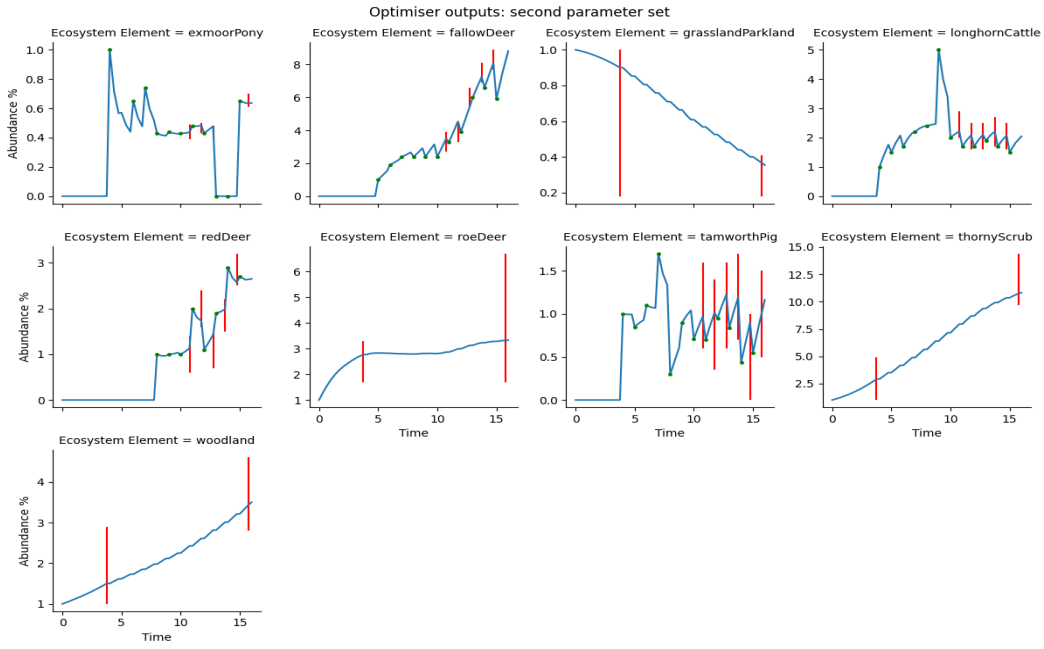


Figure A3.3: The accepted genetic algorithm time-series output (fit = 2.6). Red vertical lines denote filtering conditions and green dots are annual forcings.

Genetic algorithm parameter outputs are shown below.

- Grassland growth rate: 0.91
- Thorny scrub growth rate: 0.35
- Woodland growth rate: 0.11

	Exmoor pony	**Fallow deer**	**Grassland**	**Longhorn cattle**	**Red deer**	**Roe deer**	**Tamworth pig**	**Thorny scrub**	**Woodland**
Exmoor pony	0	0	2.7	0	0	0	0	0.17	0.4
Fallow deer	0	0	3.8	0	0	0	0	0.37	0.49
Grassland	-0.0024	-0.0032	-0.83	-0.015	-0.003	-0.00092	-0.0082	-0.046	-0.049
Longhorn cattle	0	0	4.99	0	0	0	0	0.21	0.4
Red deer	0	0	2.8	0	0	0	0	0.29	0.42
Roe deer	0	0	4.9	0	0	0	0	0.25	0.38
Tamworth pig	0	0	3.7	0	0	0	0	0.23	0.41
Thorny scrub	-0.0014	-0.005	0	-0.0051	-0.0039	-0.0023	-0.0018	-0.015	-0.022
Woodland	-0.0041	-0.0058	0	-0.0083	-0.004	-0.0032	-0.0037	0.0079	-0.0062

4. Reality check constraints

The accepted runs are passed through several ‘reality check’ constraints to ensure their dynamics are fundamentally theoretically sound (Figures A3.4-A3.8).

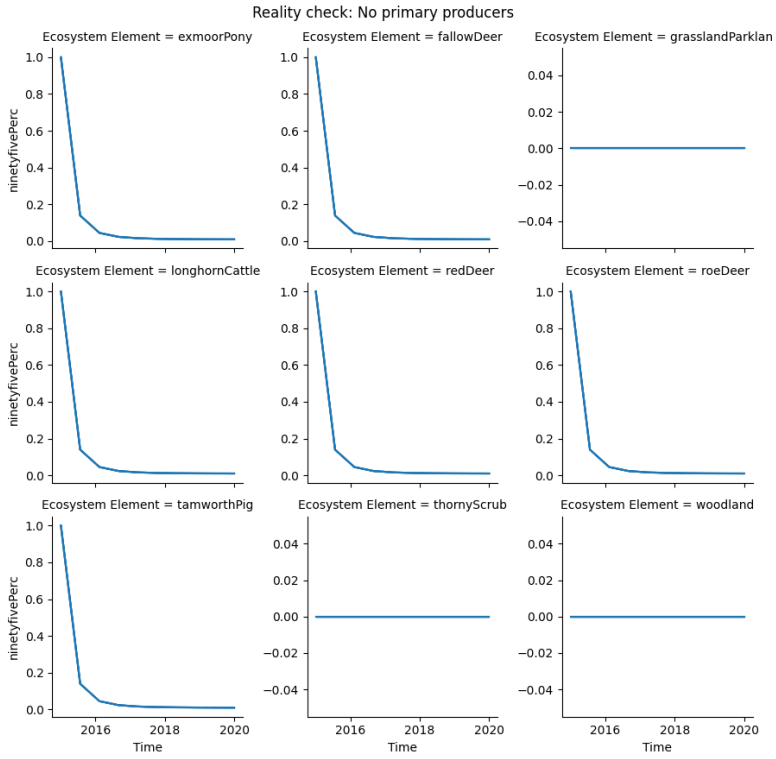


Figure A3.4: The first constraint ensures consumers fall to zero within one year if there are no primary producers present.

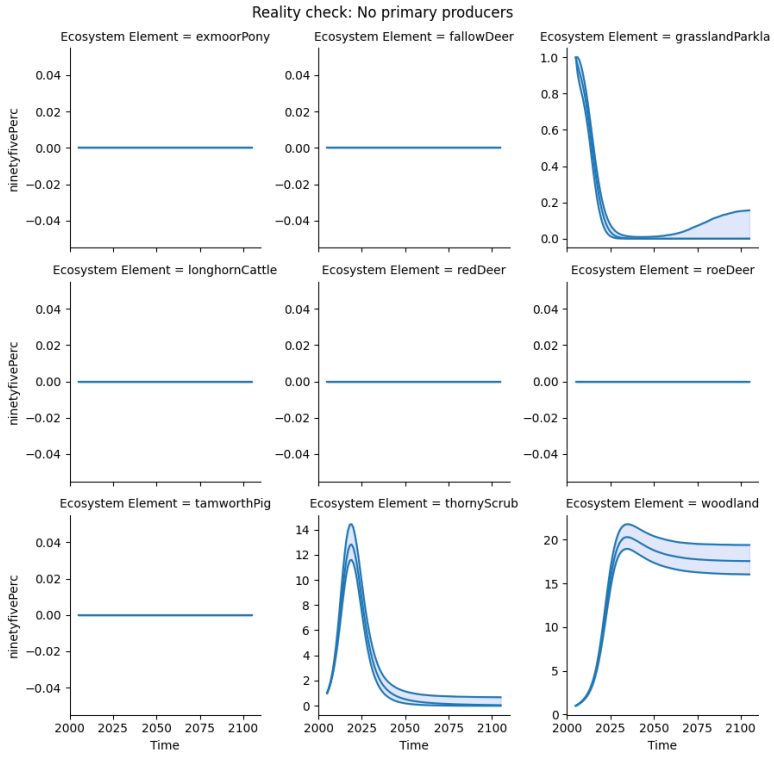


Figure A3.5: The second constraint runs the model for 100 years with no herbivory. Thorny scrubland should increase at the onset, but then eventually be outcompeted by woodland. Woodland should level out at approximately 17.2 (equivalent to 100% relative to its initial starting conditions) with no herbivory present.

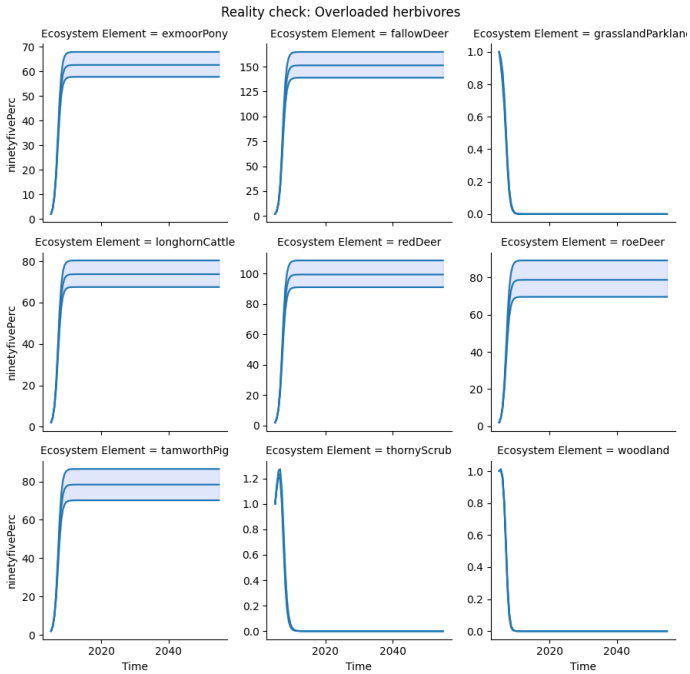


Figure A3.6: In the third constraint, herbivores are overloaded into the system, and all habitat types should decline towards zero.

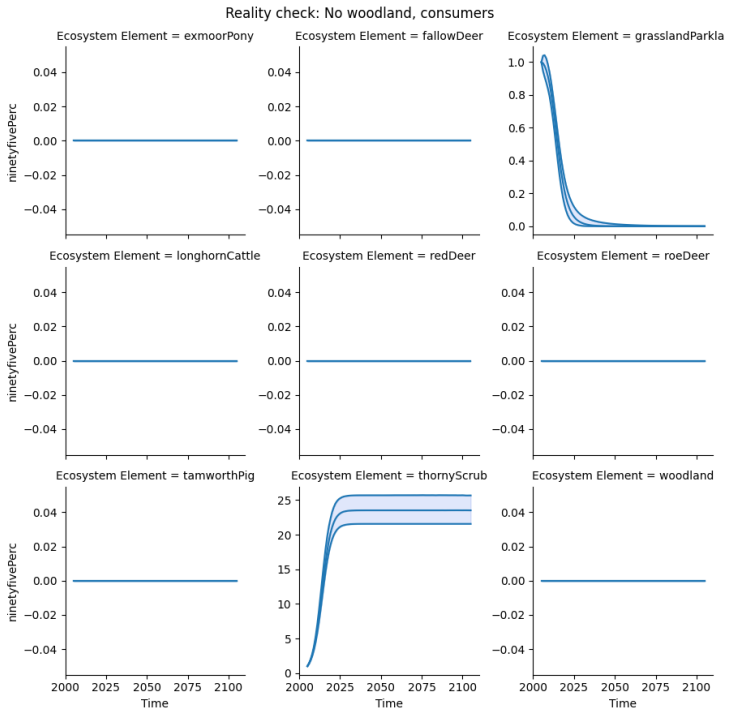


Figure A3.7: If there are no consumers present or light competition with other habitats (i.e., in this case, if no woodland is present), thorny scrubland should level out at 23.3. Relative to its initial condition, this is equal to 100%.

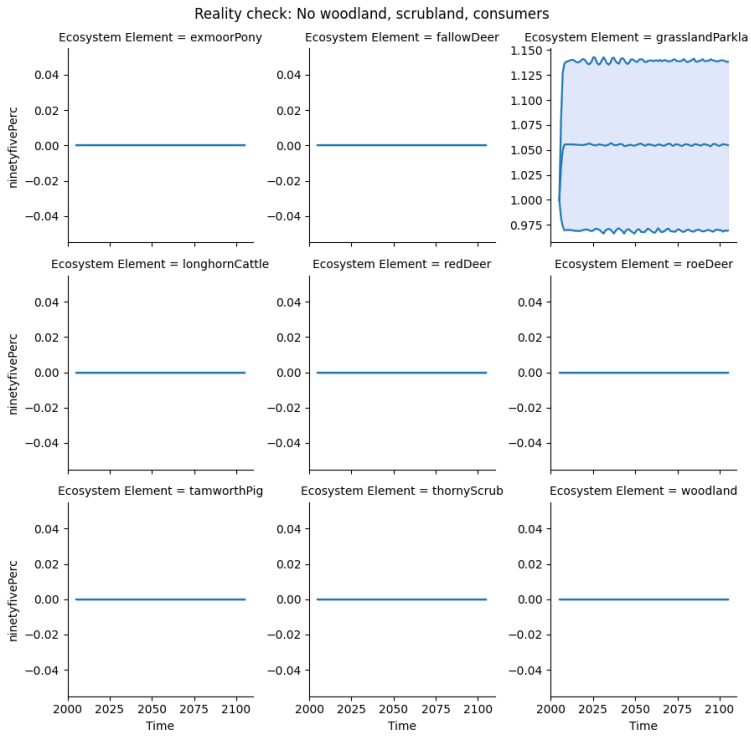


Figure A3.8: If there are no consumers or light competition (i.e., in this case, no woodland or thorny scrubland present), grassland should level out at 1. Relative to its initial condition, this is equal to 100%.

5. Choosing the bounds for the ABC Process: KS-test, histograms and correlation matrices

In the Approximate Bayesian Computation process, uniform priors on all parameters were assumed. A Kolmogorov-Smirnov (KS) test was performed (Kolmogorov, 1933; Smirnov, 1948) to find accepted parameters with non-uniform distributions (Table A3.5); these are the parameters whose posteriors were significantly affected by the rejection process (i.e., something was learned about these parameters from rejection sampling).

Table A3.5: Results of the KS-test for all accepted parameters. The nineteen identified as significant are marked with asterisks.

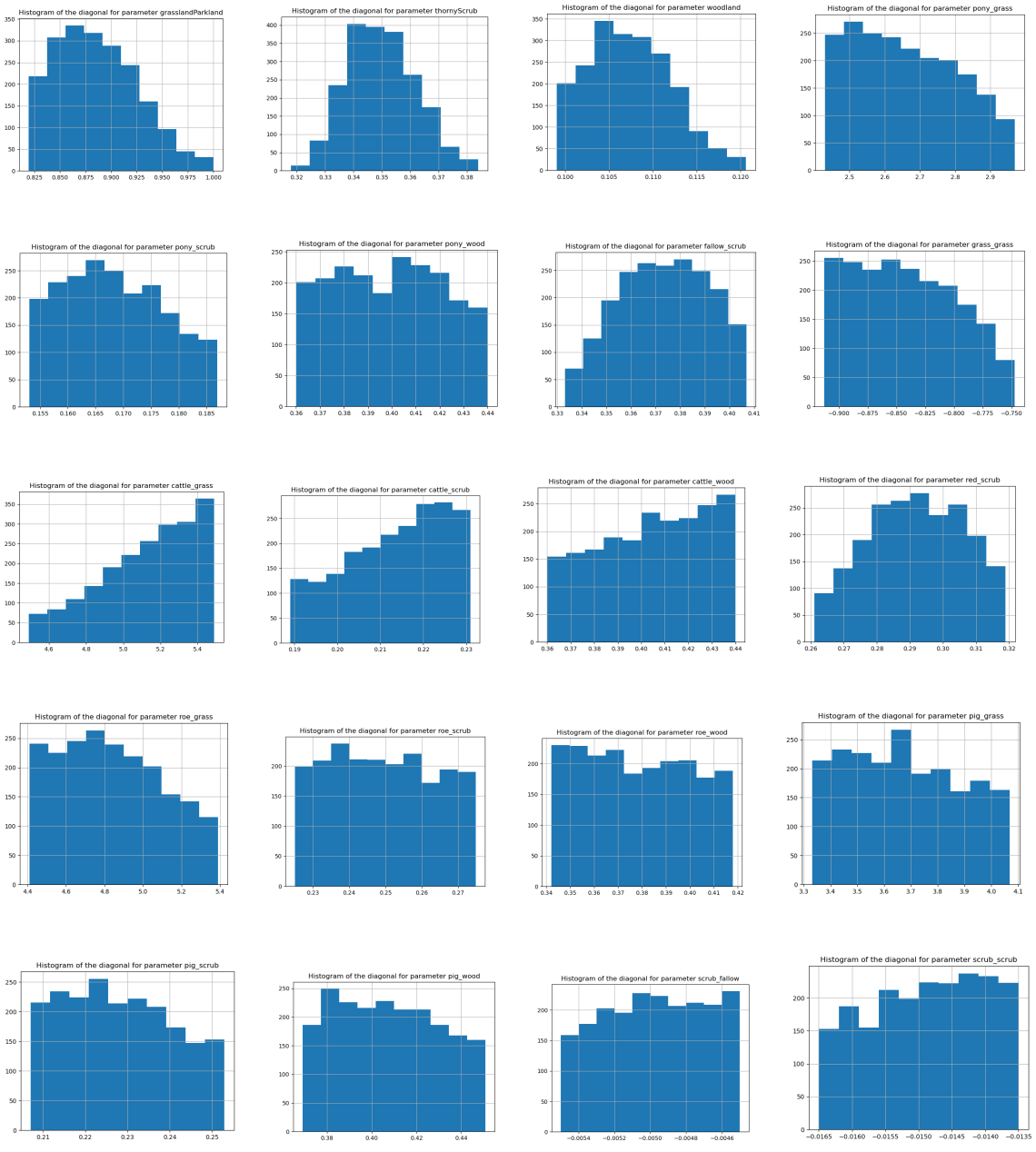
Parameter name	**P-value: PS1, no stability criteria**
Grass growth	1.2e-104*
Thorny scrub growth	1.2e-51*
Woodland growth	1.5e-92*
Pony - grassland	1.1e-22*
Pony - scrub	8.7e-16*
Pony - woodland	0.002*
Fallow deer - grassland	0.1
Fallow deer - scrubland	4.7e-25*
Fallow deer - woodland	0.46
Grassland - pony	0.92
Grassland - Fallow deer	0.15
Grassland negative	2.2e-22*
Grassland - cattle	0.48
Grassland - Red deer	0.83
Grassland - Roe deer	0.36
Grassland - pig	0.46
Grassland - Scrub	0.052
Grassland - Woodland	0.81
Cattle - grass	1.6e-81*
Cattle - scrub	2.9e-30*
Cattle - woodland	2.9e-13*
Red deer - grass	0.14
Red deer - scrub	7.3e-19*
Red deer - woodland	0.26
Roe deer - grassland	1.4e-21*
Roe deer - scrub	0.03*
Roe deer - woodland	0.004*

Pig - grassland	5.1e-08*
Pig - scrubland	6.4e-11*
Pig - woodland	4.9e-06*
Scrub - pony	0.06
Scrub - fallow deer	0.0007*
Scrub - cattle	0.82
Scrub - red deer	0.17
Scrub - roe deer	0.81
Scrub - pig	0.15
Scrub diagonal	9.5e-07*
Scrub - woodland	0.07
Woodland - pony	0.88
Woodland - fallow	0.42
Woodland - cattle	0.25
Woodland - red deer	0.4
Woodland - roe deer	0.66
Woodland - pig	0.17
Woodland - scrub	0.001*
Woodland diagonal	0.71

Choosing the bounds around each parameter output from the genetic algorithm was a trade-off between having a high number of runs accepted (assumed to be >2000) while also showing a large range of potential parameter outputs. The latter requirement is identified by assessing the histograms for the non-uniform parameters identified during the KS-test (below).

6. Histograms and Correlation Matrix

Twenty-one of the 46 (46%) parameters had non-uniform histograms as identified by the KS-test (Figure A3.9). Since all parameters were originally drawn from a uniform distribution, this means the rejection process had a significant effect on those that are now non-uniform. A correlation matrix of the accepted parameter sets is shown in Figure A3.10.



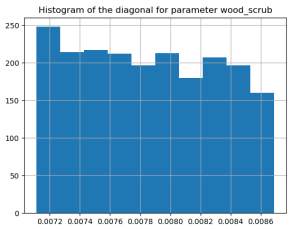


Figure A3.9 Parameters which had non-uniform distributions following ABC with rejection sampling.

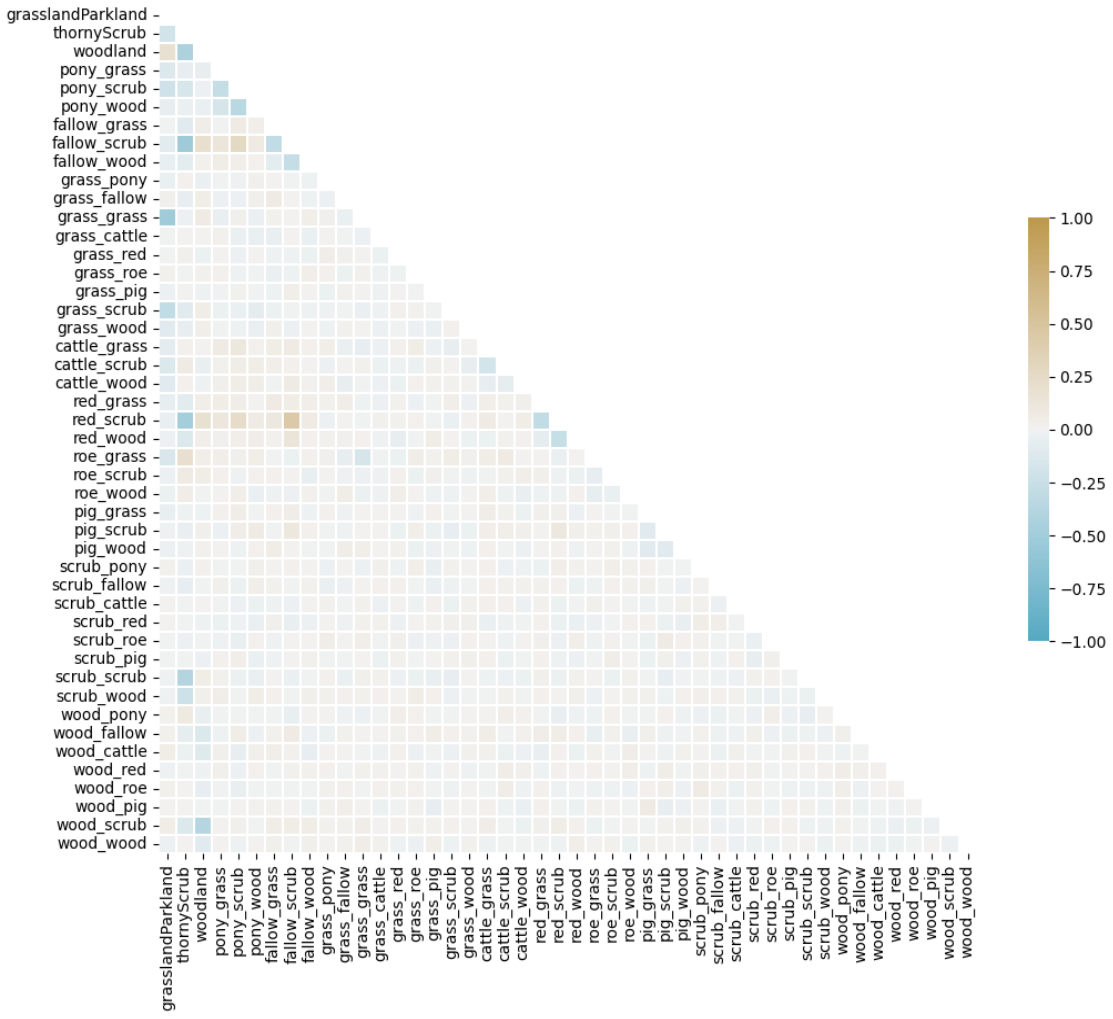


Figure A3.10 Correlation matrix of the accepted parameter sets following ABC with rejection sampling.

7. Filtering conditions

Each filtering condition was passed by at least 15.1% of runs, with the most difficult being fallow deer populations in 2018 (16.8%), and 2019 (15.1%) (Table A3.6).

Table A3.6: Percentage of runs that passed each filter in the post-reintroduction model.

Year	**Species**	**Percentage passed**
2015	Exmoor pony	46.4%
2015	Fallow deer	40.0%
2015	Longhorn cattle	34.4%
2015	Red deer	58.1%
2015	Tamworth pig	63.7%
2016	Exmoor pony	31.4%
2016	Fallow deer	27.6%
2016	Longhorn cattle	54.0%
2016	Red deer	41.0%
2016	Tamworth pig	63.3%
2017	Exmoor pony	29.9%
2017	Fallow deer	20.1%
2017	Longhorn cattle	54.9%
2017	Red deer	38.0%
2017	Tamworth pig	61.8%
2018	Fallow deer	16.8%
2018	Longhorn cattle	55.8%
2018	Red deer	40.8%
2018	Tamworth pig	63.3%
2019	Fallow deer	15.1%
2019	Longhorn cattle	55.9%

2019	Red deer	27.2%
2019	Tamworth pig	47.9%
2020	Exmoor pony	28.1%
2020	Roe deer	62.5%
2020	Grassland	55.1%
2020	Woodland	63.6%
2020	Scrubland	52.3%

8. Sensitivity test

A one-at-a-time sensitivity analysis (ten Broeke et al., 2016) was undertaken to assess how changes in parameters affect the number of filters passed. Each parameter in the genetic algorithm output was varied ±50, ±10, ±5, or ±1% around their values, the model run with the new value, and the number of filters passed recorded. A line was then fit to each parameter value and the corresponding number of filters passed (Table A3.7).

Table A3.7: The gradient of the line when assessing how changes in each of the model's parameters impact the number of filtering conditions passed.

Parameter name	**Gradient**
1. Grassland growth rate	-1.41
2. Thorny scrubland growth rate	-0.63
3. Woodland growth rate	-0.47
4. Grassland impact on pony	-0.31
5. Scrub impact on pony	-0.31
6. Woodland impact on pony	-0.47
7. Grassland impact on fallow deer	-0.47
8. Scrub impact on fallow deer	-0.31

9. Woodland impact on fallow deer	-0.31
10. Pony impact on grass	0
11. Fallow deer impact on grass	0
12. Grass diagonal	0.63
13. Cattle impact on grass	0
14. Red deer impact on grass	0
15. Roe deer impact on grass	0
16. Pig impact on grass	0
17. Scrub impact on grass	0.63
18. Woodland impact on grass	0.16
19. Grass impact on cattle	0.16
20. Scrub impact on cattle	0
21. Wood impact on cattle	0
22. Grass impact on red deer	0
23. Scrub impact on red deer	0
24. Wood impact on red deer	0
25. Grass impact on roe deer	0
26. Scrub impact on roe deer	0
27. Wood impact on roe deer	0
28. Grass impact on pigs	-0.16
29. Scrub impact on pigs	-0.16
30. Wood impact on pigs	0
31. Pony impact on scrub	0
32. Fallow deer impact on scrub	0
33. Scrub diagonal	0
34. Cattle impact on scrub	0
35. Red deer impact on scrub	0
36. Roe deer impact on scrub	0

37. Pig impact on scrub	0
38. Scrub impact on scrub	0.47
39. Woodland impact on scrub	0.16
40. Pony impact on woodland	0
41. Fallow deer impact on woodland	0
42. Woodland diagonal	0
43. Cattle impact on woodland	0
44. Red deer impact on woodland	0
45. Roe deer impact on woodland	0
46. Pig impact on woodland	0
47. Scrub impact on woodland	0
48. Woodland impact on woodland	0

9. Varying stocking densities (one at a time)

Each species' stocking density is varied one at a time to understand what level of impact each individual herbivore species has on the system, and whether they could be individually optimised towards the goal. If each species is varied one at a time, all can achieve the target of keeping woodland regeneration at 50 or 45% in the next 100 years. This can require a significant increase in stocking densities particularly for Exmoor ponies and Tamworth pigs. However, only fallow deer can achieve 25% woodland; changes in all other species' stocking densities alone were not able to reach this end goal (Table A3.8).

Table A3.8: The collective changes in stocking density (number of individuals) required to achieve a reduction in future woodland abundance.

Species	Target	Stocking density	Percentage change from current stocking densities	Woodland output value
Exmoor pony	50% woodland	237 (+222 individuals)	1620%	50%
Fallow deer		403 (+156 individuals)	163%	50%
Longhorn cattle		325 (+244 individuals)	401%	50%
Red deer		133 (+98 individuals)	380%	50%
Tamworth pig		286 (+267 individuals)	1505%	50%
Exmoor pony	45% woodland	508 (+493 individuals)	3387%	45%
Fallow deer		569 (+322 individuals)	230%	45%
Longhorn cattle		612 (+531 individuals)	756%	45%
Red deer		236 (+201 individuals)	674%	45%
Tamworth pig		561 (+542 individuals)	2953%	46%
Exmoor pony	25% woodland	762 (+747 individuals)	5040%	51.6%
Fallow deer		1511 (+1264 individuals)	612%	25%
Longhorn cattle		874 (+793 individuals)	1079%	41.8%
Red deer		386 (+351 individuals)	1103%	39.4%
Tamworth pig		561 (+542 individuals)	2953%	46.0%

10. Reintroducing new species

An experiment is run in which a hypothetical new species is reintroduced, with the parameters regarding its impacts on grassland, scrubland, and woodland (with bounds of -1 to 0), and the amount it gains from grassland, scrubland, and woodland (bounds of 0 to 5)

varied during optimisation, to achieve end-goals of reduced woodland regeneration. The optimiser parameter outputs for this new species are outlined in Table A3.9.

Table A3.9: The optimiser outputs for the hypothetical new species reintroduction experiment.

Experiment	Impact on grass	Impact on scrub	Impact on woodland	Gain from grass	Gain from scrub	Gain from woodland
25% Woodland	-0.0026	-0.098	-0.017	3.4	0.61	0.85
45% Woodland	-0.002	-0.033	-0.0029	2.1	0.24	0.76
50% Woodland	-0.0017	-0.061	-0.011	2.0	0.19	0.20

CHAPER 4

4 Assessing the impacts of rewilding at the Knepp Estate, UK, using an agent-based model with rejection sampling

Abstract

Many rewilding projects in Europe, inspired by the wood-pasture hypothesis, have reintroduced large grazers to create dynamic wood-pasture habitats and boost biodiversity. This work is occurring alongside debates around the implications of rewilding, including potential unintended consequences resulting from species reintroductions. There are also practical management uncertainties such as the functional groups or number of individuals to reintroduce; these factors can affect ecosystem outcomes. An analytic approach that can forecast the outcomes of different interventions could be an invaluable tool to support rewilding management and decision-making. Previous ensemble ecosystem models (EEMs) using the Lotka-Volterra equations have explored the ecosystem-wide impacts of species reintroductions, but these may not be best-suited for application to systems which are moderately data limited, or for exploring spatial dynamics such as the wood-pasture hypothesis. In this paper, a spatial agent-based model (ABM) using rejection sampling is developed to assess the cascading impacts of rewilding at the Knepp Estate, UK, and predict the range of possible future states under various reintroduction scenarios. Results indicate that had reintroductions not occurred, the Knepp ecosystem would trend towards woodland dominance within 25 years, supporting the idea that rewilding with large herbivores can foster habitat heterogeneity. Forecasting suggests that current grazing regimes may not sustain open areas long-term, recommending an optimised stocking

density of 0.5 Livestock Units per hectare reduce the risk of losing these. The ABM methodology had several advantages: the calibration process was improved compared to a previous EEM of Knepp, and it provided nuanced insights into the specific ecosystem impacts of hypothetical new species, such as European bison or elk. The inclusion of spatial interactions was also useful for capturing certain interactions and revealed an emergent behaviour: with large herbivores present, woodland regenerates more frequently in thorny scrubland than grassland or bare ground. The methodology is therefore promising for rewilding planning and decision-making, particularly for projects which have relatively good data availability, or are interested in the wood-pasture hypothesis or other spatially dependent interactions.

Keywords Agent-based model, approximate Bayesian computation, rejection sampling, rewilding, species reintroductions, trophic cascades, genetic algorithms

4.1 Introduction

The Knepp Estate has been home to one of the UK's most influential rewilding projects since 2001 (Tree, 2018). Once intensive arable farmland, the 3,500-acre area is now devoted to restoring dynamic, self-sustaining ecosystems through reduction of human interventions and reintroduction of large herbivore and omnivore species (Perino & et al., 2019; Svenning, 2020; Svenning et al., 2016). The project was inspired by the wood-pasture hypothesis, which proposes the primaeval European landscape was a shifting mosaic of grassland, scrubland, and woodland capable of supporting high levels of biodiversity and whose dynamics were

primarily driven by the grazing, browsing, and trampling of large herbivores (Vera, 2000). Herbivore-maintained grasslands provide opportunities for scrub re-establishment, with these unpalatable plants facilitating more palatable plants such as tree saplings. Palatable plants eventually out-shading the species that facilitated them, leading to cyclical turnover (Olff et al., 1999). Global declines and losses of megafauna beginning in the late Pleistocene, and continuing more recently with the expansion of agriculture, led to the restructuring of these biomes and a loss of wood-pasture-associated biodiversity (Kaplan et al., 2009; Vera, 2000). The wood-pasture hypothesis has been widely influential for European rewilding projects and many are reintroducing large herbivores to reinstate these habitats (Carver et al., 2021). However, the openness of Europe's primaeval landscape, and the role of large herbivores in shaping these landscapes, are under debate (Birks, 2005; Svenning, 2002). Herbivory can play a role in maintaining open habitats, but the extent of its impacts is often context and species-dependent, and dependent on the diversity and abundance of herbivore communities (Bakker et al., 2016; Kowalczyk et al., 2021).

Knepp is divided into three blocks, each of which vary in management strategy. In the Southern Block, a diverse suite of species (Old English longhorn cattle, Exmoor ponies, fallow and red deer, and Tamworth pigs) were chosen to maximise diversity of feeding strategy, and in some cases to serve as proxies for once naturally existing wild species. Roe deer were already naturally occurring at the site in low numbers. Although Knepp seeks to be process-led and reduce active management, its vision of a dynamic, mosaic habitat has guided its decision making, particularly regarding stocking densities (i.e., the number of reintroduced species present in the system). Stocking densities are continually adjusted to

generate further income via the sale of organic, pasture-fed meat (Tree, 2018), and to encourage a balance between herbivores and vegetation, while also taking into account animal welfare concerns, i.e., reducing the population to a level that can survive long, harsh winters given fodder availability (Tree, 2018). Breeding is likewise managed to support animal welfare and to prevent overpopulation: boars, bulls, and stallions are only temporarily introduced during particular times of year. The owner described the stocking density decision-making process as "... largely subjective, about a feel for the carrying capacity of the land. So we tweak the number of animals and see what happens" (Dempsey, 2021). Knepp has also been undertaking further successful reintroductions of wild species, such as white storks and beavers, and has expressed interest in understanding the potential impacts of other large herbivores, such as European bison (*Bison bonasus*) (Penny Green, pers comm., 2023).

This pioneering work is occurring alongside debates around the implications of rewilding, including potential risks and uncertainties of species reintroductions and other human interventions. Changes can have widespread and unexpected knock-on effects on ecosystems, potentially producing unintended consequences (Lovari et al., 2014; Nogués-Bravo et al., 2016; Pace et al., 1999b). Uncertainties also exist around practical management questions such as the functional groups and number of individuals to reintroduce, as these can affect outcomes (Newton et al., 2013; Scheffer et al., 2001; Tuomi et al., 2019). A lack of research on rewilding's potential impacts (Nogués-Bravo et al., 2016), and limited scientific support for facilitating sound decision-making (Pettorelli et al., 2018), have led to calls for a more systematic appraisal of its costs and benefits (Nogués-Bravo et al., 2016;

Svenning et al., 2016). An analytic approach that can forecast the outcomes of different interventions could therefore be an invaluable tool to support management and decision-making both at Knepp and other rewilding projects more broadly.

In this paper, a spatial agent-based model (ABM) is developed and applied to Knepp (Tree, 2018) with the aim of assessing the impacts of rewilding and predicting the outcomes of future decision-making. The calibration process is an extension of Lotka-Volterra-based ensemble ecosystem models (EEMs), which use a methodology similar to Approximate Bayesian Computation (ABC) with rejection sampling (Pritchard et al., 1999) to assess the impacts of decisions made under uncertainty (Bode et al., 2017). Other EEMs have been used to understand the ecosystem-wide impacts of species reintroductions (Baker et al., 2019; Baker, Gordon, et al., 2016; Bode et al., 2017), but the methodology may be limited in some cases: a previous EEM of interacting species at Knepp discussed potential difficulties with identifying suitable parameter sets in systems that are moderately data constrained (e.g., with time-series abundance data available in addition to qualitative expert knowledge), as they may not be sufficiently data-constrained for a random search with rejection, but not so data rich that acceptable models can be exclusively derived from optimisation outputs. The authors suggested a more granular approach, which can incorporate further complexity and spatially dependent interactions between species, could more easily identify acceptable models (Neil, Carrella & Bailey, in prep), while also facilitating the exploration of questions related to the wood-pasture hypothesis or other spatial dynamics.

ABMs simulate individual agents, their interactions, and the environment (Railsback & Grimm, 2011). Unlike EEMs, whose dynamics are dictated by the Lotka-Volterra equation, ABMs are driven by discrete-time, 'if-then' statements. This can give the freedom to write more reasonable rules for the system, potentially leading to more realistic results (Parunak et al., 1998). ABMs also allow for the inclusion of space and heterogeneity of individuals; in the context of rewilding, this could better capture spatial dynamics between vegetation, such as the facilitation of saplings by scrub, or individual consumer choices regarding seasonal movements and consumption preferences. ABMs have been applied to rewilding and ecosystems, for example to inform lynx reintroduction sites in Scotland (Philips, 2020), predict the conditions necessary for successful reintroductions of passenger pigeons (Elzinga et al., 2020), and to analyse food web networks (Flores et al., 2019). Other ABMs of ecological systems have been calibrated using ABC (van der Vaart et al., 2015), but to the authors' knowledge, this is the first time the EEM approach has been applied to a spatial ABM of interacting species.

4.2 Methods

A model of the Knepp Estate is developed using Mesa, an ABM framework in Python (Kazil et al., 2020). The code is open access and freely available on GitHub (Neil et al., 2022a). The aim is to simulate the dynamics of interacting species at the Knepp Estate and answer questions relevant to rewilding decision-making, such as: how have species reintroductions impacted the ecosystem, and how might they continue to impact it in the future? What is the chance of wood-pasture habitats being maintained in the long-term?

Can the addition of new species or changes to stocking densities affect this chance? The full model description following the ODD (Overview, Design Concepts, Details) protocol for describing agent-based models is available in the Supporting Information (Grimm et al., 2006, 2010).

4.2.1 Model design and initialisation

Knepp is divided into three blocks, Northern, Middle, and Southern, each of which varies in management strategy, herbivore assemblage and density, and the year in which rewilding began; this model focuses on the 450-hectare Southern Block, which has relatively more time-series data as well as the full suite of reintroduced herbivores. The model proceeds in discrete steps of one month, and covers three time-periods: the years before grazers were reintroduced (2005-2009), the years after reintroductions (2009-2020), and future projections (2020-2070). Years are assumed to begin in March, which is when the annual livestock count takes place.

There are seven model entities; six are consumers: roe, fallow, and red deer, Old English longhorn cattle, Exmoor ponies, and Tamworth pigs, and the seventh is a habitat entity. Habitats are defined by converting a shapefile of the Southern Block to $100m^2$ (1 hectare) grid cells (Figure 4.1), and classifying each as an individual agent comprising a percentage of grassland or bare ground, a number of scrub plants and trees (sapling and mature), and an overall dominant habitat condition (grassland, scrubland, woodland, or bare ground). Consumers move within and between habitat agents, and are characterised by their location

and energy levels. Pigs are additionally characterised by a sex and age description, being either a boar, sow, or piglet.

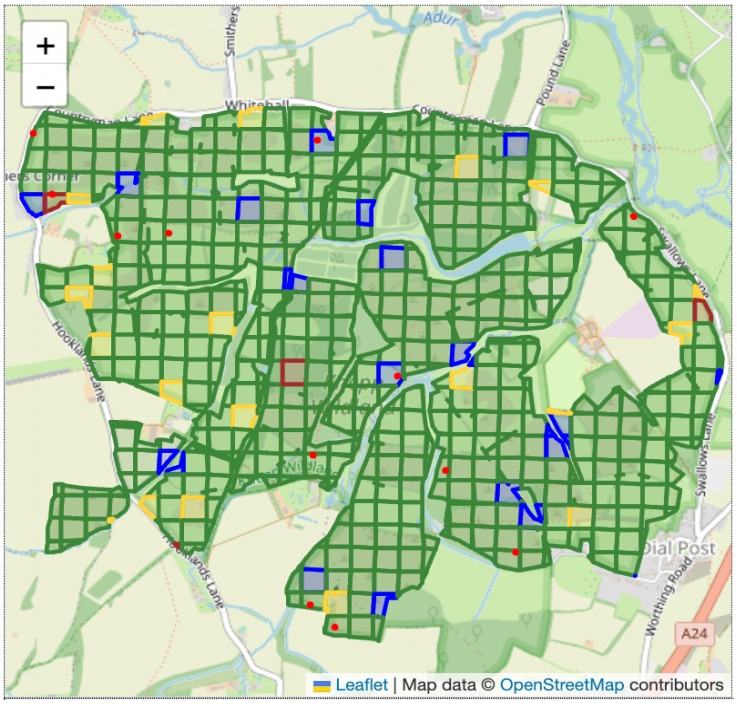


***Figure 4.1**: The Knepp Estate (Southern Block) model landscape at initialisation, with each habitat grid showing a different dominant condition (grassland as green, scrubland as blue, woodland as red, bare ground as yellow), and roe deer (red dots).*

Figure 4.2 shows the processes for consumers in the model. At the beginning of each timestep, consumers lose 1 energy and choose to move within their current cell or into a neighbouring one, depending on its dominant habitat condition. Roe deer are browsers and therefore choose to move towards scrubland or woodland if it is available; fallow and red deer are intermediate feeders, preferring grassland in the spring and summer months but randomly picking one of the habitat types to move to in the autumn and winter months; Exmoor ponies and longhorn cattle are predominantly grazers and prefer grassland year-round; and Tamworth pigs are omnivores and assumed to randomly choose any habitat,

where they rootle in the soil in search of roots and invertebrates. If the preferred habitat type is not available in theirs or a neighbouring cell, the consumer moves randomly.

Once they have moved, consumers randomly choose a vegetation component (i.e., grassland, saplings, young scrub, mature trees or scrub) in that cell and consume as much as they need for their energy to equal 1. If there is not enough of the chosen vegetation to fill their energy, they randomly choose a different component and consume it, stopping when their energy levels reach 1, or when all vegetation components in the cell have been sampled. Energy levels are capped at 1 to ensure consumers cannot survive beyond one time-step if they are unable to find any food. Scrub is assumed to facilitate sapling regeneration by preventing herbivory (King, 2019; Salek et al., 2019; Van Uytvanck et al., 2008); therefore, if consumers choose to eat saplings, the number removed from the system is scaled according to a 'facilitation' parameter and the number of mature scrub present. If a consumer's energy falls below zero, it dies and is removed from the system.

Consumer reproduction patterns are seasonal and density-dependent (i.e., the chance of reproducing decreases as the population increases) (Sibly et al., 2002), informed by monthly stocking data from Knepp. Roe, red, and fallow deer have fawns from May-July, Longhorn cattle from April-June, and Tamworth pigs 2-4 months after the introduction of a boar. Exmoor ponies do not reproduce since no stallions are present in the Southern Block. If it is the correct month, there is a probability that each consumer will produce a single offspring. The offspring's energy is randomly set between 0 and the energy level of the parent.

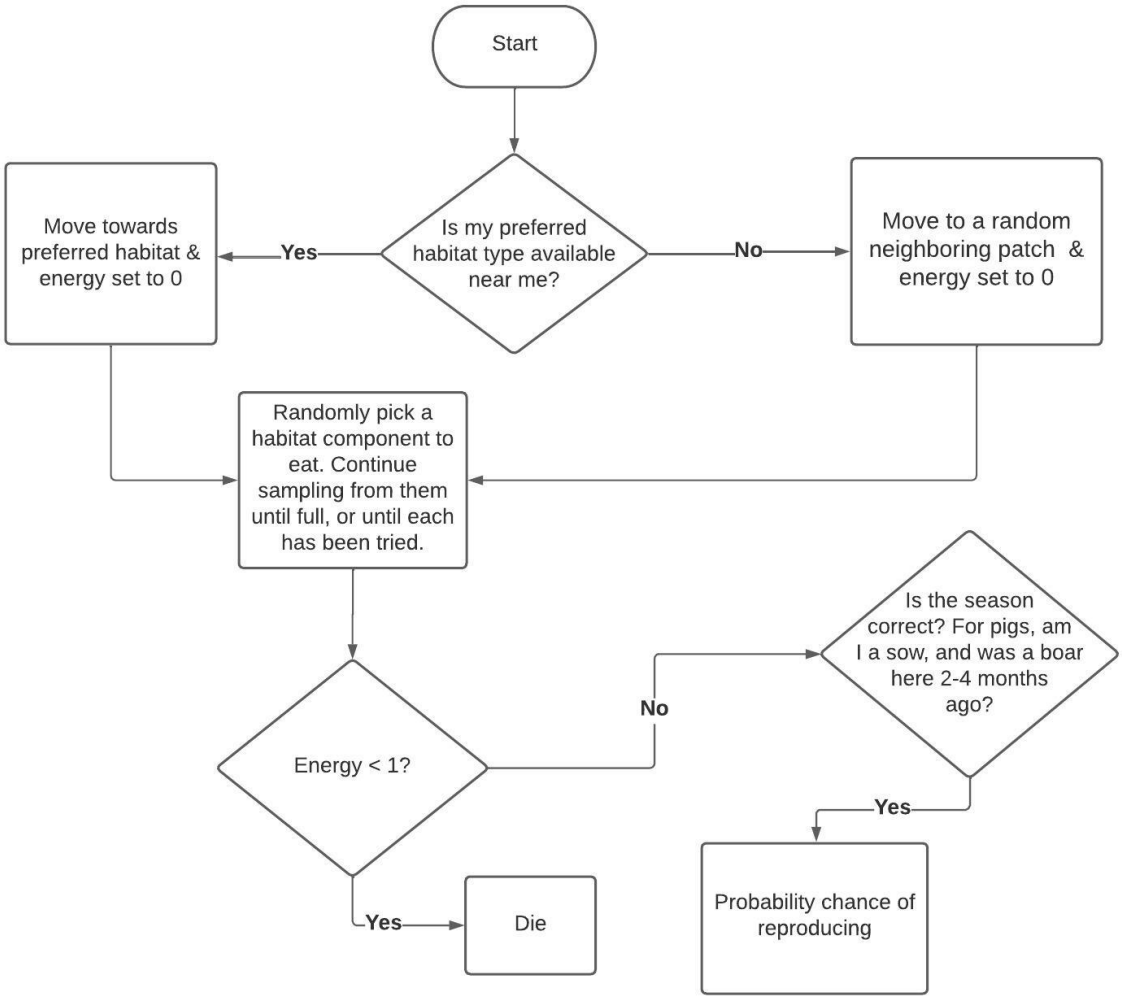


Figure 4.2*: Details of the consumer portion of the model. Diamond symbols show decisions, and rectangles actions.*

From 2005-2009, roe deer are the only consumers present in the model. In 2009, Exmoor ponies, Old English longhorn cattle, and Tamworth pigs are reintroduced, with fallow deer in 2010 and red deer in 2013. Over the course of each year, the reintroduced consumers' populations are controlled via culling or the temporary addition of breeding males. Data on each species' stocking density is available from Knepp on a yearly basis between 2009-2015, and monthly between 2015-2020 (Supporting Information). Whenever a cull or supplementation occurs, the consumer's population value is forced by adding to, or

subtracting from, the model-generated value until it equals the known number at that time-step. No data on the sex ratios of Tamworth pigs (boar, sow, piglets) are available between 2009 and 2015; it is assumed that there were between 4-8 sows, which was the minimum and maximum number in the following years, with the remaining being piglets.

Figure 4.3 shows the processes for habitat agents in the model. At every timestep, scrub and grassland have a percentage chance of being outcompeted by trees, and grassland has a percentage chance of being outcompeted by scrub; this is to simulate competition for light. If outcompeted or eaten by a consumer, the component is removed from the system. Trees and scrub have a probability of reproducing one sapling or young scrub to theirs or a neighbouring cell, and each component has a probability of regrowing or maturing, i.e., bare ground to grassland, young scrub to mature scrub, and saplings to trees. Each habitat agent can contain a maximum of 4000 mature trees and/or scrub (Fuentes-Montemayor et al., 2022), and 5000 saplings and/or young scrubs (Spracklen et al., 2013). To the authors' knowledge, no data is available for scrub density in the UK, so it was assumed to be equal to the maximum number of trees.

At the end of each timestep, the dominant habitat type of each agent is reassessed (scaled by the size of the cell). 750 trees per ha was assumed to be the start of a woodland in the model (Fuentes-Montemayor et al., 2022).

- **Bare ground**: < 750 trees; < 750 scrub; > 50% bare ground
- **Grassland**: < 750 trees; < 750 scrub; >= 50% grassland
- **Scrubland**: >= 750 scrub; < 750 trees

- **Woodland**: >= 750 trees

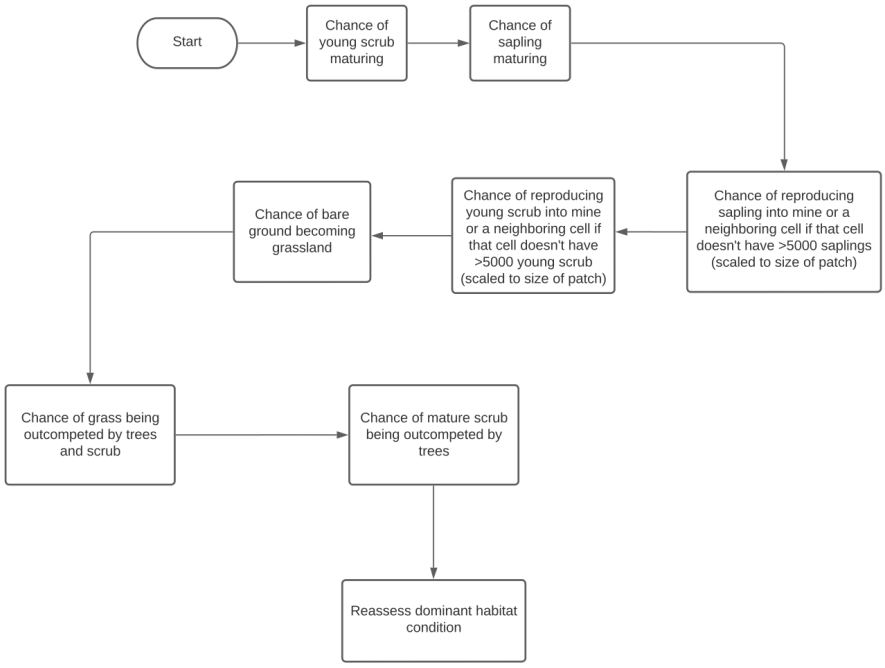


Figure 4.3: *Details of the habitat agent processes in the model, namely: reproduction, growth and maturation, and competition for light between habitat types.*

To initialise the model, the grid shapefile of the Southern Block is loaded, and each cell assigned to a habitat agent. Each habitat agent is then given a probability of being grassland, woodland, or scrubland dominant (89.9%, 4.3%, and 5.8%, respectively, based on the empirical data from Knepp) (Schulte to Bühne et al., 2022). Habitat agents are populated with vegetation components, the amount of which depends on their dominant condition. Cells <100m^2 in size are scaled by multiplying the abundance of the vegetation component by the size of the cell divided by the maximum possible area (100m^2). Grassland and bare ground areas are assumed not to have saplings and young scrub at the onset, as these were primarily agricultural fields and it is unlikely regeneration was

occurring. Roe deer, which were the only large herbivores present at Knepp in 2005, are then initialised at 12 individuals (Greenaway, 2006).

4.2.2 Calibration using genetic algorithms and ABC

To find simulations which match the data from Knepp, ABC with rejection sampling is used (Pritchard et al., 1999): many simulations are run that randomly sample from the parameters' prior distributions, and outputs are filtered against empirical data from the Knepp Estate. The posterior joint distribution of parameters is built using only the acceptable simulations, and the accepted parameters are then used to forecast and perform experiments on the system. However, the size of the parameter space (44 parameters) makes filtering too demanding to pass a simple accept/reject scheme. Optimization using genetic algorithms (GA) is therefore used (Bremermann, 1958; Fraser, 1957; Holland, 1975). The objective function specifically focuses on the first (March 2009) and last (May 2020) sets of filtering conditions for roe deer and habitats, and the final two filtering conditions for reintroduced species, so that each node has two observations targeted. The value *a* is minimized during the optimization process by varying all parameters (outlined in Supporting Information), to identify parameter sets that produce outputs (x) closely matching the data (y) for each species over time (Equation 4.1):

$$a = \min \sum_{i=1}^{N} ((x - y) / y)^2 \qquad \text{(Eqn 4.1)}$$

Where *N* is the number of outputs with associated filtering conditions. In the absence of any other food, consumer species are assumed to need >10 young scrub or saplings per month, and >3 trees or mature scrub per month to survive; these parameters are therefore bounded at 0-0.1 and 0-0.33 respectively. Young scrub and saplings are assumed to mature after 5-50 years (Murphy et al., 2022; Van Uytvanck et al., 2008). All other parameters are given wide bounds of 0-1.

To obtain a diversity of solutions and prevent collapse on a single local minimum, 100 separate GAs are run (Williams et al., 2020). The outputs are used to build a prior on which to run ABC to identify additional suitable parameters and model outputs, and to allow for the quantification of risks in terms of probability with respect to the posterior distribution. A wide uniform posterior is generated around the minimum and maximum distributions of the GA outputs, and 100,000 simulations are run by randomly drawing all parameter values from these distributions.

Several system- and individual- level reality checks are performed on the outputs to ensure the model behaves realistically (Supporting Information). Rejection sampling is then used with a $\boldsymbol{\delta}$ of 0.1% and the requirement of passing all habitat conditions. The second requirement exists because reintroduced grazers are continuously observed and have relatively more filters, so the top 0.1% of runs could be skewed towards correctly fitting these species. However, a key goal of the model is to assess the effect of grazers on habitat regeneration and composition; a usable model must therefore be able to correctly replicate

habitat dynamics. The posterior joint distribution of parameters is then built using only the accepted simulations.

A one-at-a-time sensitivity analysis (ten Broeke et al., 2016) is undertaken with the accepted simulations to assess how changes in parameters affect the number of filters passed. For the 'best' run, defined as the run that passes the most filtering conditions, each parameter is varied ±10, ±5, or ±1% around its values. The model is run with the new value, and the number of filters passed is recorded. The process is then run three more times with randomly-chosen accepted parameter sets to compare whether the sensitive parameters differ.

Table 4.1 shows the filtering conditions that simulations must pass through for roe deer and habitats. Reintroduced species' filtering conditions are targeted towards replicating observed natural population growth (outlined in the Supporting Information). To account for model noise, simulations that produce consumer values within the following bounds around the known values are assumed to have passed the filter:

- Exmoor pony: ±1 individual
- Fallow deer: ±25 individuals
- Longhorn cattle: ±25 individuals
- Red deer: ±5 individuals
- Tamworth pigs: ±10 individuals

Table 4.1: *The 2009 and 2020 filtering conditions for roe deer and habitat agents which each model run must pass through. These are informed by empirical data or, in some cases, expert on-site knowledge.*

Ecosystem element	Filtering conditions (2009)	Filtering conditions (2020)
Roe deer	12-40 individuals (Penny Green, *pers. comm*)	20-80 individuals (Penny Green, *pers. comm*)
Grassland	26.8-89.9% (wide bounds between the initial condition and lowest value in 2020 were used) (Schulte to Bühne et al., 2022)	26.8 +-10% (Schulte to Bühne et al., 2022)
Scrubland	4.3 - 51.8% (wide bounds between the initial condition and lowest value in 2020 were used) (Schulte to Bühne et al., 2022)	51.8 +- 10% (Schulte to Bühne et al., 2022)
Woodland	5.8% (Schulte to Bühne et al., 2022) - 17% (Müller, 2019)	21.5% +-10% (Schulte to Bühne et al., 2022; Wheldon, 2019)

4.2.3 Forecasting and experiments

Accepted simulations are used to forecast the range of potential future dynamics of the ecosystem in the long-term, and to explore questions relevant to rewilding management. The first experiment forecasts twenty-five years into the future (2020-2045) to assess how rewilding and current consumer stocking densities may continue to shape the ecosystem within a time-frame that is useful for decision-making. Reintroduced species are gradually culled back over the course of the year in these simulations to keep populations at approximately their 2020 values, which Knepp seeks to maintain (Penny Green, *pers comm*., 2021). The schedule of culling is: fallow deer between August and April (except for rutting season in October), cattle between June and February, red deer between August and April (except for rutting season in September and October), and pigs between December

and February (Knepp Estate, *unpublished data*). The difference between the model-generated values and the 2020 stocking density for each consumer species is calculated, and a random value between 1 and that number is culled. In the last month, they are culled back to the 2020 stocking values. Boars are temporarily added to the system each December for one month, and all culled pigs are assumed to be piglets. In March, consumers are 'restocked' to the desired densities if their populations fell below. This is then compared to what may have happened had species reintroductions never occurred.

The second explores how hypothetical future reintroductions could affect the ecosystem: fifty individuals of a new consumer species are added to the system, either European bison (large intermediate feeders) or European elk (large browsers) (Bocherens et al., 2015). A density of fifty individuals was chosen as it was assumed Knepp would want to reintroduce less than the 2020 population of the next largest consumer, Longhorn cattle. European bison are assumed to impact vegetation at rates equal to, or 10% above, Longhorn cattle. Bison reproduction probabilities are assumed to be +-10% that for Longhorn cattle. Elk are assumed to impact vegetation at rates equal to, or 10% below, red deer (the next largest deer species). Their reproduction probabilities are likewise assumed to be +-10% compared to red deer. Populations grow between April-June, which is when they are assumed to give birth. In March (the stock assessment month), they are culled back to fifty individuals. Finally, an optimisation experiment is run to explore how management can engineer the system towards a mosaic ecosystem containing at least 10% grassland.

4.3 Results

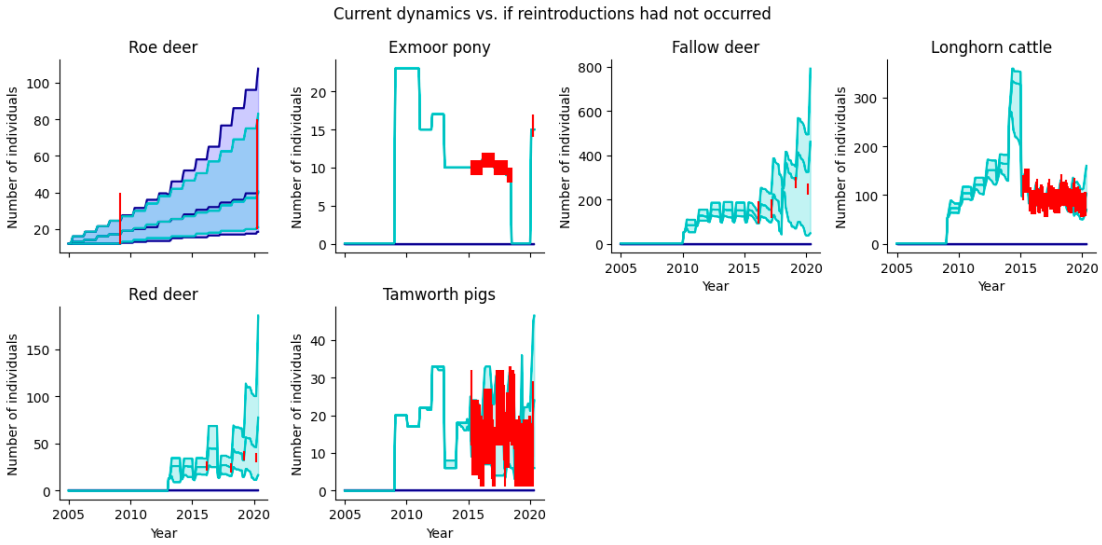
4.3.1 Accepted simulations

Outputs of the GA process are used to build a prior for running ABC to identify additional suitable models. Rejection sampling allowed simulations to be identified which pass many more filtering conditions: the GA parameter sets pass 2-94% of the filters, whereas the 'accepted' 100 models after rejection sampling pass 68-97%. Histograms for the parameters of the accepted runs are generated (Supporting Information); these suggest the search is primarily driven by a few parameters related to sapling, young scrub, and consumer reproduction, the chance that saplings and young scrub mature, and the probability that scrub is outcompeted by trees. Overall, distributions of the remaining parameters are relatively broad and uniform, suggesting many parameters are still uncertain (Supporting Information).

Results of the sensitivity test revealed that in three of the four runs, the parameter which most impacted the number of filters passed is the chance of reproducing saplings. Two of the runs shared six impactful parameters: the chance of cattle reproducing, the chance that grass will be outcompeted by trees, and four related to vegetation consumption, all of which are still relatively unknown based on their histogram outputs (amount of energy roe deer gain from grass and saplings, pigs gain from young scrub, and cows gain from young scrub) (Supporting Information).

4.3.2 Assessing the impacts of species reintroductions

Several experiments are run using the accepted parameters. The first assesses how rewilding has affected the ecosystem to-date, and predicts what may have occurred if species reintroductions had not taken place (hereafter referred to as the counterfactual) (Figure 4.4). With no reintroduced large herbivores, woodland was modelled to cover an area between 16 and 83%, while in the presence of reintroduced large herbivores woodland had a lower coverage of 12 to 32% (Figure 4.4). Thorny scrub has a much wider spread if no reintroduced large herbivores are present (1-74%) and the overall trend is declining, potentially due to competition with increasing woodland (Figure 4.4). These results suggest that large herbivores and omnivores are reducing vegetation succession, particularly in palatable species such as saplings and mature trees, which is consistent with the literature (Kowalczyk et al., 2011). Grassland and roe deer have similar trajectories whether reintroduced large herbivores are present or not (Figure 4.4).



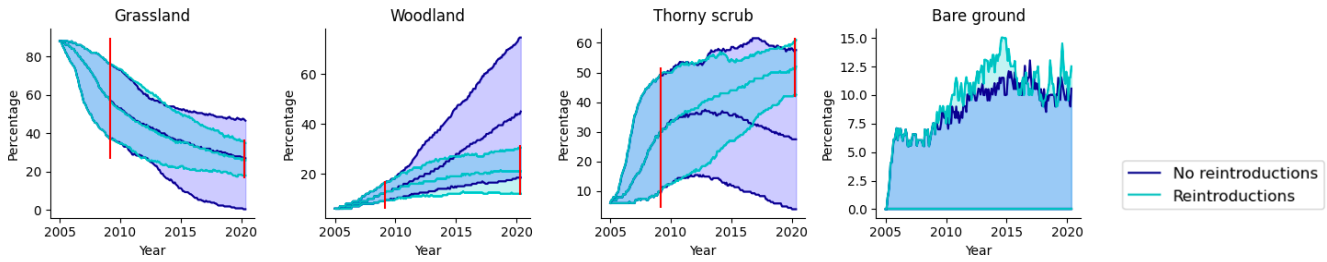
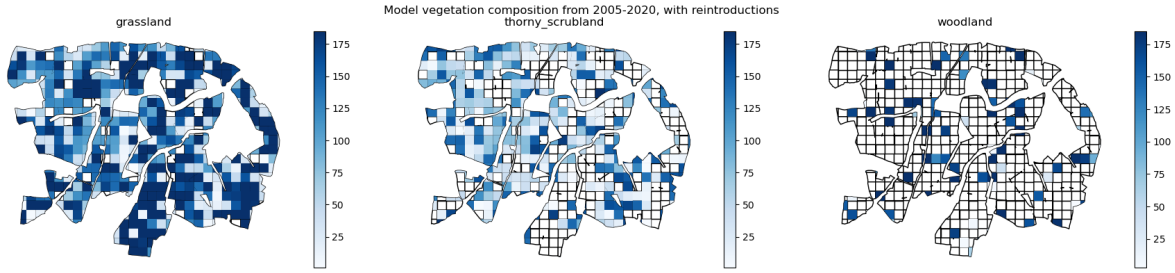


***Figure 4.4**: Time-series of Knepp ecosystem elements from 2005-2020 (light blue), compared to what may have occurred if species reintroductions had not taken place (dark blue). Top panels show the population dynamics (number of individuals) of the six consumer species. Bottom panels show the percentage of each of the four habitat types. Graphs show the median and 95th percentile (shaded areas). Red vertical lines show the filtering conditions which the runs must pass through.*

The 'best' parameter set, which passed 97% of filtering conditions, is then used to visualise the spatial composition of habitat components under current dynamics versus if no reintroduced species are present (Figure 4.5). In this particular run, grassland is much higher when the reintroduced large herbivores and omnivores are not present (55% vs. 30%) and thorny scrubland is reduced (24% vs. 58%). Since roe deer numbers are similar (40 vs. 33 individuals), this could be due to increased woodland coverage (21% vs. 12%) and high inter-habitat competition between trees and scrub. These results suggest that in the model, the behaviours of large herbivores and omnivores can foster environmental heterogeneity and may not have consistently negative impacts on woody vegetation.



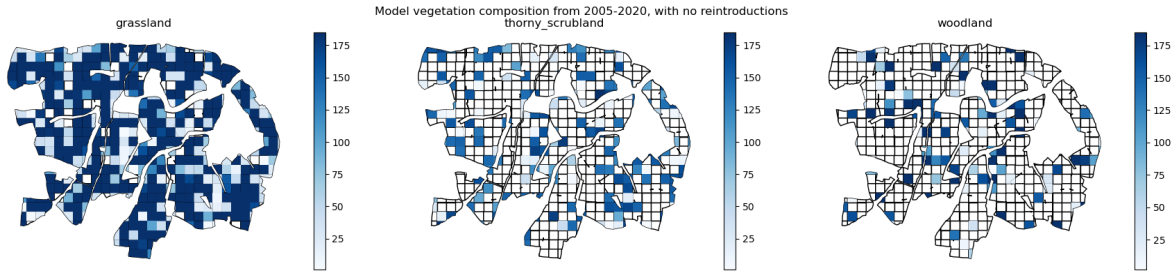


Figure 4.5: *Spatial heatmap of the best parameter set (i.e., the one which passes the most filtering conditions), showing Knepp's vegetation composition from 2005-2020 (top), compared to what may have occurred if species reintroductions had not taken place (bottom).*

Outputs also suggest that the system's spatial composition is affected by the relationship between thorny scrub and woodland: across all runs, woodland regenerated, on average, 42% of times in cells which were previously scrubland, as opposed to grassland or bare ground. In contrast, without reintroduced species present, woodland regenerated only 27% of the time in scrubland.

4.3.3 Species reintroduction and wood-pasture experiments

Next, the impacts of two hypothetical reintroductions - European bison (large intermediate feeders) and European elk (large browsers) - are explored and compared to current conditions, forecasted 25 years into the future. Since Knepp aims to have a mosaic ecosystem comprising woodland, scrubland, and grassland, the number of runs where a habitat type falls to < 10% is assessed (Table 2). The most frequent outcome of the models under current conditions is a reduction in grassland, with 60% of the runs leading to < 10% grassland in 25 years; this suggests that given the current model structure and parameters, herbivory levels may not be sufficient to maintain open areas in the long-term. Woodland

falls below 10% in 19% of the model runs, and thorny scrub in only 1%. Reintroducing European elk increases the chance of grassland and woodland collapsing (66% and 26%, respectively). Of the three scenarios, reintroducing European bison results in the fewest runs (54%) with grassland declining to less than 10%. Bison have an impact on woodland regeneration but less so than elk, with 23% of runs leading to collapse in 25 years.

Increasing stocking densities of the species currently at Knepp can impact the risk of grassland loss in unexpected, nonlinear ways, in some cases increasing the risk and in others reducing it (Table 4.2). High stocking densities (200% above current levels) can reduce the risk of grassland collapse to almost 50% of runs, but this may have unintended consequences on woodland (Table 4.2). To identify stocking densities which reduce the risk of grassland collapsing, optimisation with genetic algorithms is run with the 'best' parameter set (which has 2% grassland in 25 years). The objective function minimises the value a by varying all reintroduced species' stocking densities between 0-3x their current levels, to identify parameter sets that produce outputs (x) resulting in a target of 10% grassland (y) in 25 years (Equation 4.1). The optimal solution had increased stocking densities at varying amounts for all species: fallow deer and cattle densities were most increased to 667 and 194 individuals (an addition of 419 and 113, respectively, compared to current levels), followed by Exmoor ponies at 21 individuals (an addition of 6), red deer at 46 individuals (an addition of 11), and Tamworth pigs at 8 individuals (an addition of 1). These changes led to 10% grassland and no adverse impacts on woodland for the best run, but did not significantly change the long-term grassland outcomes when applied to all 100 accepted runs (Table 4.2).

Table 4.2: *Probability that any of the four habitat types (grassland, thorny scrub, woodland, or bare ground) will decline to <10% in 25 years, under six different scenarios.*

Scenario	Grassland	Thorny Scrub	Woodland	Bare ground
Current dynamics	60%	1%	19%	100%
Bison reintroduction	54%	1%	23%	100%
Elk reintroduction	66%	1%	26%	100%
Increasing stocking densities by 50%	59%	1%	22%	100%
Increasing stocking densities by 100%	67%	1%	32%	100%
Increasing stocking densities by 200%	53%	1%	44%	99%
Optimised stocking densities	59%	1%	30%	100%

Finally, to understand under what conditions herbivory is sufficient for maintaining open grassy areas, the accepted runs are split into two categories - those that have >10% grassland after 25 years and those that do not - and their inputs and outputs compared. Three parameters had divergent trends between the two groups, all of which were related to herbivory levels (Figure 4.6; full outputs in Supporting Information). These could therefore act as indicators as to whether open areas will be maintained in the long-term: if cows and fallow deer gain high amounts of energy from scrub and trees, respectively (meaning they eat relatively few), and if Tamworth pigs gain little energy from saplings (meaning they eat large amounts, in this case consuming up to 100 per month per individual), grassland is unlikely to collapse.

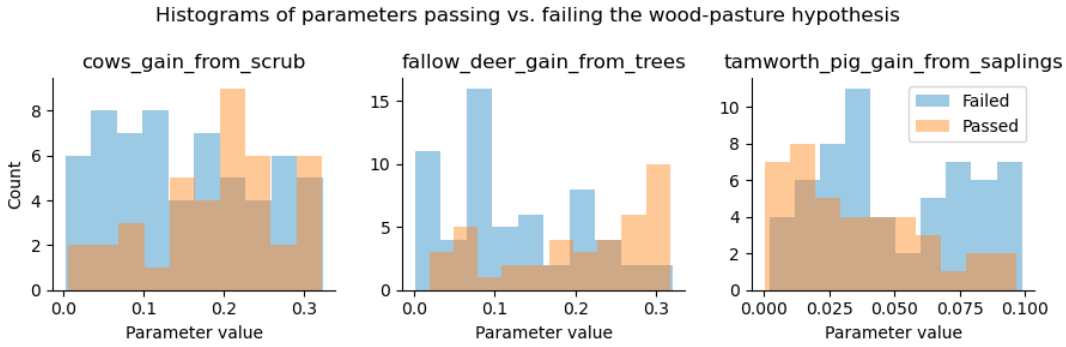


Figure 4.6: *Accepted runs are split into two categories: those that pass the wood-pasture hypothesis, and those that fail (defined as those that have <10% grassland after 25 years). This figure shows the histograms for the three parameter sets which diverge between these two categories: the energy cows gain from scrub, the energy fallow deer gain from trees, and the energy Tamworth pigs gain from saplings.*

Next, time-series outputs are compared. Results suggest that around the year 2021-2022, it will become apparent whether the system will have maintained grasslands or not (Figure **4.7**). In runs where the wood-pasture hypothesis fails, the system becomes dominated by approximately 80% thorny scrubland. In runs where it passes, there is still predominantly scrubland at about 50%, however there is a balanced mixture of the other habitat types with grassland maintained at about 20% and woodland at 30%.

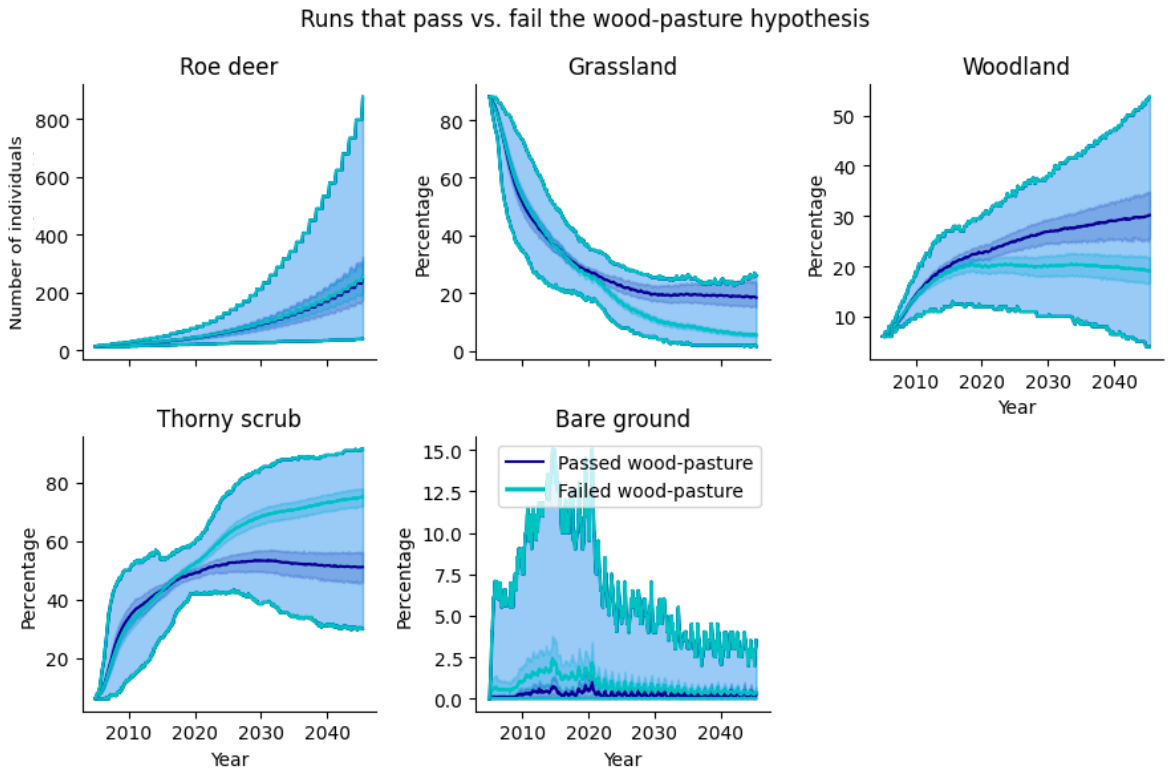


Figure 4.7*: When accepted runs are categorised as either passing (dark blue) the wood-pasture hypothesis or failing it (defined as those that have <10% grassland after 25 years; shown in light blue), the time-series dynamics will begin to diverge around the year 2021 for grassland, woodland, and thorny scrubland. Graphs show the median and 95th percentile (shaded areas).*

4.4 Discussion

In this paper, a new ABM using rejection sampling is developed to inform decision-making in a dynamic rewilding ecosystem. The methodology is an extension of the Lotka-Volterra ensemble ecosystem modelling (EEM) literature: both approaches involve generating many quantitative models, which are then filtered through plausible constraints to provide a range of future ecosystem states (Baker et al., 2016, 2019; Bode et al., 2017). The model can produce a range of outcomes consistent with the known information from Knepp and other

sites, namely, that large herbivores and omnivores can prevent the formation of woodland-dominant ecosystems and foster habitat heterogeneity through the maintenance of open or scrubby areas in the short to medium-term (Kowalczyk et al., 2021). If species reintroductions had not occurred, results indicate the ecosystem would trend towards becoming woodland-dominant in 25 years, with declines in scrubland and grassland. This outcome aligns with those found in a Lotka-Volterra based EEM of the Knepp Estate (Neil et al., in prep). Since habitat heterogeneity strongly correlates with species richness (Bakker et al., 2016; Stein et al., 2014), this result supports the idea that rewilding with large herbivores can positively impact biodiversity.

The ABM builds on the EEM literature by incorporating complexities such as space and heterogeneity of individuals. This was useful for capturing certain interactions and spatial components; for example, an interesting emergent behaviour appeared from the inclusion of spatial interactions between woodland and thorny scrub: with large herbivores present, woodland regenerated more frequently in areas of thorny scrubland, likely due to the protection that scrub provides saplings. Without large herbivores, woodland regenerates more frequently in grassland and bare ground. This is consistent with a rewilding experiment which found that sapling survival is higher in lawn than rough areas when herbivores are excluded (Smit et al., 2015). Spatial models may therefore be well-suited to assessing the wood-pasture hypothesis and formation of mosaic ecosystems. They also open the possibility of exploring spatial experiments, such as the importance of grazing refuges for wood-pasture formation (Smit et al., 2015). Additional granularity around herbivore movement and dietary preferences was also useful for understanding the impacts

of future reintroductions. Consumers in the model have different movements and dietary preferences and therefore differing impacts on vegetation; in some cases, this requires species-specific management interventions. For example, European elk increased the risk of grassland and woodland collapsing in the long-term, whereas bison increased the risk for woodland but decreased grassland.

An ensemble of genetic algorithm (GA) outputs and Approximate Bayesian Computation with rejection sampling are used to fit the model. GAs are typically run once to identify a single optimal set of input variables (D'heygere et al., 2006), but this approach can mean uncertainty is lost, and risk may therefore be underestimated. In a previous EEM of the Knepp Estate, manual searching was necessary during the calibration process, and only one GA output could be found that replicated the data while also passing simple 'reality check' constraints. By comparison, the 'if-then' statements driving the ABM provided freedom to write more sensible rules and simplified the calibration process: no manual searching was necessary despite being fit to the same data and exploring similar questions to the EEM, and 100 distinct GA outputs could be generated, providing a diversity of solutions and helping prevent collapse on a single local minimum. For moderately data-limited systems, relatively complex models such as ABMs therefore show promise for identifying solutions that can fit the available information. However, the added complexity of the ABM undoubtedly comes with the trade-off of added time and computational intensity to run simulations (Colon et al., 2015; Parunak et al., 1998).

At Knepp, the risk of losing open grassy areas is an important factor in decision-making around stocking densities and further species reintroductions. Model forecasting experiments suggest that current grazing regimes may not maintain open areas in the long term: over half the runs failed the wood-pasture hypothesis with grassland declining to <10%. The number of individual reintroduced species could be optimised to reduce this risk. Stocking densities are often expressed as Livestock Units (LUs) per hectare (ha); the Southern Block of Knepp had approximately 0.22 LUs/ha in 2020 and optimisation suggests an increase to 0.51/ha to reduce the risk of losing open grassy areas (Supplementary Information). This LU is slightly above those observed in other rewilding projects which typically range from 0.1-0.4 LUs/ha (Fløjgaard et al., 2022); however, it is within the range for moderate conservation grazing levels (Mason et al., 2019), and well below the average stocking rate for traditional agriculture in England such as lowland dairy farms (2 LUs/ha) (Natural England, 2009). Fallow deer had the highest percentage increase following optimisation (1.5 individuals/ha) but were still below the estimated natural numbers of 2.5 individuals/ha during the last interglacial in Britain (Fløjgaard et al., 2022).

Species reintroductions and changes in stocking densities can reduce the risk of losing grassland areas, but the outcomes are not always straightforward or intuitive: increasing all stocking densities did not consistently reduce the risk, nor did reintroducing any arbitrary large herbivore species. These quantitative predictions about the range of possible future system states can give managers a better understanding of uncertainty and possible negative outcomes, while informing future research. By comparing the runs which passed versus failed the wood-pasture hypothesis, three parameters and an approximate time-frame were

identified as indicators for the future state of grassland. Sensitivity analyses and histograms of the accepted parameters also revealed several parameters which are still relatively unknown but important for overall model results, particularly those related to consumers' impacts on vegetation components. Directing future research to these areas can help managers get the most benefit per observation and better predict future ecosystem states (LeBauer et al., 2013).

An advantage of this model is it can be easily updated to incorporate more data and qualitative expert opinion, including additional rejection filters for long-term projections. This is useful because experts may not have information about a single parameter, but can identify when some simulations are unrealistic. In this model, experts may identify a need for an additional filter for roe deer, as their populations have wide long-term posteriors. This gives the methodology considerable potential for continuous improvement and encouraging participative collaboration. With sufficient data, future work could fine-tune the parameters regarding consumer effects on vegetation, many of which the model is sensitive to, and incorporate more granular information on their behaviours and impacts. One option could be to estimate the metabolic rates of different reintroduced species (see Pedersen et al., 2023) and use these to inform herbivory parameter bounds during optimisation. Similarly, collective vegetation consumption rates by large herbivores, as estimated by Pedersen et al. (2023), could be used to validate and refine model assumptions, or act as a filtering condition to ensure future model runs are within realistic bounds. The ABM presented here captures different foraging preferences of consumers and therefore their variable impacts on wood-pasture formation (Lamoot et al., 2005), but

additional species-specific behaviours such as coppicing by Longhorn cattle, debarking by red deer, and rootling by Tamworth pigs, can also have large impacts on the ecosystem while potentially leading to interesting emergent properties, such as plant regeneration occurring primarily in bare soil exposed by rootling (Tree, 2018).

Spatial movement decisions could also be fine-tuned in future. The model currently assumes that consumers move towards a preferred hectare habitat patch at each monthly-time step, but this is likely overly simplistic. A rich literature in movement ecology indicates that individual consumer movement decisions can be influenced by factors such as seasonal variations in resource availability and memories of the landscape over time (Jeltsch et al., 2013), risk avoidance and human impacts (Bull et al., 2019), energy costs (Berti et al., 2022), and densities of other competitors present in a given location (Morales et al., 2010). Movement types also vary depending on different needs and goals (i.e., breeding dispersal, migration, foraging, nomadic versus home range movements) (Jeltsch et al., 2013; Schlägel et al., 2020) and are impacted by the dynamics of social groups (Morales et al., 2010). Since the reintroduced species at Knepp typically live in herds, movement decision-making may be more collective than is currently modelled. Incorporating these complexities could lead to the emergence of feedback loops where consumer movements impact the environment, in turn influencing future movements, potentially with broader impacts on the ecosystem (Bull et al., 2019; Jeltsch et al., 2013; Schlägel et al., 2020).

The methodology presented here can also be used with variegated data, although a potential limitation of this is that it allows for some user choice. For example, the chosen acceptable bounds for reintroduced consumer populations and the thresholds for dominant habitat category were largely arbitrary, as it is difficult to determine exactly how many trees and shrubs it takes to make a woodland or shrubland. Future work could integrate further data and expert knowledge to revise these assumptions, and explore model sensitivity to them. Another opportunity for further research is to run the models until they reach equilibrium, to assess whether, for example, grassland can naturally increase again in the long-term without need for intervention, and how long this may take to occur. In this case, stocking density interventions at Knepp are ongoing and relatively frequent to facilitate a shifting mosaic of wood-pasture, so a collapse in a vegetation component at any time-point was considered undesirable, and a shorter time-frame of 25 years was chosen to ensure utility for management decision-making.

The model presented in this study confers several advantages for rewilding science and management: it can make use of limited and variegated data to capture spatial interactions between ecosystem components and assess the range of possible futures under different interventions. The methodology is therefore promising for rewilding planning and decision-making, particularly for projects which are interested in the wood-pasture hypothesis or other spatially-dependent interactions. For systems like Knepp, which have time-series data in addition to expert knowledge, simple random searches with rejection using the EEM Lotka-Volterra-based approach could be difficult; ABMs can improve the calibration process and identify a wider range of suitable parameter sets. Since concerns have been

raised about a lack of research and empirical evidence on the potential outcomes of rewilding (Nogués-Bravo et al., 2016; Svenning et al., 2016), the increased use of models such as these can assist with increasing the evidence-base of the field.

Summary: Paper 2

Paper 2 focusses on developing a spatial agent-based model (ABM) using rejection sampling to explore the ecosystem-wide effects of different management interventions at the Knepp Estate. There are some similarities between the outputs of the ABM and the ODE (Paper 1): both found, for example, that grazing with large herbivores can foster wood-pasture ecosystems and prevent the system from becoming woodland dominant, and reintroducing European bison or elk can enhance environmental heterogeneity. Both models make use of limited and variegated data to capture interactions between ecosystem components and are therefore promising for rewilding planning and decision-making.

The ABM was more computationally intensive than the ODE, but overall, it was found to have several advantages when applied to a system, like Knepp, with relatively good data availability. The calibration process was easier than the ODE, which facilitated the identification of many different acceptable parameter sets. This allowed the model to provide quantitative predictions about the range of possible future system states, identifying risks and uncertainties with future management interventions and indicators for whether mosaic wood-pasture ecosystems will be maintained in the long-term. The inclusion of space was useful for capturing interactions and dynamics relevant to the wood-pasture hypothesis, and it revealed an emergent behaviour: with large herbivores present, woodland regenerated more frequently in thorny scrubland than grassland or bare ground. This supports the idea that thorny scrubland can protect saplings from herbivory. Additional granularity around herbivore movements and dietary preferences was also useful for understanding the impacts of future reintroductions; for example,

European elk was found to increase the risk of grassland and woodland collapsing in the long-term, whereas bison increased the risk for woodland but decreased grassland.

Direct comparisons between model methodologies are uncommon. To gain a better understanding of the differences between the ODE and ABM, in Paper 3 they are both applied to questions about resilience, and their outputs compared to assess under what conditions they are meaningfully different. In Paper 2, it is noted that snapshots of the medium- to long-term may not be representative of the system's final state, and that roe deer may need an additional long-term filter to prevent population explosions. Therefore, in Paper 3 both models are run to equilibrium to assess their end conditions, and additional long-term filters are added.

4.5 Supporting Information

1. Model description following the ODD protocol

A model of the Knepp Estate is developed using Mesa, an ABM framework in Python (Kazil et al., 2020). The code is open access and freely available on GitHub (Neil et al., 2022a). The model description follows the ODD (Overview, Design Concepts, Details) protocol for describing agent-based models (Grimm et al., 2006, 2010).

a. Purpose

The purpose of the model is to simulate the dynamics of interacting species at the Knepp Estate, using a mixture of quantitative time-series data and qualitative expert knowledge,

and to answer questions relevant to rewilding decision-making, such as: how have species reintroductions impacted the ecosystem, and how might they continue to impact it in the future? What impact might future species reintroductions, such as European bison, have? How can the system be engineered towards a particular end goal, such as having a mosaic habitat in the long-term?

b. Entities, state variables, and scales

Knepp is divided into three blocks, Northern, Middle, and Southern, each of which varies in management strategy, herbivore assemblage and density, and the year in which rewilding began. The model focuses on the 450-hectare Southern Block, which has relatively more time-series data as well as the full suite of reintroduced herbivores. The model proceeds in discrete steps of one month, and covers three time-periods: the years before grazers were reintroduced (2005-2009), the years after reintroductions (2009-2020), and future projections (2020-2070). Years are assumed to begin in March, which is when the annual livestock count takes place.

There are seven model entities; six are consumers: roe, fallow, and red deer, Old English longhorn cattle, Exmoor ponies, and Tamworth pigs, and the seventh is a habitat entity. Habitats are defined by converting a shapefile of the Southern Block to $100m^2$ (1 hectare) grid cells, and classifying each as an individual agent comprising a percentage of grassland or bare ground, a number of scrub plants and trees (sapling and mature), and an overall dominant habitat condition (grassland, scrubland, woodland, or bare ground). Grazers move

within and between habitat agents, and are characterised by their location and energy levels. Pigs are additionally characterised by a sex and age description, being either a boar, sow, or piglet.

c. Process overview and scheduling

At the beginning of each timestep, consumers lose 1 energy, and move towards their preferred habitat; if it is not available, they move randomly. Roe deer are browsers, preferring scrubland and woodland year-round in the model. Fallow and red deer are intermediate feeders, preferring grassland in the spring and summer months but randomly picking one of the habitat types to move to in the autumn and winter months. Exmoor ponies and Longhorn cattle are grazers and choose grassland year-round if available. Tamworth pigs are omnivores and assumed to randomly choose any habitat, where they rootle in the soil in search of roots and invertebrates.

Once they have moved, consumers randomly choose a vegetation component (i.e., grassland, saplings, young scrub, mature trees or scrub) in that cell and consume as much as they need for their energy to equal 1. If there is not enough of the chosen vegetation to fill their energy, they randomly choose a different component and consume it, stopping when their energy levels reach 1, or when all vegetation components in the cell have been sampled. Energy levels are capped at 1 to ensure consumers cannot survive beyond one time-step if they are unable to find any food. Scrub is assumed to facilitate sapling regeneration by preventing herbivory (King, 2019; Salek et al., 2019; Van Uytvanck et al.,

2008); therefore, if consumers choose to eat saplings, the number removed from the system is scaled according to a 'facilitation' parameter and the number of mature scrub present. If a consumer's energy falls below zero, it dies and is removed from the system.

Consumer reproduction patterns are seasonal and density-dependent (i.e., the chance of reproducing decreases as the population increases), informed by monthly stocking data from Knepp. Roe, red, and fallow deer have fawns from May-July, Longhorn cattle from April-June, and Tamworth pigs 2-4 months after the introduction of a boar. Exmoor ponies do not reproduce since no stallions are present in the Southern Block. If it is the correct month, there is a probability that each consumer will produce a single offspring. The offspring's energy is set randomly between 0 and the parent energy levels.

From 2005-2009, roe deer are the only consumers present in the model. In 2009, Exmoor ponies, Old English longhorn cattle, and Tamworth pigs are reintroduced, with fallow deer in 2010 and red deer in 2013. Over the course of each year, the reintroduced consumers' populations are controlled via culling or the temporary addition of breeding males. Data on each species' stocking density is available from Knepp on a yearly basis between 2009-2015, and monthly between 2015-2020 (Supporting Information). Whenever a cull or supplementation occurs, the consumer's population value is forced by adding to, or subtracting from, the model-generated value until it equals the known number at that time-step. No data on the sex ratios of Tamworth pigs (boar, sow, piglets) are available between 2009 and 2015; it is assumed that there were between 4-8 sows, which was the minimum and maximum number in the following years, with the remaining being piglets.

At every timestep, scrub and grassland have a percentage chance of being outcompeted by trees, and grassland has a percentage chance of being outcompeted by scrub; this is to simulate competition for light. If outcompeted or eaten by a consumer, the component is removed from the system. Trees and scrub have a probability of reproducing one sapling or young scrub to theirs or a neighbouring cell, and each component has a probability of regrowing or maturing, i.e., bare ground to grassland, young scrub to mature scrub, and saplings to trees. Each habitat agent can contain a maximum of 4000 mature trees and/or scrub (Fuentes-Montemayor et al., 2022), and 5000 saplings and/or young scrubs (Spracklen et al., 2013). To the authors' knowledge, no data is available for scrub density in the UK, so it was assumed to be equal to the maximum number of trees.

At the end of each timestep, the dominant habitat type of each agent is reassessed (scaled by the size of the cell). 750 trees per ha was assumed to be the start of a woodland in the model (Fuentes-Montemayor et al., 2022).

- **Bare ground**: < 750 trees; < 750 scrub; > 50% bare ground
- **Grassland**: < 750 trees; < 750 scrub; >= 50% grassland
- **Scrubland**: >= 750 scrub; < 750 trees
- **Woodland**: >= 750 trees

d. Design concepts

i. Basic principles

The model is built on the assumption that large consumers are the primary drivers of landscape composition by preventing regeneration via browsing pressure, therefore helping to maintain a dynamic mosaic ecosystem of grassland, scrubland, and woodland. This is a leading rationale for many rewilding projects in Europe (Vera, 2000).

ii. Emergence

Spatial habitat composition and the rate at which scrub and woodland regenerate emerge from adaptive, seasonal decisions made by consumers regarding which habitat type to move towards, and which component(s) of the habitat to eat, as well as intra-habitat spatial dynamics of competition and facilitation.

iii. Objectives

The objective is to identify simulations which can replicate the time-series data from Knepp, while also behaving realistically (as defined by qualitative expert knowledge, and several system- and individual-level 'reality checks'). These acceptable simulations are then used to forecast and answer questions related to rewilding management and decision-making.

iv. Sensing

Consumers are assumed to sense the dominant habitat type of the cell it occupies, and its neighbours.

v. Interaction

Consumers directly interact with primary producers via herbivory, and indirectly with each other via competition for food. Primary producers directly interact with each other via competition and/or facilitation.

vi. Stochasticity

Fine-scale movements related to species-level habitat preferences, the spatial composition of habitat types and grazers upon initialisation, and habitat composition driven by herbivory, competition, and facilitation, are all stochastic.

vii. Collectives

Habitat agents are super-individuals representing a given number of mature trees, saplings, mature and young scrub, and percentage of grassland and bare ground.

viii. Observation

Consumer populations and the percentage of dominant habitat types (i.e., grassland, woodland, scrubland, bare ground) are recorded monthly to compare to the time-series data from Knepp. The spatial locations of agents, the number or percentage of vegetation components within habitat agents, and causes of mortality are also recorded at each time-step to perform 'reality checks' and ensure the model is behaving as expected.

e. Initialization

To initialise the model, the grid shapefile of the Southern Block is loaded, and each cell assigned to a habitat agent. Each habitat agent is then given a probability of being grassland, woodland, or scrubland dominant (89.9%, 4.3%, and 5.8%, respectively) (Schulte to Bühne et al., 2022). Habitat agents are populated with vegetation components, the amount of which depends on their dominant condition, scaled to the size of the cell. Grassland and bare ground areas are assumed not to have saplings and young scrub at the onset, as these were primarily agricultural fields and it is unlikely regeneration was occurring. Roe deer, which were the only large herbivores present at Knepp in 2005, are then initialised at 12 individuals (Greenaway, 2006).

2. Model variables

There are 44 variables used in the model; their descriptions and values are outlined in Table A4.1.

Table A4.1: Descriptions of the variables used in the model, and the range of their values.

Entity	Description	Values
Consumers	Initial energy	0-1
	Sex [Tamworth pigs only]	Sow, boar, piglet
	Energy gained from consuming 1% grassland	0-1
	Energy gained from consuming 1 mature tree	0-1
	Energy gained from consuming 1 mature scrub	0-1
	Energy gained from consuming 1 sapling	0-1
	Energy gained from consuming 1 young scrub	0-1
	Probability of reproducing	Percent
Habitat	Dominant condition	Grassland, scrubland, woodland, bare ground
	Number of mature trees	0-400
	Number of saplings	0-5,000
	Number of mature scrub	0-800
	Number of young scrub	0-5,000
	Amount grassland	Percent
	Amount bare ground	Percent
	Chance of tree spawning a sapling	Percent
	Chance of scrub spawning young scrub	Percent
	Chance of grass regrowing	Percent
	Chance of sapling becoming mature	Percent
	Chance of young scrub becoming mature	Percent
	Chance of mature scrub being outcompeted by trees	Percent
	Chance of grass being outcompeted by trees	Percent
	Chance of grass being outcompeted by mature scrub	Percent
	Chance of mature scrub facilitating saplings	Percent

3. Filtering conditions and forcings

The forcings and filtering conditions for reintroduced species are shown in Table A4.2. Between 2009 and 2015, data is only available on an annual basis, and the number of animals culled and born each month are not known; there are therefore no filtering conditions for consumers' population growth during this time-frame. Between 2015 and 2020, reintroduced species generally have monthly filters. However, red and fallow deer have one filtering condition per year, as their stock assessments only occur in March (i.e., the number of individuals culled each month is recorded, but no population growth is observed until the annual stock assessment).

Table A4.2: Model filtering conditions (black) and forcings (red).
** It's not clear how many were culled to arrive at this value (due to lack of data on population growth over the course of the year), so the number is a forcing rather than a filtering condition.*

***The model was never able to pass this filtering condition, and the number seems too high to constitute natural population growth. It is possible there was a stock supplement during this time. The number is therefore a forcing rather than a filtering condition.*

	Exmoor pony	**Fallow deer**	**Longhorn cattle**	**Red deer**	**Tamworth pigs**
2009 March	23	0	53	0	20
2010 March	13	42	77	0	17
2011 March	15	81	92	0	22
2012 March	17	100	116	0	33
2013 March	10	100	129	13	6
2014 March Jan Feb	10	100	264	13	18 +1 boar -1 boar
2015 March April May June July Aug Sept Oct Nov Dec Jan Feb	10 9-11 9-11 9-11 9-11 9-11 9-11 9-11 9-11 9-11 9-11 9-11 [+1]	100 -2 culled -2 culled -3 culled -7 culled -6 culled -7 culled -10 culled	107 90-140 104-154 [-5 culls] 104-154 104-154 104-154 [+1 added] 105-155 [-39 culled] 66-116 66-116 [-5 culled] 61-111 61-111 61-111	13	18 [-1 culled] 12-32 [-8 culled] 4-24 4-24 4-24 4-24 4-24 4-24 [-1 culled] 3-23 3-23 [-4 culled, +1 boar added] 1-20 [-2 culled] 1-20 [-3 culled, -1 boar, +3 added]

2016					
March	10-12	115-165	61-111 [+1 added]	21-31	1-19
April	10-12		78-128 [-2 culled]		1-19
May	10-12		83-133 [-30 culled, +4 added]		7-27
June	10-12		64-114 [-2 culled]		7-27
July	10-12	-5 culled	62-112		7-27
Aug	10-12		62-112 [-13 culled, +22 added]		7-27
Sept	10-12		72-122		7-27
Oct	10-12	-3 culled	72-122 [-5 culled]		7-27
Nov	10-12	-9 culled	67-117 [-13 culled]		7-27[-4 culled]
Dec	10-12		54-104		3-23 [-4 culled +1 boar]
Jan	10-12	-8 culled	54-104		1-19 [-2 culled, -1 boar]
Feb	10-12 [-1]		54-104		1-17
2017					
March	9-11	140-190	54-104 [+3 added]	14*	1-17
April	9-11		75-125		12-32
May	9-11		84-134 [-24 culled, +3 added]		12-32
June	9-11		69-119		12-32
July	9-11	-16 culled	69-119		12-32
Aug	9-11	-5 culled	69-119 [-25 culled, +23 added]		12-32
Sept	9-11	-4 culled	65-115 [-2 culled]		12-32
Oct	9-11	-2 culled	63-113		12-32
Nov	9-11	-46 culled	63-113	-1 culled	12-32 [-4 culled]
Dec	9-11		63-113		8-28 [-9 culled, +1 boar]
Jan	9-11	-14 culled	63-113	-1 culled	1-21 [-1 boar]
Feb	9-11 [-1]		63-113		6-26
2018					
March	8-10	251**	63-113 [+1 added]	19-29	6-26
April	8-10		76-126		6-26
May	8-10		92-142 [-20 culled, +2 added]		13-33
June	8-10		78-128	-1 culled	13-33
July	8-10 [-9]	-15 culled	78-128 [-1 culled]	-1 culled	12-32 [-1 culled]
Aug	0	-19 culled	77-127 [-16 culled, +20 added]		12-32
Sept		-4 culled	81-131 [-5 culled]		12-32
Oct			76-126 [-7 culled]		11-31 [-1 culled]
Nov		-19 culled	68-118 [-5 culled, +1 added]	-1 culled	1-19 [-12 culled]
Dec			64-114		1-19
Jan			64-114 [-2 culled]		1-19 [+1 boar]
Feb		-7 culled	62-112	-7 culled	1-20

2019					
March		253-303	62-112	32-42	1-19 [-1 boar]
April			76-126		1-18
May			85-135 [-28 culled]		1-18
June			64-114 [-2 culled, +6 added]		1-18 [-27 culled]
July			66-116		1-19
Aug		-15 culled	66-116 [-23 culled, +25 added]		1-19
Sept			68-118 [-5 culled]		1-19
Oct		-7 culled	63-113 [-1 culled]	-3 culled	1-19
Nov		-12 culled	62-112 [-7 culled]	-4 culled	1-19 [+1 boar]
Dec		-24 culled	55-105		1-20
Jan		-12 culled	55-105 [-1 culled]	-2 culled	1-20 [-1 culled, -1 boar]
Feb			54-104 [-1 culled, +3 added]		1-18 [-1 culled]
2020					
March	15	222-272	56-106	30-40	1-17
April	14-16		56-106		1-17
May	14-16		56-106		9-29

4. Genetic Algorithm – 100 outputs

The correlation matrix and histograms for the 100 GA outputs are provided in Figures A4.1 and A4.2, respectively. 2-92% of filtering conditions were passed. The best fit (indicated with the red vertical line) is typically towards the middle of the distribution, suggesting these are likely good estimates of uncertainty. Consumers generally have negative correlations with other consumers regarding the amount of energy they gain from vegetation components.



Figure A4.1: Correlation matrix for the 100 genetic algorithm outputs.



Figure A4.2: Histograms for the 100 accepted genetic algorithm outputs. The 'best fit' result is outlined with a red vertical line.

5. ‘Accepted’ simulation outputs

Figure A4.3 shows the percentage of filtering conditions passed by each of the runs, and whether the run was accepted or rejected following the Approximate Bayesian Computation process. Some runs were rejected despite passing many filtering conditions because they did not successfully pass both habitat filters (this was the other model requirement as outlined in the manuscript).

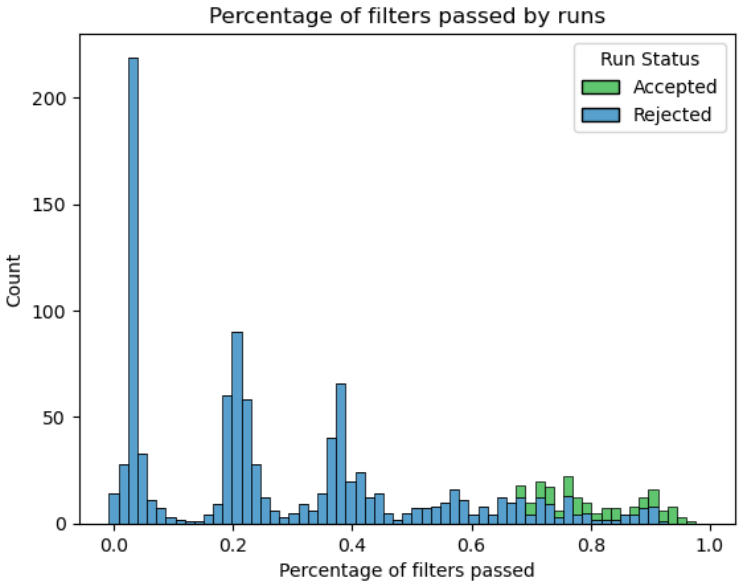


Figure A4.3: Percentage of filtering conditions passed by the runs. The 100 accepted simulations passed 68-97%.

Histograms are, for the most part, relatively broad and uniform, showing that some parameters are still unknown (Figure A4.4).

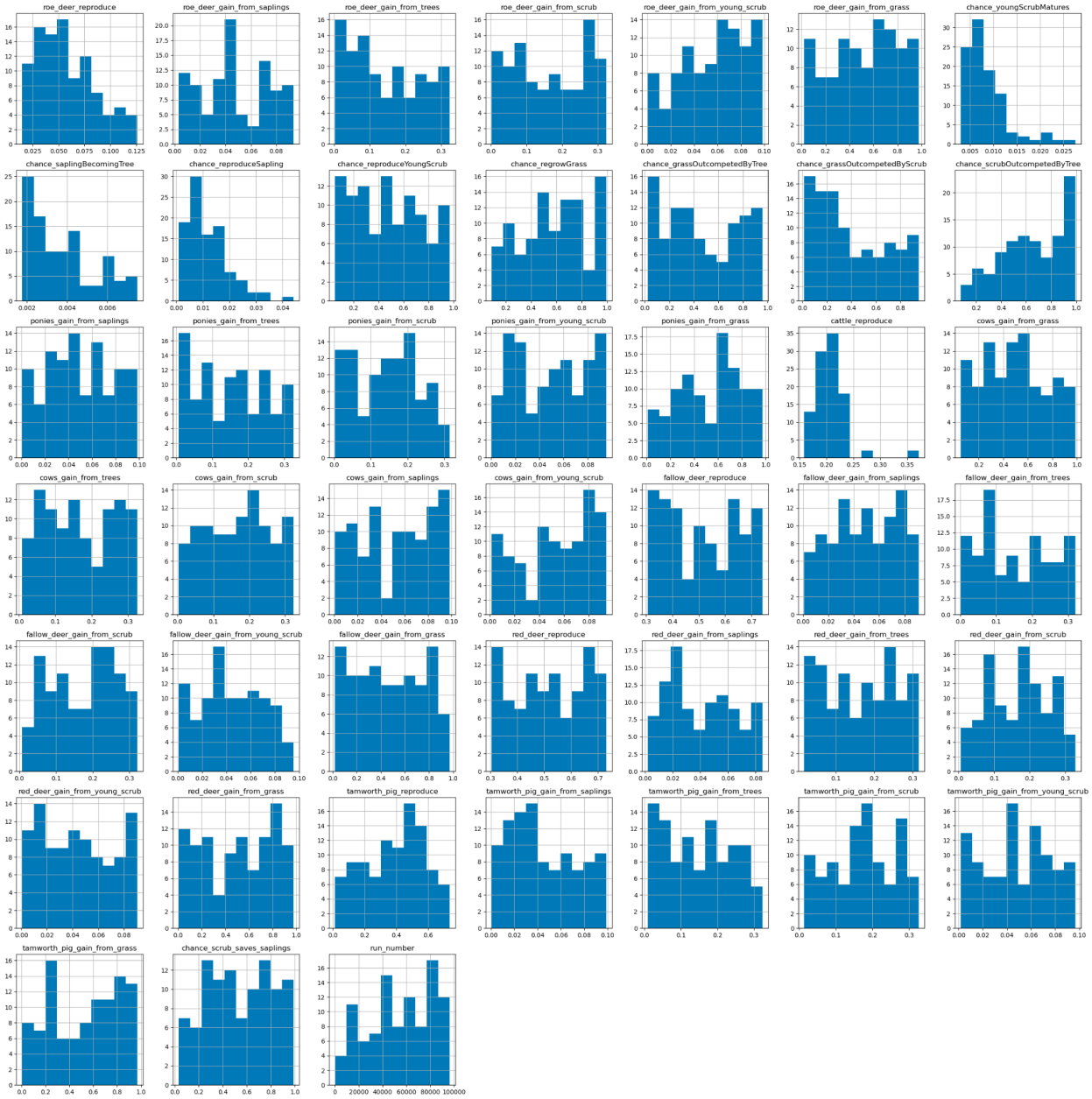


Figure A4.4: Histograms of the 100 accepted parameter sets.

Unlike the correlation matrix of the GA outputs, there are no patterns of negative correlations between consumers regarding the amount of energy they gain from vegetation components from the ABC outputs (Figure A4.5).



Figure A4.5: Correlation matrix of the 100 accepted parameter sets.

6. Validation of accepted parameter sets

As a first-order validation of the model, several system-level and/or individual-level reality checks' are performed using the output parameters, to ensure the model behaves as expected

(Sargent, 2013). These checks are based on empirically known features of the system, that if not present in the model, would signal significant problems. They are as follows:

1. If all primary producers are removed, consumers should decline to zero within one time-step. This is based on simple physiological needs of the animals (Figure A4.6).

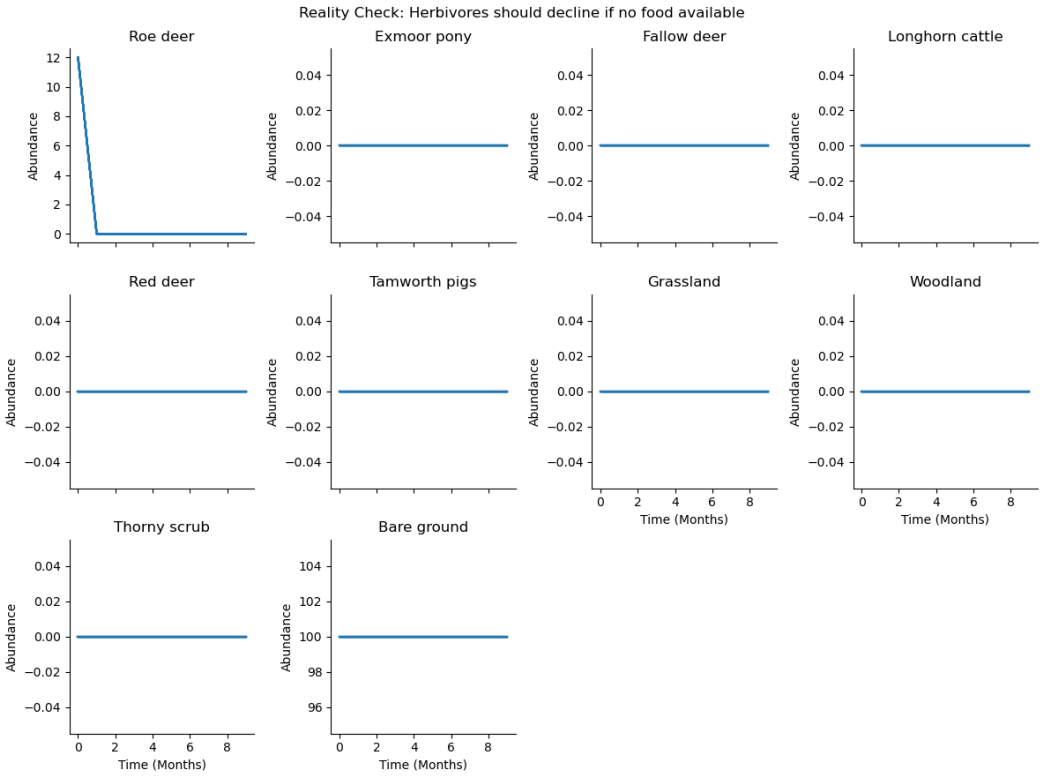


Figure A4.6:In the first reality check, all herbivore populations should decline towards zero in the absence of any food.

2. If the model is run for 50 years with no herbivory, thorny scrubland should increase at the onset, but then eventually be outcompeted by woodland. This is based on expert knowledge and empirical evidence from other rewilding projects in England (Broughton et al., 2021) (Figure A4.7).

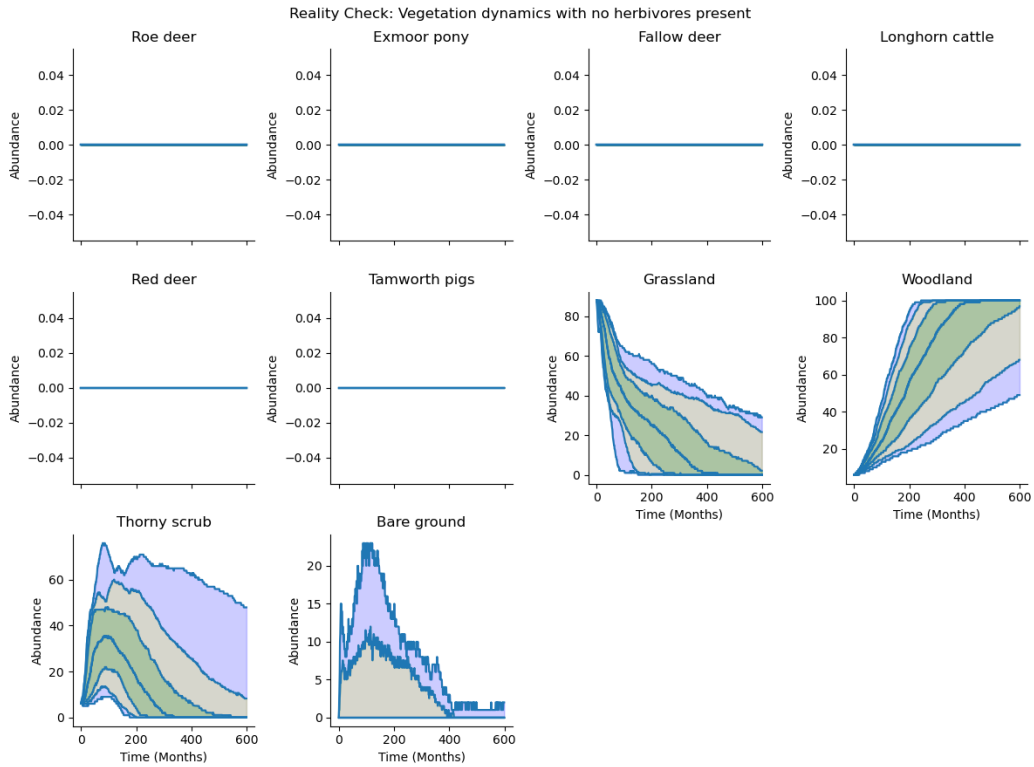


Figure A4.7: In reality check 2, in the absence of herbivory, thorny scrub should increase at the outset but eventually be outcompeted by woodland.

3. If herbivores are overloaded into the system (stocking densities set to 5x higher), woodland should decline. This is based on studies in the UK which show excessive grazing can reduce structural complexity and species richness, and suppress tree regeneration (Anderson & Radford, 1994; Kinnaird, 1974; Pollock et al., 2005). (Figure A4.8).

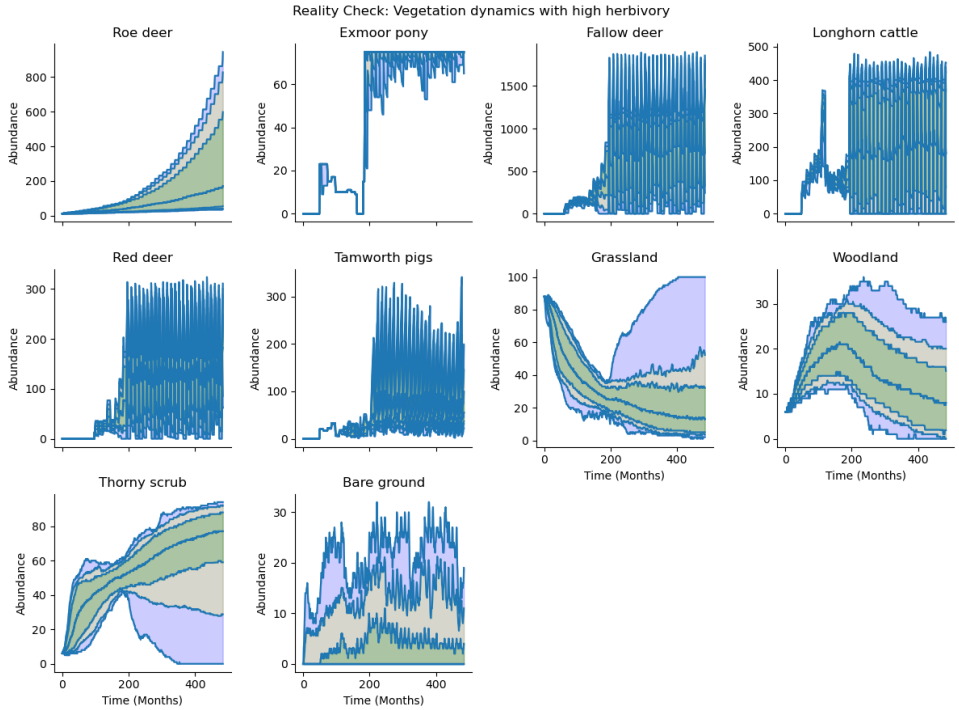
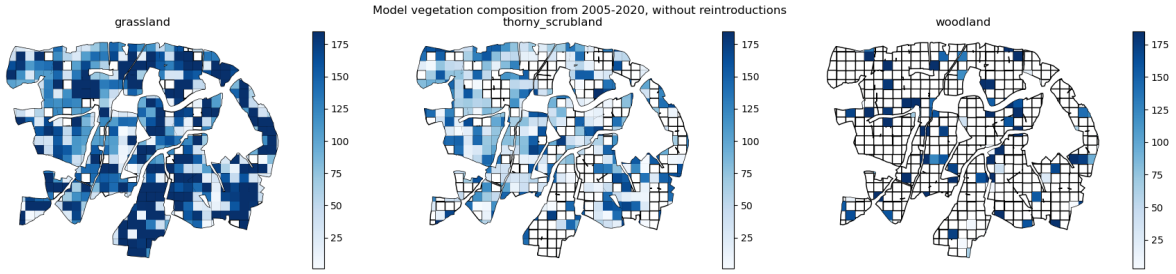


Figure A4.8: In reality check 3, woodland should decline with an overabundance of herbivores.

4. Grazers and browsers should search for their preferred habitat (grassland and woodland/scrubland, respectively), and stay in these areas if available. This is based on the dietary preferences of the consumers present at Knepp (Rewilding Europe, 2015) (Figure A4.9).



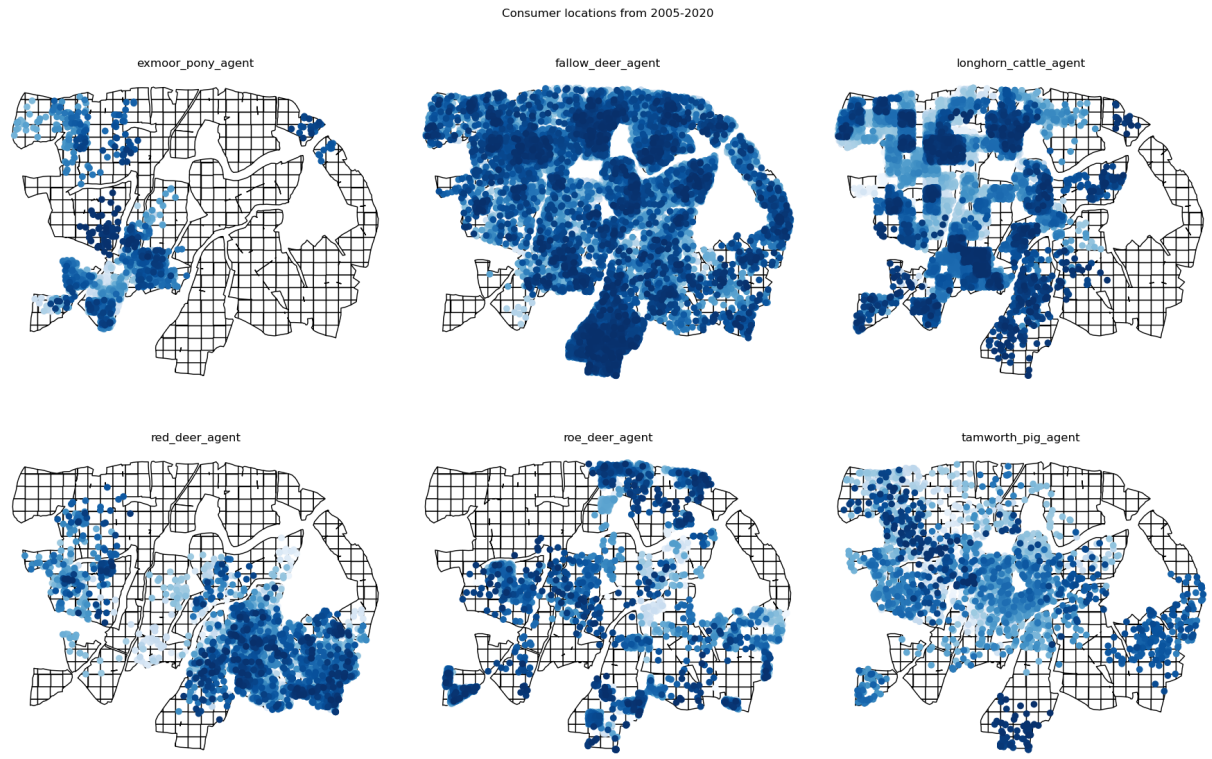
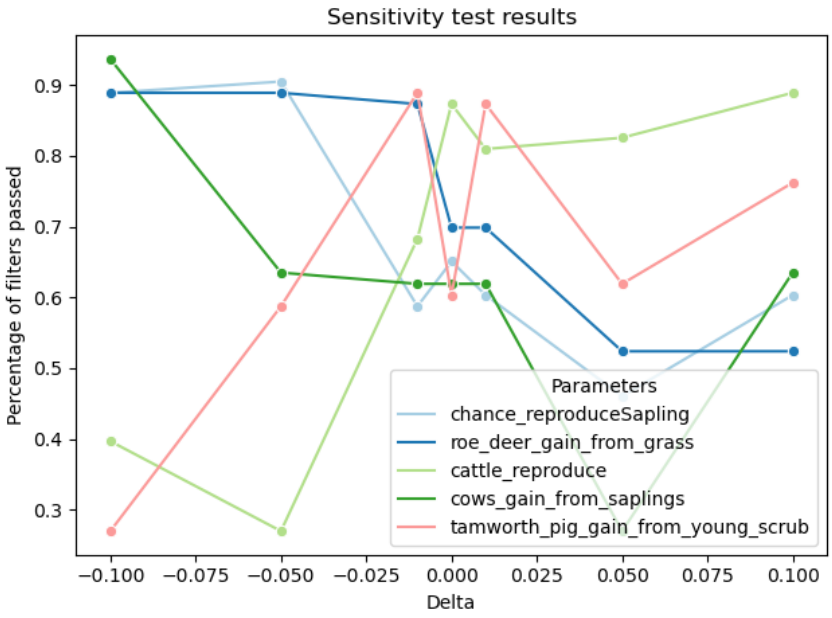
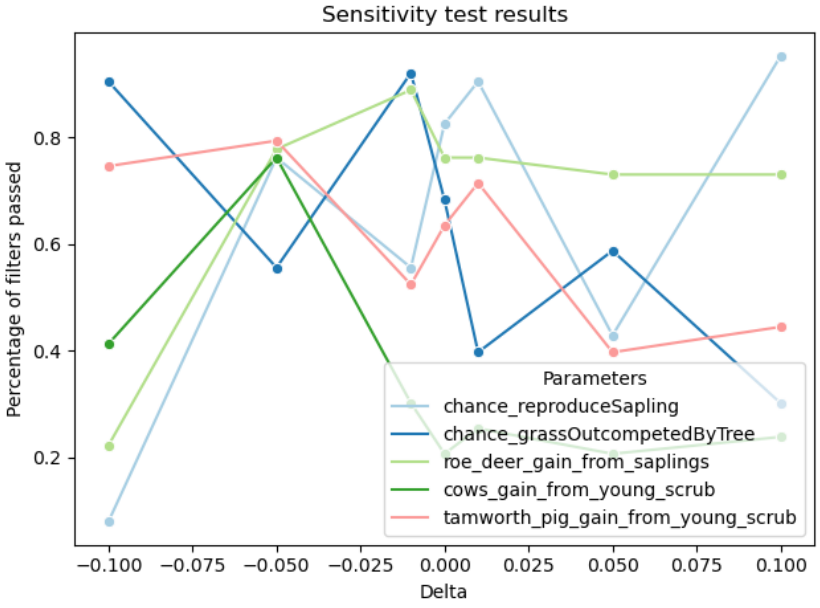


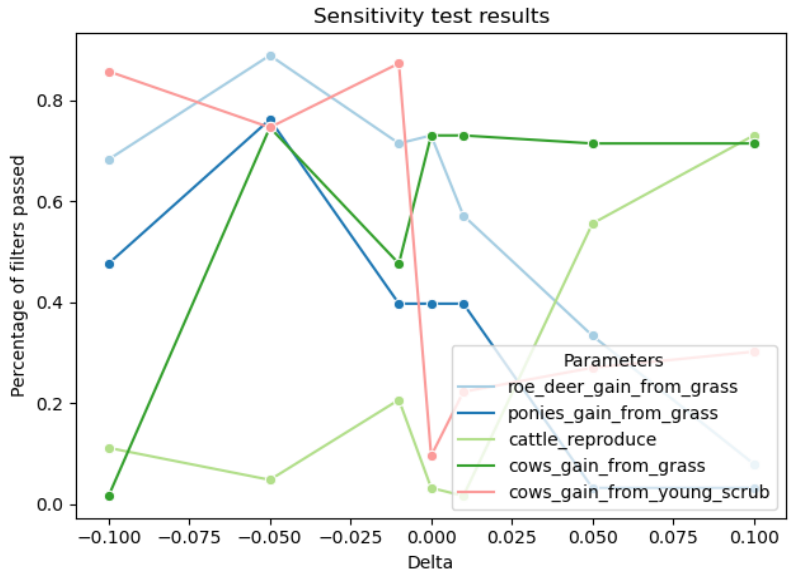
Figure A4.9: A visualisation of reality check 4, in which grazers and browsers should locate their preferred habitat and stay in these areas if possible. The top three panels show a heatmap of vegetation locations, and the bottom 6 panels show the point locations of consumers for the best run (i.e., the one which passed the most filtering conditions)

7. Sensitivity tests

A one-at-a-time sensitivity test was run on four model parameters: the 'best' one (which passed the most filtering conditions), and three randomly chosen ones (Figure A4.10). In three of the four runs, the parameter which most impacted the number of filters passed is the chance of reproducing saplings. Two of the runs shared six impactful parameters: the chance of cattle reproducing, the chance that grass will be outcompeted by trees, and four related to vegetation consumption.


Sensitivity test results
Percentage of filters passed
Delta
Parameters
chance_reproduceSapling
roe_deer_gain_from_grass
cattle_reproduce
cows_gain_from_saplings
tamworth_pig_gain_from_young_scrub


Sensitivity test results
Percentage of filters passed
Delta
Parameters
chance_reproduceSapling
chance_grassOutcompetedByTree
roe_deer_gain_from_saplings
cows_gain_from_young_scrub
tamworth_pig_gain_from_young_scrub



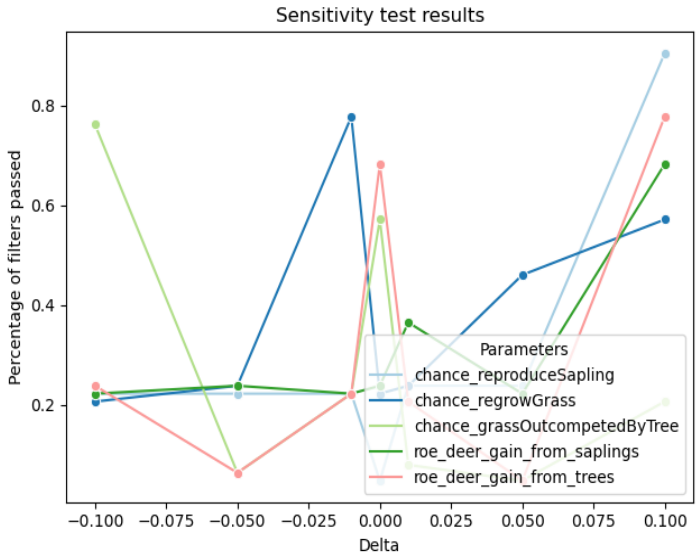


Figure A4.10: This figure shows the top five most impactful parameters in the 'best' run (i.e., the one which passed the most filtering conditions) at the top. The bottom three are the top parameters in randomly chosen runs. The x-axis shows the percent change from the actual parameter value, and the y-axis shows the percentage of filters passed.

8. Calculating Livestock Units

Livestock units (LU) were provided by Knepp (*2022, unpublished data)* and are calculated based on weight, rather than fodder consumed. They are categorised by species, sex, and in some cases, age or additional impacts and behaviours (e.g., rootling). The averages of these LUs per species were used in this paper (Table A4.3).

Table A4 3 Livestock units per species used in this paper.

Species	Livestock Unit per individual
Fallow deer	0.1
Longhorn cattle	0.73
Red deer	0.13
Tamworth pigs	0.75
Exmoor ponies	0.5

CHAPER 5

5 Exploring the impacts of rewilding on ecosystem resilience: a comparison of two model methodologies

Abstract

Rewilding has been proposed as a means of enhancing ecosystem resilience amid the climate and biodiversity crises, but its effectiveness and the impacts of management interventions remain unclear. This paper explores the application of two models, an ordinary differential equation (ODE) and an agent-based model (ABM), to study resilience at the Knepp Estate rewilding project in the UK. The models explore alternative end states and transitions under future scenarios, evaluate current management's ability to maintain desired states, and assess whether resilience can be built into the system. Despite differing levels of complexity, both models produced similar and intuitive high-level insights, indicating the simpler ODE might often be preferable. They showed that end states largely depend on the number of reintroduced species and highlighted the need for adaptive management under novel conditions. The models can help managers optimise stocking densities to increase resilience or drive the system towards a desired outcome. Several practical advantages and disadvantages to each model are discussed: the ODE is faster and easier to use but may be too simplistic for systems, like Knepp, which have moderate data availability. The ABM is computationally intensive but could more easily fit the available data, and it offers a wider range of end states, capturing more uncertainty in predictions. A benefit of exploring the same questions with multiple models is the ability to compare results and understand which elements are missing. If applied to moderately data-rich systems, the inclusion of additional mechanisms in the ODE could be a valuable next step,

combining the relative speed and simplicity of the ODE with the realism and flexibility of the more complex ABM.

Keywords Ecosystem resilience, ensemble ecosystem modelling, agent-based modelling, rewilding, species reintroductions, climate change

5.1 Introduction

The ongoing biodiversity and climate crises are having profound and irreversible consequences for ecosystem structure and function (Malhi et al., 2020; Maxwell et al., 2019; Smith et al., 2015). Changes in climatic conditions affect vegetation composition, growth rates, and the suitable ranges of species (Zhu et al., 2016), and can result in ecosystem phase-shifts; a famous example is the bleaching of coral habitats and declines in biodiversity due to rising ocean temperatures (Glynn, 1993). Possibly a bigger threat to ecosystems than changes in average conditions are extreme weather events such as flooding, wildfires, and heat waves (Jentsch & Beierkuhnlein, 2008), which are expected to increase in magnitude and frequency with climate change (IPCC, 2022; Myhre et al., 2019; Williams et al., 2019). At the same time, biodiversity loss can reduce the ability of an ecosystem to adapt and reorganise following a disturbance (Elmqvist et al., 2003), and disrupt the provisioning of key ecosystem functions and services (Oliver et al., 2015). Consequently, increasing resilience, defined as the ability of a system to maintain its function and structure when subjected to a disturbance, has become a global concern (Angeler & Allen, 2016; Holling, 1973).

Rewilding, which aims to rebuild self-sustaining ecosystems via the restoration of natural processes and trophic webs, has been proposed as a means of enhancing resilience (Carver et al., 2021; Morel et al., 2020; Sheehan et al., 2021; Svenning, 2020). Initiatives have shown promise for increasing biodiversity, which can improve an ecosystem's ability to adapt to change by buffering against declines and losses of individual species (Jia et al., 2021; Maia et al., 2021), and increasing response diversity as different species have varying tolerances to stressors (Elmqvist et al., 2003). Reintroductions of species may also reduce the risk of high-magnitude flooding and wildfire events (Johnson et al., 2018; Rewilding Britain, 2016), and provide increased resilience to climate extremes (Isbell et al., 2015; Svenning et al., 2016).

However, assessing resilience is a challenging problem. Its underlying mechanisms are often poorly understood (Egli et al., 2019), and although leading indicators can be used to act as 'early warning signals' of a potential regime shift with sufficient monitoring (Scheffer et al., 2009), identifying and detecting these in practice is difficult, and the system may already be poised to change by the time the signal is noticeable (Carpenter et al., 2007; Donangelo et al., 2010). In the context of rewilding, the extent to which natural processes alone can push a system towards a healthy equilibrium is also not well understood, nor are the impacts of any ongoing management interventions. Defining the existence and boundaries of stable states, the factors that confer resilience within stable states, and the extent to which environmental changes erode resilience, can allow management to actively help the system move towards a healthy equilibrium and avoid undesirable changes, while also increasing awareness of the shifts that may occur with ongoing anthropogenic stressors (Beisner et al., 2003).

Models can be useful for assessing resilience and forecasting the range of possible ecosystem responses to novel future stressors (Bailey & van der Grient, 2020). In this study, two ecosystem models are used to assess the resilience of a rewilding ecosystem. The rationale for using two models is to explore the importance of model choice and complexity: many consider simpler models to be the 'gold standard' as they typically have a smaller parameter space, less uncertainty, and require less data and computational power, yet can answer many questions just as well as complex models (Evans, 2012; Harrison et al., 2011). However, the relative simplicity of a model could abstract or exclude important mechanisms, and restrict the applicability of the results (D. DeAngelis, 1988; Parunak et al., 1998). Using "the simplest accurate model" is typically recommended (Hunter-Ayad et al., 2020), but choosing between model options is not always a straightforward process, and direct comparisons between methods are uncommon. The models in this paper are on either end of the complexity scale but can be fitted to the same data while exploring the same questions, allowing for a comparison of their outputs.

The first model is an ordinary differential equation (ODE); it uses the ensemble ecosystem modelling methodology (Baker, Bode, et al., 2016) based on the continuous-time, generalised Lotka-Volterra equations (Lotka, 1925; Volterra, 1926). This approach is computationally straightforward, and can capture trophic and non-trophic interactions between species; it has been used in similar studies to assess the ecosystem-wide impacts of perturbations such as species reintroductions (Baker, Bode, et al., 2016; Baker et al., 2019; Bode et al., 2017). The second is a more complex agent-based model (ABM), which incorporates space, increased granularity in temporal scales and habitat components, and heterogeneity of individuals; this means it may be able to better capture certain relationships and ecosystem dynamics. ABMs are more

computationally intensive and can have more uncertainty in results (Parunak et al., 1998). They are capable of producing emergent properties like resilience (Egli et al., 2019), and have been applied to rewilding and ecosystems, for example to inform lynx reintroduction sites in Scotland (Philips, 2020), and assess ecosystem responses to interventions or stressors (Bartlett et al., 2016; Purves et al., 2013).

The two models are applied to a rewilding case study at the Knepp Estate, United Kingdom. Previously managed as an intensive arable and dairy farm, in 2001 the owners decided to devote the 3,500-acre area to a pioneering rewilding project, with an aim of creating self-sustaining wood-pasture ecosystems and restoring biodiversity through the reintroduction of large herbivore and omnivore species (Tree, 2018). To facilitate a wood-pasture habitat and ensure animal welfare standards are met, introduced species are maintained at specific, relatively low densities via annual culling or the removal of breeding males. Since the system has this ongoing management, true ecosystem equilibriums are likely not reached; they are therefore referred to as 'end states' in this paper. The models are used to 1) investigate the existence of alternative end states at Knepp and possible transitions between them under relevant future forcing scenarios, 2) understand whether current management interventions are sufficient for maintaining desired states under novel future environmental conditions, and 3) assess the extent to which resilience can be built into the system, i.e., whether interventions can be optimised to move the system towards desirable states. Lastly, the outputs of the two models are compared to assess whether they are meaningfully different.

5.2 Methods

5.2.1 ODE and ABM network structure

This study adapts the ODE described in (Chapter 3: Neil et al., in prep) and an updated version of the spatial ABM described in (Chapter 4: Neil et al., in prep); full model descriptions are in the respective papers. The two main changes to the ABM are the addition of natural mortality for roe deer and a simplified process for updating consumer energy levels, both of which are further outlined in the Supporting Information. The models were developed in Python and are open access (Neil et al., 2022b, 2022a).

Knepp is inspired by the wood-pasture hypothesis, which proposes primaeval Europe would have been a shifting mosaic of grassland, scrubland, and woodland, with dynamics driven primarily by the behaviours of large herbivores (Vera, 2000). Both models therefore focus on the interactions between grazers and their habitat (referred to as ecosystem elements), and the cyclical turnover between vegetation components due to facilitation and competition (Figure 5.1) (Olff et al., 1999; Olff & Ritchie, 1998; Putman, 1986). They have the same six grazing species and three habitat types, but habitats in the ABM have more granularity than the ODE, assessing a number of mature trees, scrub, saplings, young scrub, and a percentage of grass or bare areas in addition to the overall habitat type in the ABM. This is to explore whether the inclusion of these finer-scale details can better capture dynamics such as vegetation facilitation and competition. The basic outputs are time-series of the abundance of each node, and the models cover three time-periods: the years before large herbivores were reintroduced to Knepp (2005-2009), the years after large herbivores were reintroduced (2009-2020), and future projections.

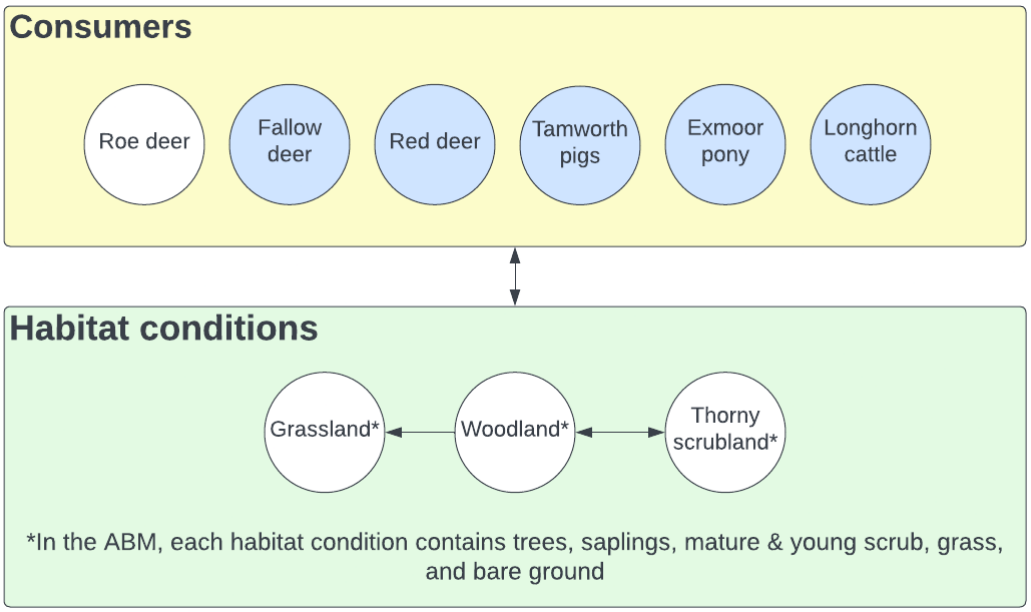


Figure 5.1: *The ecological network of the Knepp Estate. Blue circles are species that were reintroduced to Knepp and whose numbers are continually managed. White circles were already present at Knepp and their populations are un-managed. Consumers are assumed to negatively impact, and be positively impacted by, each of the three habitat types. Habitats can negatively impact each other via competition for light. Thorny scrubland is assumed to positively impact woodland via facilitation of saplings. Consumer species are the same in both the ODE and ABM network, but the ABM has more granularity for primary producers.*

There are several common processes and interactions between the ODE and ABM: for example, consumers reproduce and are assumed to negatively impact primary producers via herbivory, and die from annual culls or lack of food; primary producers reproduce and die from herbivory or competition with other plants; and thorny scrub is assumed to facilitate saplings by protecting them from herbivory (Salek et al., 2019; Smit & Ruifrok, 2011). However, the way in which the networked interactions are modelled differ. The ODE is based on the continuous-time, generalised Lotka-Volterra equations (Equation 5.1; Lotka, 1925; Volterra, 1926):

$$\frac{dn_i}{dt} = r_i n_i + \sum_{j=1}^{N} \alpha_{i,j} n_i n_j \qquad \text{Eqn. 5.1}$$

Where n_i is the total amount of ecosystem element i (relative population size, i.e., relative number of individuals or percentage habitat type), r_i is the growth rate (growth of the relative population per year), $\alpha_{i,j}$ is the strength of the interaction between nodes i and j (number of individuals^{-1}year^{-1}), and N is the total number of ecosystem elements. Population sizes are rescaled to 1 so that the model tracks relative changes over time. Similar Lotka-Volterra models typically have positive intrinsic growth rates and negative diagonals of the α matrix for all ecosystem elements (Baker et al., 2016, 2019; Bode et al., 2017); however, this allows consumer populations to survive without any primary producers for several years and was considered too unrealistic for this model (see Chapter 3: Neil et al., in prep). Primary producers are therefore given positive r values between 0 and 1 and are assumed to be self-limiting, i.e., with diagonals of the matrix between -1 and 0, whereas consumers are assumed to have negative r values, diagonals equal to zero, and interaction strengths between -1 and 5 depending on the sign of the interaction.

In contrast, the ABM's dynamics are driven by discrete-time, 'if-then' statements, which can give the freedom to write more detailed and possibly discontinuous rules for the system, potentially leading to more realistic results (Parunak et al., 1998). The ABM also has some added complexity in that it incorporates space, increased granularity in temporal scales (monthly as opposed to yearly time-steps) and habitat components, and heterogeneity of individuals; this means it may be able to better capture spatial dynamics between habitat components, such as light competition or the facilitation of saplings by thorny scrub, as well as individual consumer choices regarding seasonal movements, or habitat preferences based on whether the species is a grazer, browser, or intermediate feeder.

5.2.2 Calibration

Both the ODE and the ABM have the same approach to fitting the data. The parameter space is large with 46 parameters in the ODE and 44 in the ABM. Optimisation using genetic algorithms (GA) (Bremermann, 1958; Fraser, 1957; Holland, 1975) is used to explore the space and identify a parameter set that produces outputs closely matching the empirical time-series data from Knepp, while also passing two ecological filters:

1. Roe deer populations should never collapse to 0 or explode beyond >500 individuals. This is based on population density surveys from elsewhere in Europe (Borkowski et al., 2021; Valente et al., 2014; Watson et al., 2009).
2. The system must reach its end state within 500 years. This is based on studies from other ecosystems in which equilibrium could be reached within several hundred years or in some cases, decades (Dodds et al., 2004; Ficetola et al., 2018). In the ODE, true equilibriums are ordinarily found by solving Equation 1 for the new steady state, which is obtained by setting $\frac{dn_i}{dt}$ equal to zero (Equation 5.2):

$$r_i n_i + \sum_{j=1}^{N} \alpha_{i,j} n_i n_j = 0 \qquad \text{(Eqn. 5.2)}$$

However, a different approach is required in this case, as true equilibriums are not reached at Knepp due to tight control of grazer populations. For both the ODE and the ABM, the model is therefore run for five hundred years, and the system assumed to be

stable if a line fit to the last hundred years for habitat nodes has a gradient with an absolute value of <= 0.01.

The objective function focusses on minimising the value *a* by varying all parameters to identify sets that produce outputs (*x*) closely matching the data (*y*) for each species over time (Equation 5.3):

$$a = \min \sum_{i=1}^{N} ((x - y) / y)^2 \qquad \text{(Eqn 5.3)}$$

Where *N* is the number of outputs with associated filtering conditions. If the additional ecological criteria are failed, a high number is returned.

The GA output provides a 'best' parameter set, but many more may exist which can pass the filters while having low calibration error. To avoid under-identification, the GA output is used as a prior to run Approximate Bayesian Computation (ABC) with rejection sampling for identifying additional suitable parameters and model outputs (Pritchard et al., 1999). The ABC process is as follows: 100,000 simulations are run by randomly drawing all parameter values from their prior distributions to model the abundance of ecosystem elements over time. In the ABM, to obtain a diversity of solutions and prevent collapse on a single local minimum, 100 separate GAs are run and a prior is generated around the minimum and maximum distributions of the outputs (Williams et al., 2020). In the ODE, due to challenges with finding solutions that replicate the data while also passing the ecological constraints (see Chapter 3: Neil et al., in prep), a single GA is run, and the neighbourhood of the parameter set returned is explored: this is done so by assuming, for each parameter, a uniform prior ranging ±10% of the value returned by the GA.

The 100,000 simulations are filtered through constraints based on the time-series data from Knepp, of which there are 32 in the ODE and 63 in the ABM (see Chapter 3: Neil et al., in prep; Chapter 4: Neil et al., in prep for further details), and the posterior joint distribution of parameters is built using only those simulations that pass the filters. The output therefore includes an expression of the parametric uncertainty in the results. Accepted simulations are defined as the top 100 runs which pass all ecological, habitat, and roe deer conditions, and the most filters. The requirement for passing the latter two conditions exists because reintroduced grazers are continuously observed and have relatively more filters, so the top 100 runs could be skewed towards correctly fitting these species rather than also replicating the dynamics of uncontrolled ecosystem elements. Specific differences between the ODE and the ABM related to their structures, equilibrium assumptions, and the GA and ABC processes, are outlined in **Table 5.1**.

Table 5.1: *Differences in the structures and processes of the ODE versus the ABM.*

	ODE	**ABM**
Structural differences	Relies on Lotka-Volterra equations	Relies on 'if-then' statements
	Continuous, yearly time-steps	Discrete, monthly time-steps
	Each habitat is represented by a single variable, describing its general abundance.	More granular assessment of vegetation components. Each habitat cell is classified as either woodland, scrubland, grassland, or bare ground, and has a number of individual trees, saplings, mature or young thorny scrub plants, and a percentage of grassland vs. bare ground.
	No space included	Space is included, e.g., incorporating spatial dynamics of habitat competition and facilitation, and movements of consumers.
	No heterogeneity of individuals	Heterogeneity of individuals, e.g., individual consumers make choices regarding seasonal movements and habitat preferences based on

		whether the species is a grazer, browser, or intermediate feeder.
Objective function	Focusses on each of the annual empirical filtering conditions, the two ecological criteria, and the following constraint: in the absence of consumers or other habitat types (i.e., no intra-habitat competition or facilitation), woodland, grassland, and scrubland should each level out at 100%. Empirical data for habitat types are available as percentages, but these are rescaled to 1 in the ODE, so it is theoretically possible that output values could be far above or below 100% without this constraint.	Focusses on the ecological criteria, the first two filtering conditions for roe deer and habitats, and the final two monthly filtering conditions for each reintroduced species, so that each node has two observations targeted.
GA bound assumptions	All bounds between -1 and 5 as applicable.	In the absence of other food, consumer species are assumed to need >10 young scrub/saplings per month, and > 3 trees/scrub per month to survive. Young scrub and saplings are assumed to mature after 5-50 years (Murphy et al., 2022; Van Uytvanck et al., 2008). All other parameters have wide bounds of 0-1.
Priors for ABC	Single GA output, with uniform prior ranging ±10% of the value returned by the optimiser.	Randomly generated values between the max and min of the 100 separate GA outputs.

5.2.3 Landscape experiments

The ‘best’ parameter set per model, defined as the accepted simulation that passes the most filtering conditions, is used to investigate possible alternative end states at Knepp. If there are multiple candidates for the best parameter set (i.e., if several runs pass the same amount of filtering conditions), one is randomly chosen. Alternative end states are explored by varying the vegetation starting conditions (between 0-100%) and stocking densities for all reintroduced consumers and running the model for 500 years. Stocking densities are all varied, at the same time, between 0-100 times their 2020 levels, which Knepp seeks to maintain in future: 247 fallow deer, 81 cattle, 35 red deer, 7 Tamworth pigs, and 15 Exmoor ponies. Testing very high

stocking densities, even if ecologically unrealistic (Fløjgaard et al., 2022; Santini et al., 2022; Stephens et al., 2019), can be useful for understanding tipping points and the resilience of the system under extreme pressure, and for testing the robustness of the model in predicting ecosystem responses. Due to the slower runtime of the ABM, 150 different initial conditions and stocking densities are explored as opposed to 1,000 in the ODE.

Optimisation using GAs is then used to identify whether species' stocking densities can be varied at different levels (rather than changing all by the same amount) to achieve three alternative end states per model, based on the possible range of end states identified in the previous landscape experiment. In the objective function, the value a is minimised by varying species' stocking densities beginning in 2020 and running it to its end state, to identify densities that produce outputs (x) closely matching the desired end state (y) (Equation 5.3). This is compared to a scenario in which manual controls of grazer populations are removed, to understand the true equilibrium of the system under its current conditions. Stocking density ranges in the ABM are limited to at most 3 times their 2020 levels (as opposed to 0 to 100 times in the ODE) to reduce the number of agents and therefore the model runtime.

5.2.4 Perturbation experiments

Next, the system is subject to various disturbances to 1) investigate possible transitions between alternative end states under changing environmental conditions, and 2) understand how far a controlled ecosystem can be pushed until current management tactics cannot maintain the same

end state. To better understand the potential of these models for assessing and quantifying resilience mechanisms, different perturbations and resilience properties are considered (Egli et al., 2019). From the year 2020, and using the 'best' parameter set per model, the system is subjected to the following disturbances:

1. Vegetation reproduction rates are temporarily changed at 100 different sets of magnitudes and durations (1-50 years). In the ABM, the following parameters are altered: the chance of reproducing saplings or young scrub, and the chance of grass growing from bare ground. This is meant to simulate the effects of a drought or flood, which can have positive or negative impacts on plant biomass (Garssen et al., 2017; Seleiman et al., 2021; Visser et al., 2003);
2. Vegetation reproduction rates are subjected to increasing amounts of noise over time to simulate stochasticity in temperatures and rainfall under climate change (Dore, 2005; Thornton et al., 2014). After 100 years, woodland percentages are decreased by 50% to simulate an extreme event, such as a drought or wildfire (S. L. Stephens et al., 2018). In the ABM, this shock is done by setting the number of trees and saplings in 50% of woodland patches to 0.

For both perturbations, the system is run for 500 years, and the response is assessed, either the recovery rate to the original state, or if it recovered to a new state, the magnitude required to push it there and the composition of the new state.

Next, an experiment is run to identify whether changes in stocking densities can achieve a hypothetical end goal despite perturbations. Each experiment identifies an objective, representing a 'desirable' or 'undesirable' state which the model is guided towards. Undesirable states are assumed to be dominated by one vegetation type, as Knepp aims to have a mosaic of grassland, scrubland, and woodland, in part because environmental heterogeneity strongly correlates with species richness (Bakker et al., 2016; Stein et al., 2014). Using the best parameter set as a starting condition, the model is guided towards the undesirable state by applying a perturbation of sufficient size to shift the ecosystem. GAs then optimise stocking densities, varied between 0-100x their 2020 values, to avoid the undesirable state and instead move towards the desirable one over 500 years. The objective function focuses on minimising a to achieve output values at the end state (x) which match the habitat composition in the desirable state (y) (Eqn. 5.3). Finally, optimised stocking changes are re-run across all acceptable parameter sets, to test policy robustness to uncertainty and parameter misspecification.

5.3 Results

5.3.1 Alternative end states

After 100,000 runs following the ABC process, 100 acceptable parameter sets could be found which passed 97-100% of filtering conditions in the ODE, and 79-95% of filtering conditions in the ABM, including all ecological, habitat, and roe deer criteria (Supporting Information). With current stocking densities, the best parameter set in the ODE has a single end state of a mosaic, woodland-dominant ecosystem with approximately 5% grassland, 27% scrubland, and 56%

woodland regardless of initial condition (**Figure 5.2**). The remaining 12% is assumed to be bare ground, although habitats are tracked as relative changes over time in the ODE and may not necessarily add up to 100%. In the ABM, the best parameter set under current conditions has four woodland-dominant end states with between 1-4% grassland and 96-99% woodland, depending on the initial conditions (**Figure 5.2**).

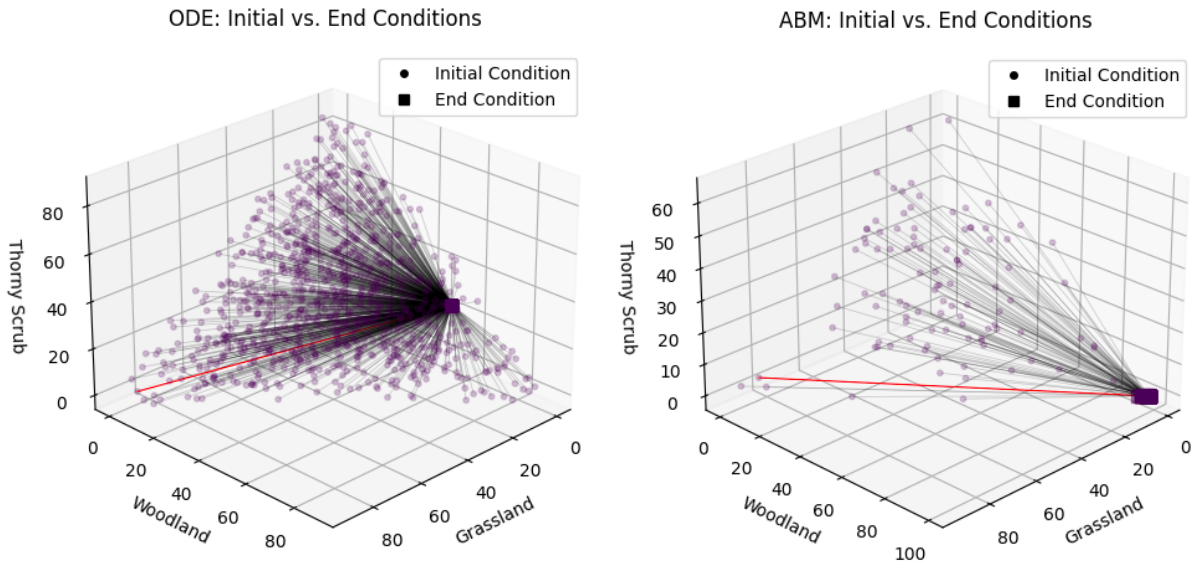
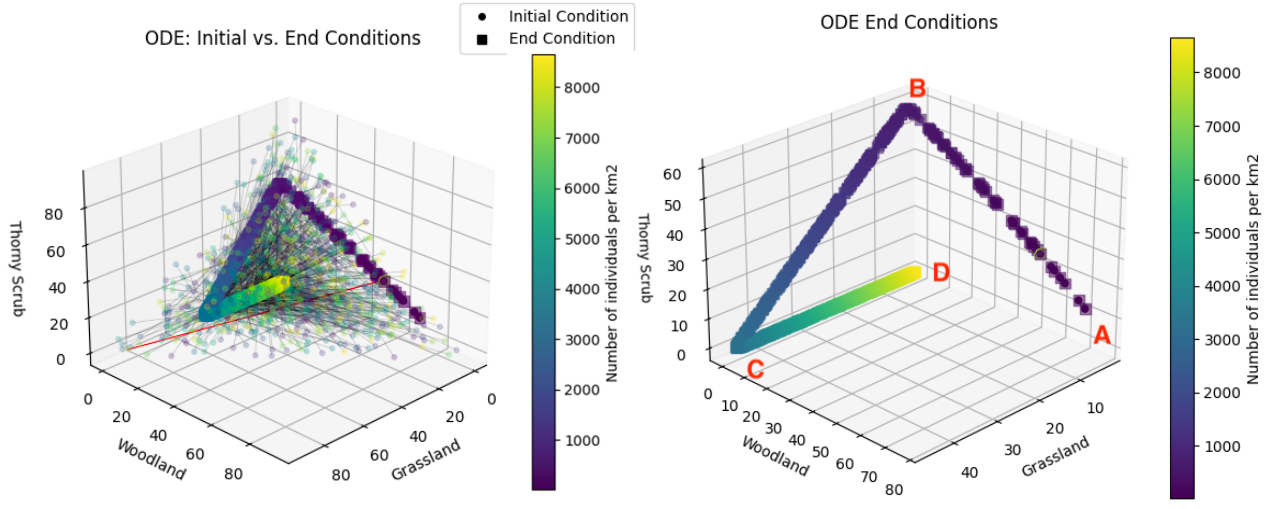


Figure 5.2*: End states in the best parameter set (defined as the one which passes the most filtering conditions) of the ODE (left) and the ABM (right) with varying initial abundances. The red line denotes the actual observed initial abundances.*

The 100 accepted parameter sets in both models generally favour a woodland-dominant end state, but the outcomes of the ABM are more variable. In the ODE, all 100 parameter sets have woodland-dominant end states (50-62%) with lesser amounts of thorny scrub (13-30%) and grassland (0-24%) (Supporting Information). In the ABM, 66% of parameter sets are woodland-dominant (having >50% woodland), 28% scrubland-dominant (>50% scrubland), 1% grassland-dominant (>50% grassland), and 5% mosaics with lesser percentages (<50%) of wood, scrub, and grassland (Supporting Information). The ODE is more likely to favour mosaic end states,

with 0% of accepted parameters leading to the dominance (>= 99%) of a single habitat type. This contrasts with the ABM which had 18% of runs as completely (>= 99%) woodland and 15% completely scrubland.

Both the ODE and ABM end states are largely driven by the stocking densities of reintroduced grazers. With increasing numbers of grazers, the system in both models shifts from woodland (point A shown in Figure 5.3) to scrubland (point B) to grassland-dominant (point C), moving towards bare ground at very high densities (point D). This suggests that managers can exert significant control by using species' densities to drive the system into a desired final state. However, in some cases the required densities are very high, exceeding those found in traditional agriculture or natural systems (Eurostat, 2020; Fløjgaard et al., 2022; Santini et al., 2022; P. A. Stephens et al., 2019): the ABM requires >14 times 2020 stocking densities to consistently achieve a 0% woodland end state (regardless of initial condition) as opposed to 9 times in the ODE, and >50 times to hit a 0% scrubland state as opposed to >45 times in the ODE.



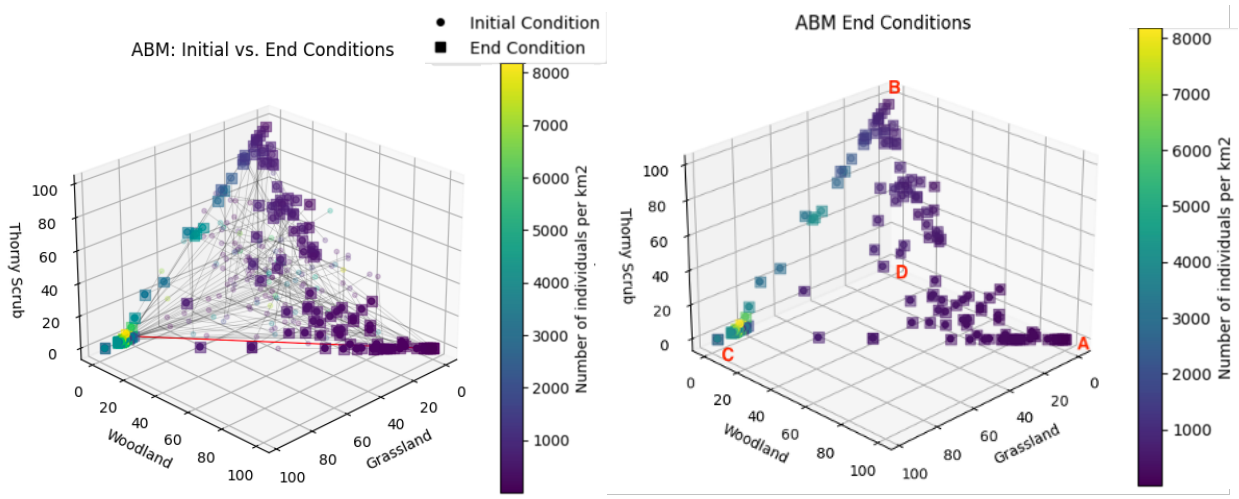


Figure 5.3 A landscape analysis of alternative end states in the ODE (top) and ABM (bottom) at Knepp. The graph shows the trajectories from various initial conditions to end states after 500 yea rs (left) and end states with descriptions of each dominant category: A) woodland, B) scrubland, C) grassland, and D) bare ground (right). 1,000 initial vegetation conditions and stocking densities for reintroduced species are explored in the ODE, and 150 in the ABM. The red line denotes the trajectory of the ecosystem under its current conditions.

Unlike the ODE, which reaches 0% of each habitat type at very high stocking levels (> 80 times current numbers), the ABM does not reach a fully bare ecosystem under current parametric conditions. This is likely due to spatial effects of the model: for example, consumers move towards their preferred habitat type at each time-step, and since none prefer bare ground, these patches are typically empty in the initial steps after annual reintroductions. Bare areas therefore experience little to no herbivory and can recover to grassland. If consumers move randomly with no preference for any habitat type, bare ground in the end state is 27% vs. 12% when consumers move preferentially (Supporting Information). A secondary spatial effect explored is related to reintroduction assumptions: consumers of the same species are reintroduced to a single, randomly chosen field each year, and at very high stocking densities, localised mass die-offs occur as resources are eaten faster than consumers can spread out, potentially leaving some areas with sufficiently low herbivory impacts for grassland maintenance (Supporting Information). After ten runs, 11% of the system is bare ground after 100 years under current assumptions,

versus 16% if consumers are reintroduced to different random fields. Differences in final habitat compositions varied between 0-200%, indicating the model is sensitive to these spatial decisions (Supporting Information).

5.3.2 Engineering end states

Alternative end states can be achieved by varying species' stocking densities in both models, indicating the ecosystem can be steered towards, or away from, desirable or undesirable states. GAs were used to optimise stocking densities towards the following states (identified based on the outputs of Figure 5.3): in the ODE, increased woodland (75%), a scrubland-dominant state (50%), and a state with 45% grassland, which is the maximum possible under current model conditions; and in the ABM, increased grassland (33%), a prevention of collapse of thorny scrub (33%), and a woodland-dominant mosaic habitat (50%) with lesser amounts of scrub and grassland (25% each).

Overall, optimisation could effectively be used to engineer the system. Shifting towards grassland or thorny scrubland required large increases in stocking densities for most species in the ODE (up to 30 times 2020 levels), whereas the ABM required smaller increases in only two species (1.6 times fallow deer and 1.7 times Tamworth pigs for grassland; 1.8 times Exmoor ponies and 2.3 times red deer for thorny scrubland) (Figure 5.3, Figure 5.4). Moving towards woodland in the ODE required reduced consumer numbers for all species except Longhorn cattle (Figure 5.3). This is only one of potentially many suitable outputs but indicates that cattle, which

have the highest impact on woodland of all species in the best parameter set of the ODE, can only be increased if all other species are significantly reduced.

Reducing woodland to create a woodland-dominant mosaic in the ABM required decreased Exmoor ponies (0.4 times) and red deer (0.72 times), and increased Tamworth pigs (2 times) (Figure 5.4). This result warrants further investigation as it suggests that at higher densities, pigs can significantly restrict woodland regeneration. In reality, pigs are known to damage woodland vegetation and disturb soil through their rootling behaviour, which at high frequencies could restrict sapling regeneration; however, other evidence suggests they can create suitable conditions for thorny scrub survival, which then protect saplings from herbivory (Johnson, 2011; Vera, 2000).

When stocking density outputs are applied to all 100 accepted parameter sets, the ABM has a much wider spread in end states than the ODE: in most experiments it was unable to predict whether the end state would be woodland or scrubland dominant (Figure 5.4). This result can help to guide future research as it indicates more data and expert knowledge are needed around the factors influencing woodland and scrubland survival. With all controls removed, the ODE system reaches a woodland-scrubland dominant stable state, with slightly more scrubland and less woodland than current trajectories with ongoing management, whereas the ABM becomes a scrubland-grassland mosaic[1].

[1] In the ABM, Longhorn cattle populations consistently exploded in number with no ongoing culling; this significantly slowed down the model runtime and therefore only 5 of the 100 accepted parameter sets were run.

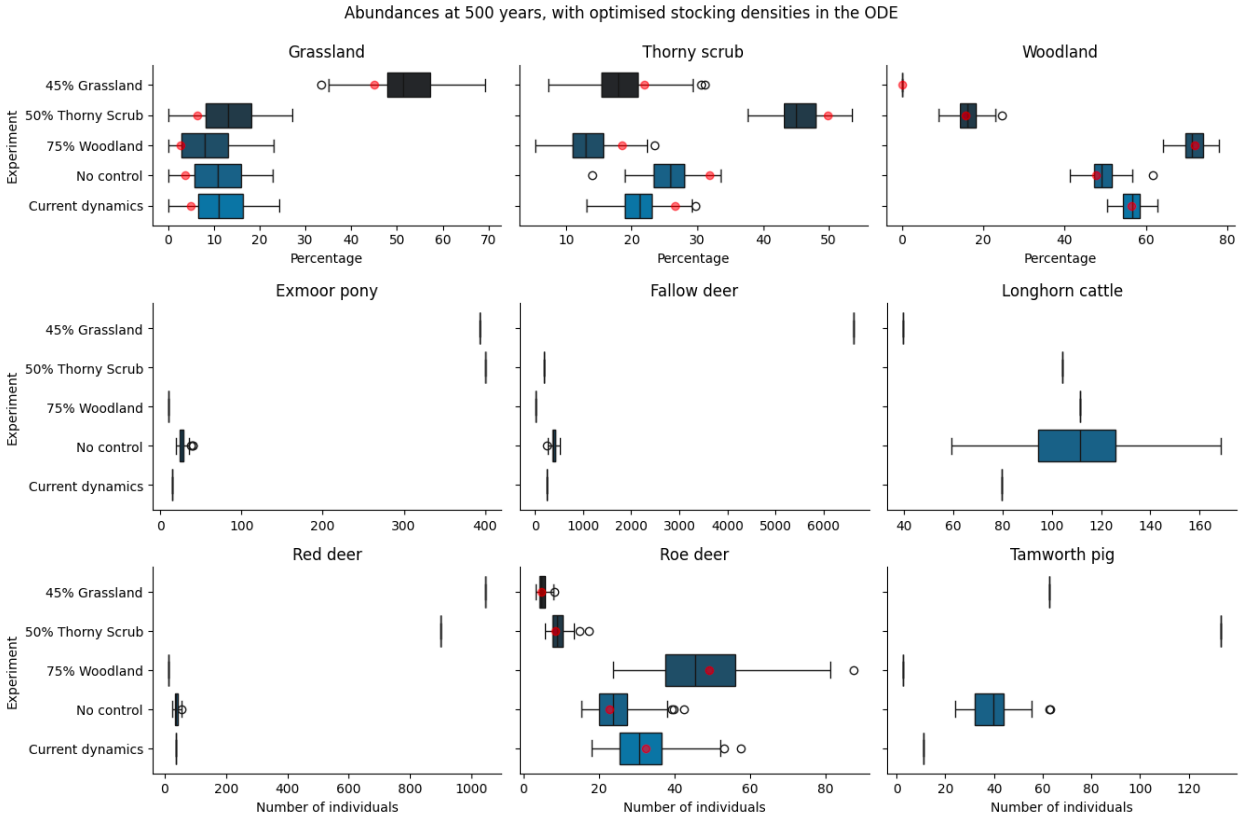
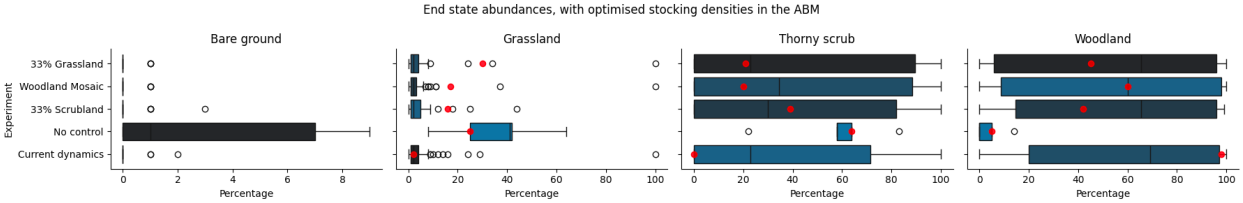


Figure 5.3: *GAs were used on the 'best' parameter set (defined as the one which passed the most filtering conditions) to optimise stocking densities and achieve various end goals in the ODE. The optimised output was then applied to all 100 accepted parameter sets. This graph shows the end states of the 100 parameter sets, with percentages of each habitat type (top) and number of individual consumers (bottom). The red dots indicate the output of the best parameter set.*



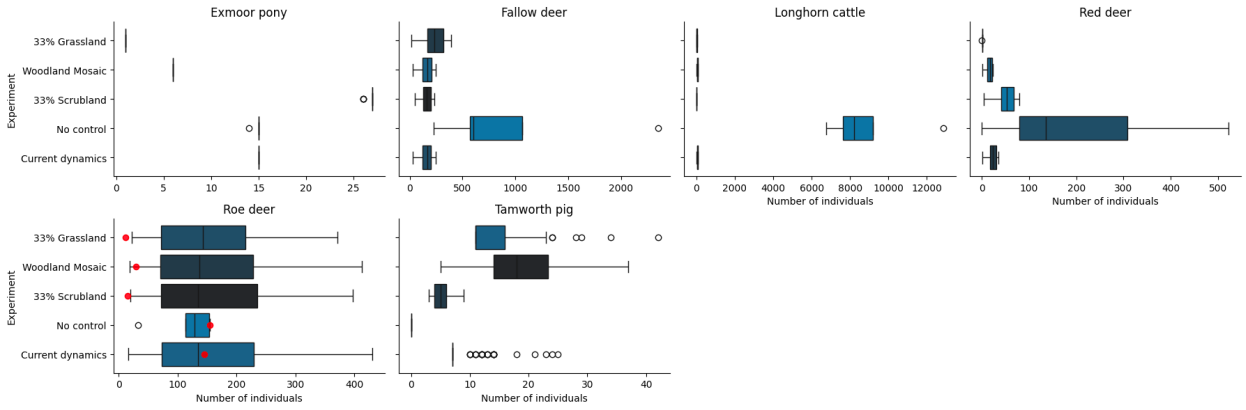


Figure 5.4*: GAs were used on the 'best' parameter set (defined as the one which passed the most filtering conditions) to optimise stocking densities and achieve various end goals in the ABM. The optimised output was then applied to all 100 accepted parameter sets. This graph shows the end states of the 100 parameter sets, with percentages of each habitat type (top) and number of individual consumers (bottom). The red dots indicate the output of the best parameter set.*

5.3.3 Perturbation experiment 1

In 96% of the ODE runs, the system returns to its original end state following small or moderate perturbations to vegetation growth rates (Figure 5.5). However, larger disturbances lead to a collapse in grassland (0% vs. 7.3%) and push the system into a new state characterised by reduced thorny scrubland and roe deer populations (26.4% vs. 28.7%, and 28 vs. 38 individuals, respectively) and increased woodland (58.4% vs. 54.6%) (Table 5.2). The new end state represents a model and mathematical boundary but is unlikely to happen in reality, as the tipping point occurs when grassland reaches zero, at which point it never recovers. Unless a perturbation can permanently remove an ecosystem element, the system in practice appears to be resilient to changes in vegetation growth rates. This resilience may be facilitated by the managed nature of the ecosystem: stocking densities affect the most change in end states (**Error! Reference source not found.**), leaving less room for perturbations to affect the system in the long-term.

Table 5.2: *End states in the ODE and ABM resulting from the first perturbation experiment, in which vegetation growth rates are shifted at various magnitudes and durations. The table also describes the thresholds required to push the systems to the new end state (magnitude and duration), and the percentage of runs that reached the state.*

Model	**End State**	**Magnitude**	**Duration (years)**	**Percentage of runs**
ODE	Original	-	-	96
	No grassland	-0.5	>38	4
ABM	Original, or regenerating towards it	-	-	90
	No woodland	0.01	>36	3
	No roe deer	0	>43	7

The ABM has similar trends in that longer and higher-magnitude perturbations can lead to a dramatic shift in ecosystem state, but overall, the system appears to be resilient to changes in vegetation reproduction. Three end states are identified: at, or moving towards, the original woodland-dominant state, a scrubland-dominant state with 0% woodland, and a state in which woodland is regenerating but roe deer populations have dropped to zero (Table 5.2; Figure 5.5).

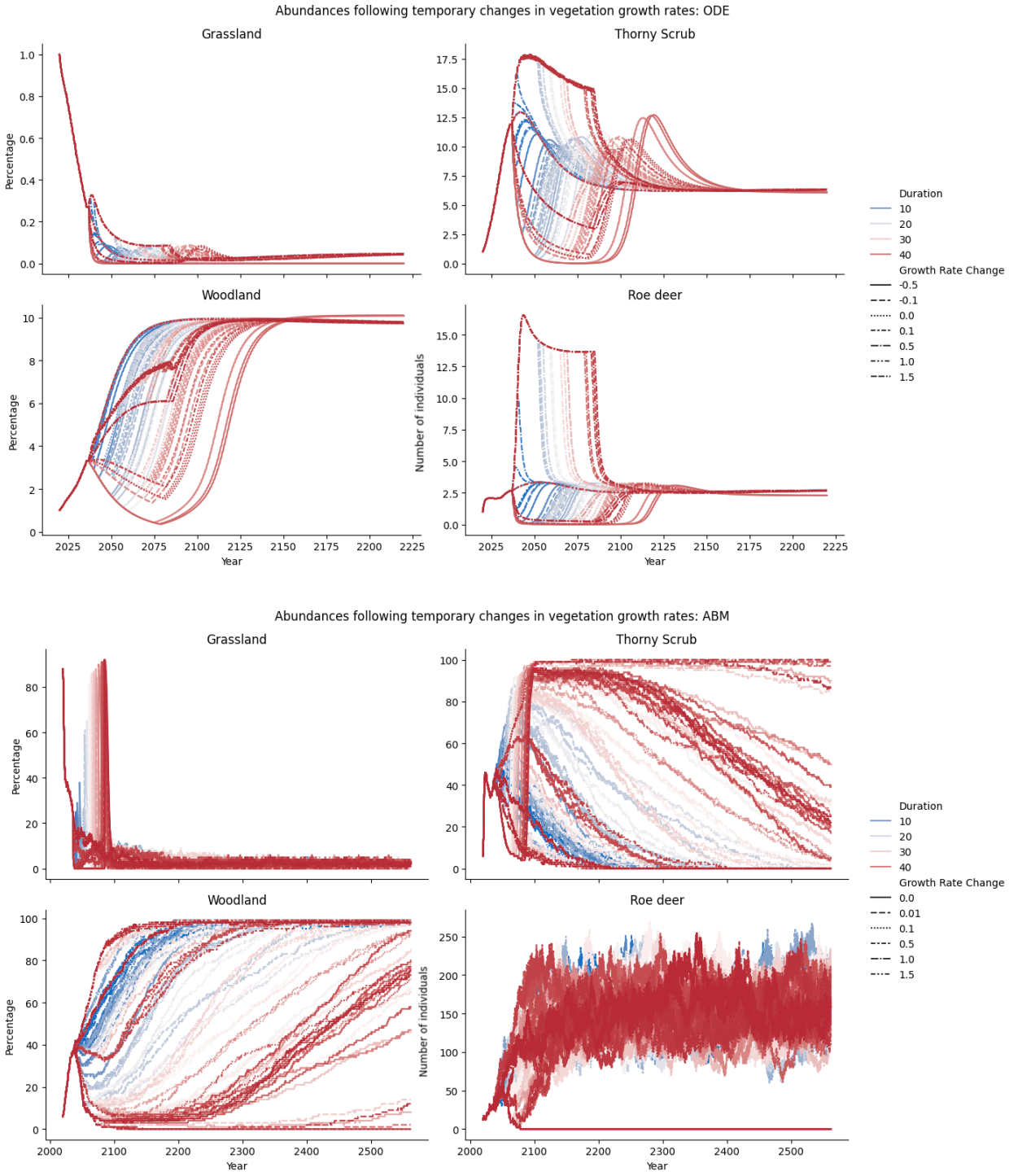
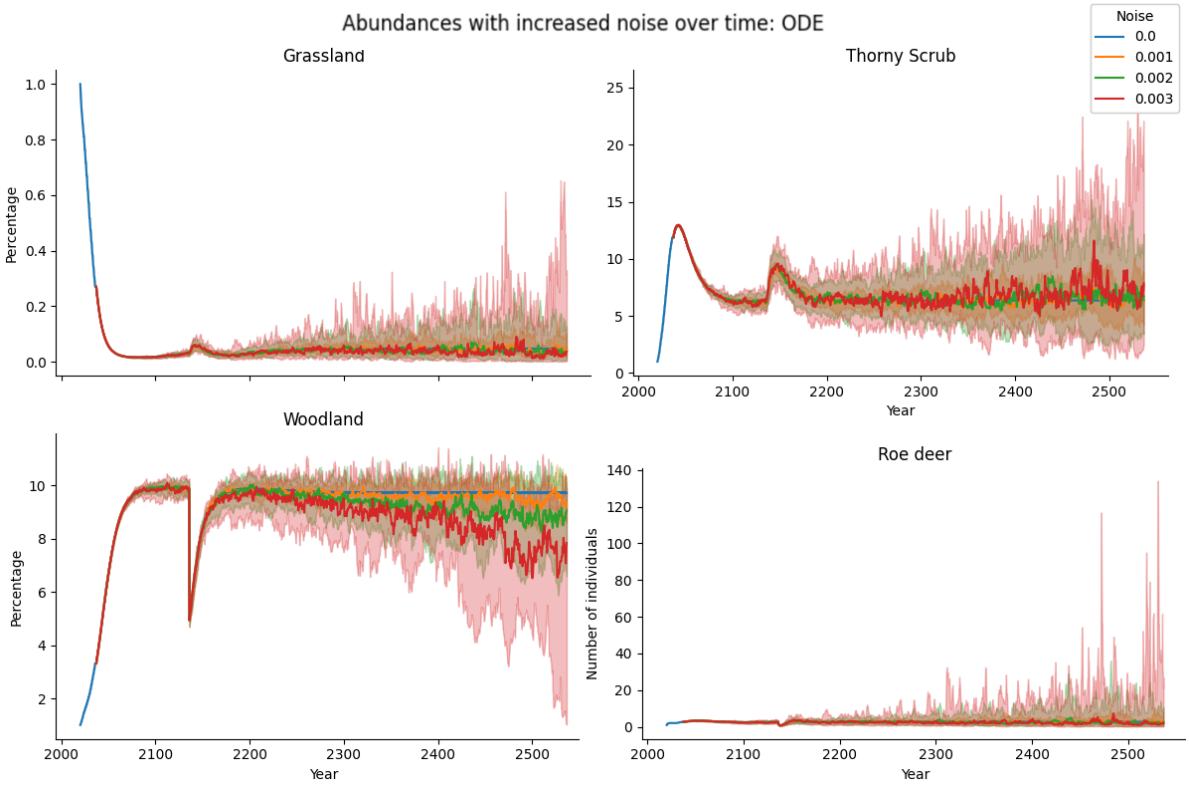


Figure 5.5: *Results of the first perturbation experiment, in which vegetation growth rates are changed at different magnitudes and durations, for the ODE (top) and ABM (bottom). The graphs show the four ecosystem elements whose populations are not managed by humans. The other species' stocking densities are assumed to be forced down to their 2020 levels for each year in future.*

5.3.4 Perturbation experiment 2

The ODE system appears to be resilient to small increases in noise and can return to the previous state following woodland loss, regardless of whether the perturbation occurs in the near or long-term (Figure 5.6; Supporting Information). However, with higher levels of noise, woodland cannot fully recover to its previous equilibrium and the system shifts to grassland and scrubland dominant. Since stocking densities are the primary driver of end states in the ODE, this result suggests that under future environmental conditions, consumer numbers may need to be adjusted to hold the ecosystem in its current end state.

Conversely, higher noise levels facilitate a faster rate of return to the original woodland-dominant state in the ABM (Figure 5.6). This is likely because noise only impacts the 0-1 probability that a vegetation element will be reproduced, as opposed to the ODE in which a negative *r* is possible, directly removing some of these elements. Although noise can shift this parameter to 0 for a given time-step in the ABM, stochastic increases in its value compensate for this and allow saplings to quickly regenerate (Supporting Information). If these disturbances occur in the long-term in the ABM (after the system has reached its end state), the loss of 50% woodland with no noise creates a new end state with higher levels of grassland; the addition of noise increases the system's resilience by facilitating its return to the original woodland state (Supporting Information).


Abundances with increased noise over time: ODE
Grassland
Thorny Scrub
Woodland
Roe deer
Noise
0.0
0.001
0.002
0.003
Percentage
Number of individuals
Year

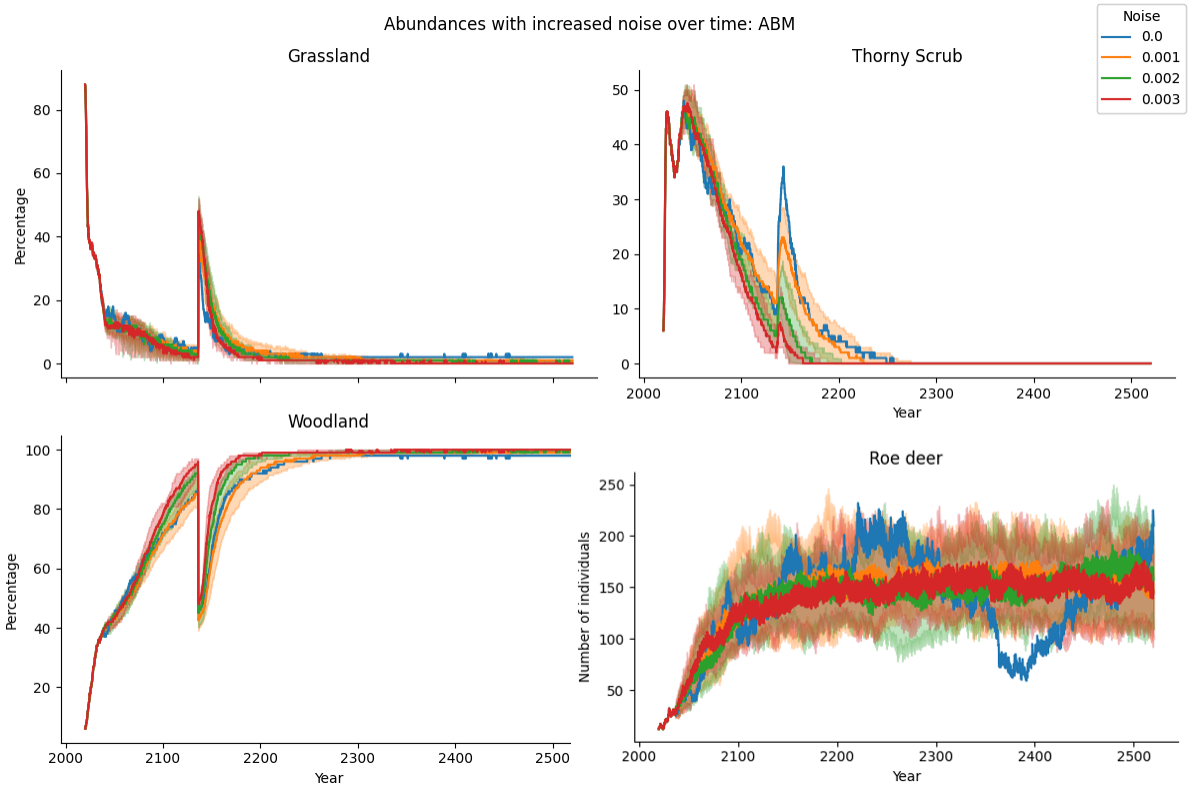

Abundances with increased noise over time: ABM
Grassland
Thorny Scrub
Woodland
Roe deer
Noise
0.0
0.001
0.002
0.003
Percentage
Number of individuals
Year

Figure 5.6: *Results of the second perturbation experiment, in which the system is subjected to annual increases in noise. Graphs show a time-series of changes to each ecosystem element's abundance in the ODE (top) and ABM (bottom) given different noise levels. After 100 years, 50% of woodland is lost to simulate an extreme event and assess the extent to which the ecosystem can recover. Plots show the median and 95th percentile (shaded areas).*

5.3.5 Perturbation experiment 3: optimising resilience

Optimisation with GAs is to explore whether resilience can be built into a system by optimising grazer stocking densities. In the ODE, this is done by running the model with +0.003 increases in noise per timestep and altering all stocking densities to reduce the severity of woodland decline. In the ABM, the first perturbation experiment is run with growth rate changes of 0.01x and durations of 37 years, to assess whether woodland collapse can be avoided. In both models, stocking densities can be optimised to increase resilience (

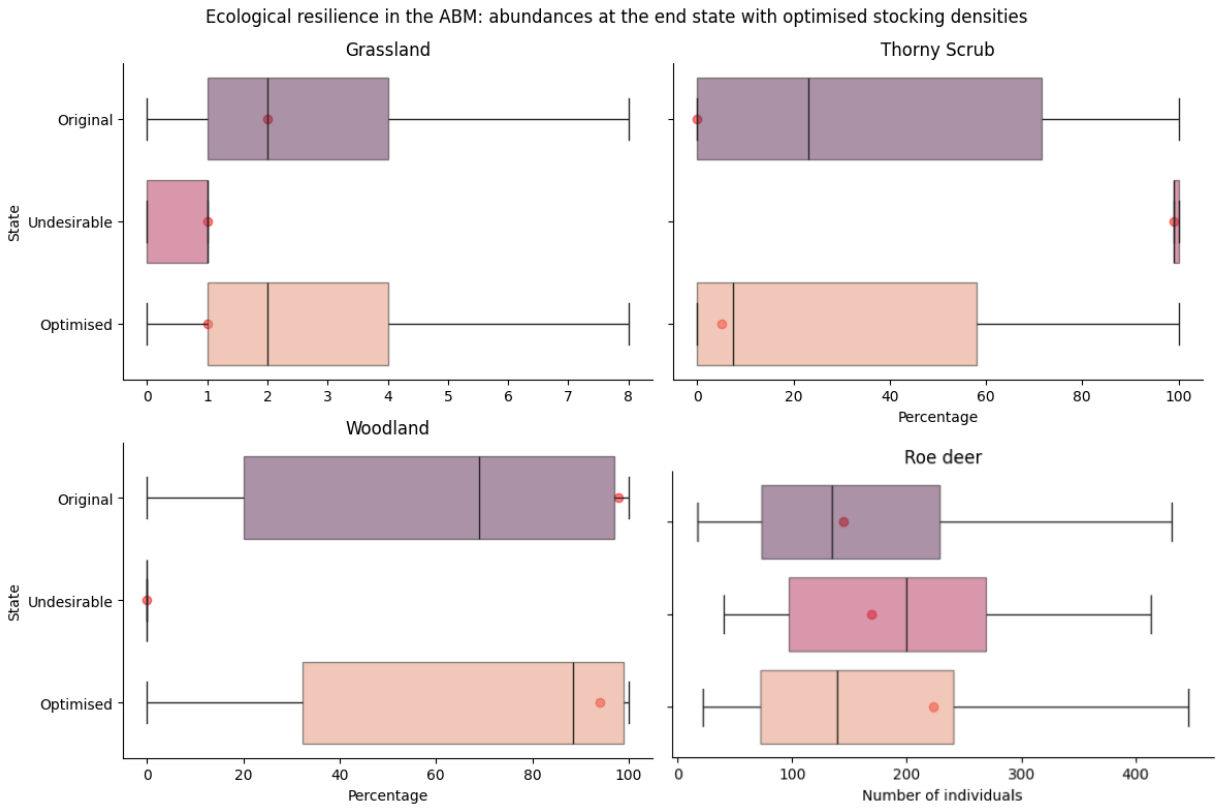


Figure **5.7**). They had similar trends for which species' densities would need to be changed to prevent woodland decline; these were: increased densities of Exmoor ponies (1.4-1.9 times 2020 values, 21-28 individuals in the ABM vs. ODE) and Tamworth pigs (1.4-1.7 times, 9-11 individuals in the ODE vs. ABM), and decreased densities of fallow deer (0.07-0.5 times, 17-123 individuals in the ABM vs. ODE) and Longhorn cattle (0.06-0.8 times, 4-64 individuals in the ABM vs. ODE). In the ODE, red deer populations were slightly increased (1.2 times, 42 individuals) to reduce the chance of woodland loss, whereas in the ABM they were decreased (0.44 times, 15 individuals) (

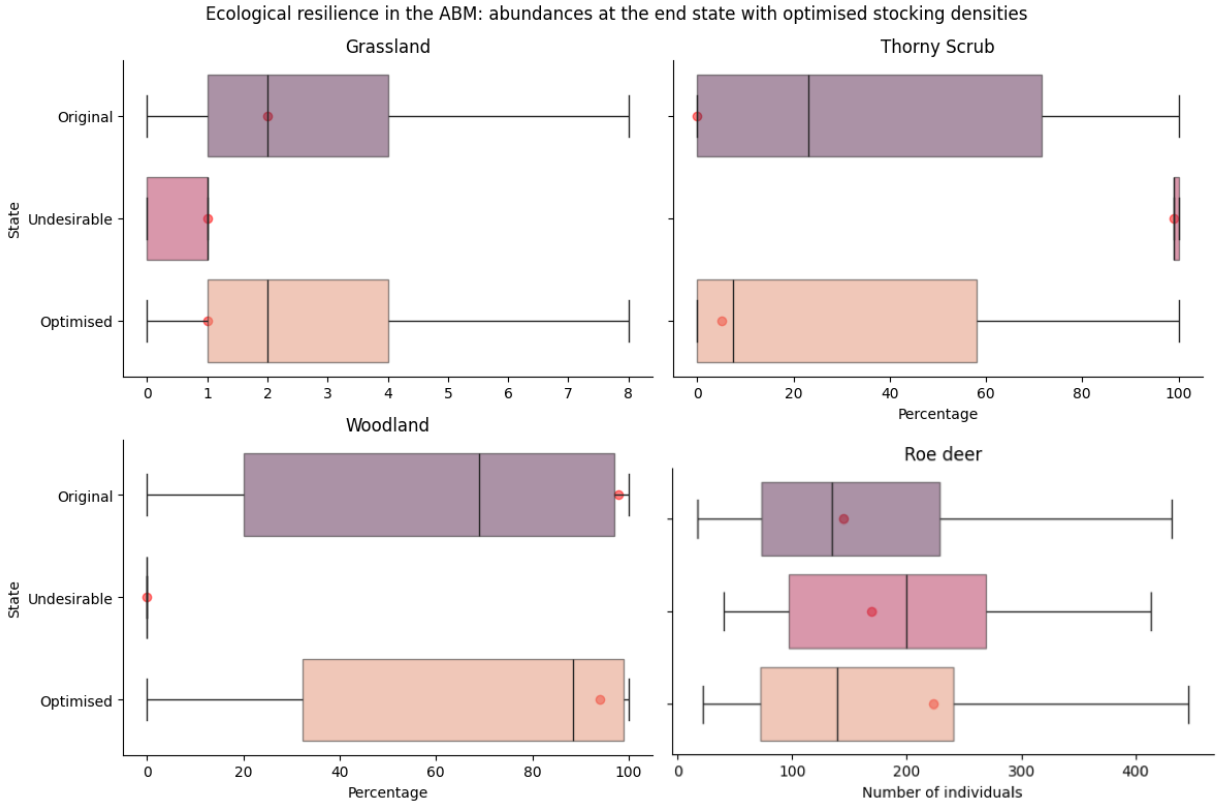
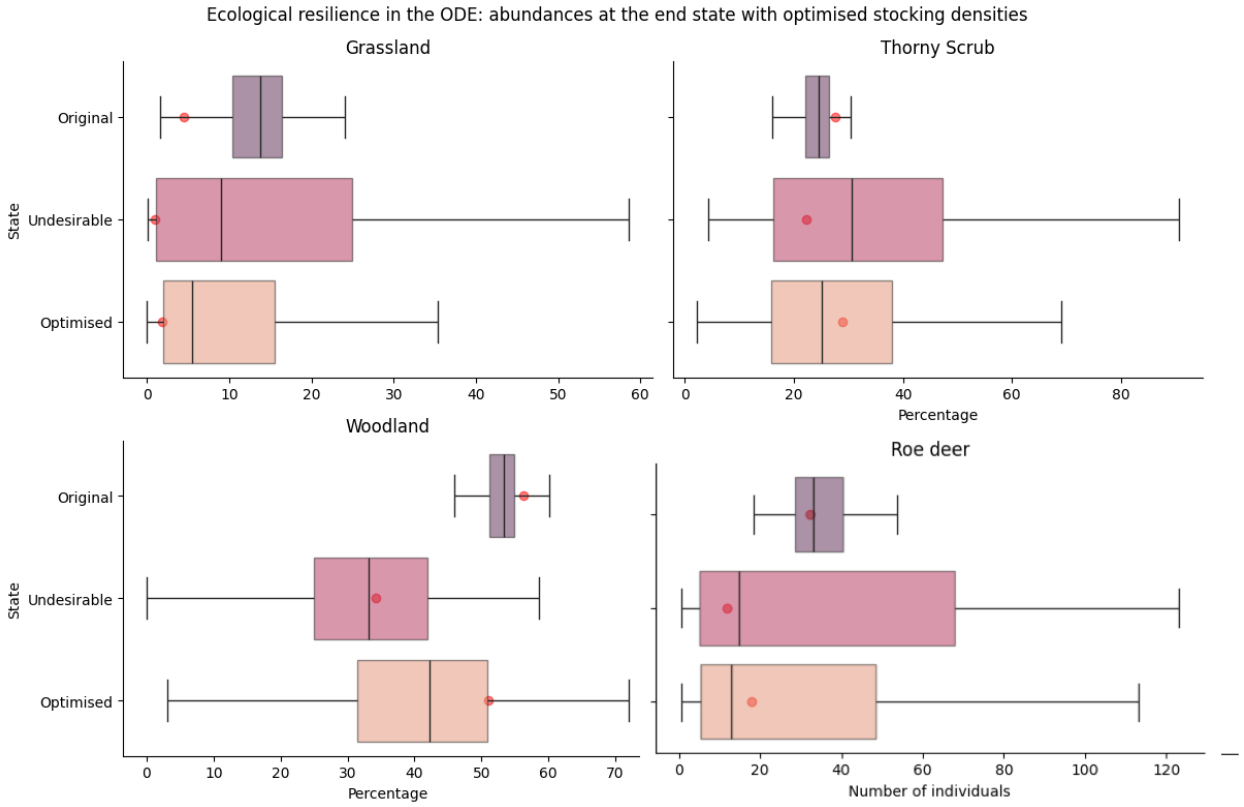


Figure **5.7**). When applied to all 100 accepted parameter sets, end states in the ABM were much more varied than the ODE: the median amount of woodland was higher in the optimised state, but some parameter sets were still scrubland dominant (>50% scrub).


Ecological resilience in the ODE: abundances at the end state with optimised stocking densities
Grassland
Thorny Scrub
Woodland
Roe deer
State
Original
Undesirable
Optimised
Percentage
Number of individuals

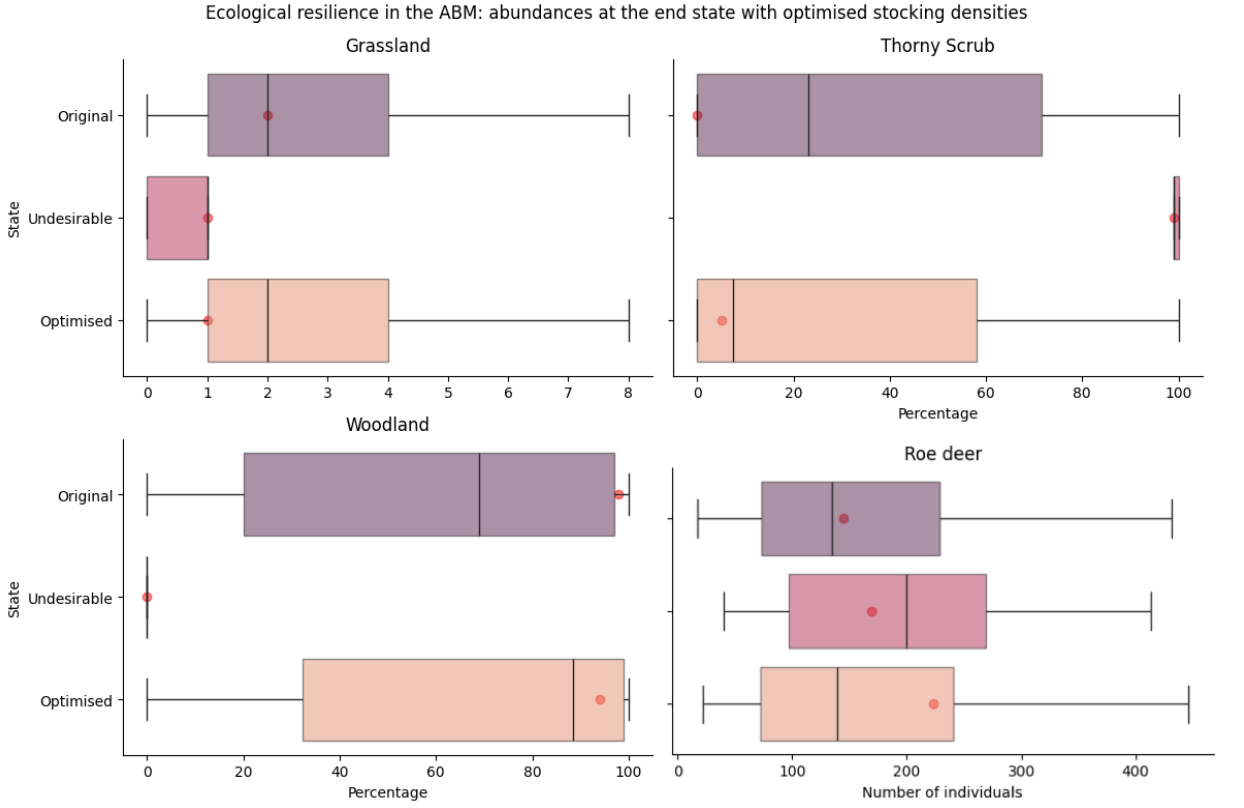

Ecological resilience in the ABM: abundances at the end state with optimised stocking densities
Grassland
Thorny Scrub
Woodland
Roe deer
State
Original
Undesirable
Optimised
Percentage
Number of individuals

Figure 5.7 *GAs were used on the 'best' parameter set (defined as the one which passed the most filtering conditions) to optimise stocking densities with an aim of restoring the original stable state following a perturbation. The optimised output was then applied to all 100 accepted parameter sets. This graph shows the end state abundances for all 100 parameter sets, for ecosystem elements whose abundances are unmanaged by humans: habitat types (percentage) and roe deer (number of individuals) under three scenarios: 1) current dynamics, 2) the undesirable state following a perturbation, and 2) the state after stocking densities are optimised. Outcomes of the ODE are shown at the top, and the ABM at the bottom. Red dots depict the outputs using the 'best' parameter set.*

5.4 Discussion

The models presented in this paper demonstrate the existence of a series of end states at Knepp which are largely dependent on management decision-making regarding stocking densities. Initial conditions have some bearing on the end state of the ABM but not in the ODE; this could indicate the ODE is not sufficiently complex, as in reality, reintroducing grazers to ecosystems at different stages of succession could impact the factors driving habitat formation and vegetation heterogeneity, the colonisation times of other species, and therefore overall composition and biodiversity (Gorman, 2018; Plieninger et al., 2014). Further, the high impacts of herbivory limit the maximum possible amount of grassland in the ODE at 45%, after which the system moves towards bare ground; the likelihood of this outcome could be revisited with further data and expert knowledge. Overall, both the ODE and the ABM systems have similar high-level insights and dynamics despite varying levels of complexity, shifting from woodland, to scrubland, to grassland-dominant with increasing numbers of grazing species and moving towards bare ground at very high stocking densities. This aligns with studies showing that grazing can increase biodiversity and habitat heterogeneity (Bakker et al., 2016), but too much can have negative effects (Mills et al., 2020) and lead to homogenisation of the environment (Beguin et al., 2022; Côté et al., 2004; Iida et al., 2016). Very high stocking densities of 9-14 and 45-50 times the collective 2020 Knepp stocking levels were needed to shift to end states of 0% woodland or 0%

scrubland, respectively, indicating these extreme model end states are difficult to achieve without exceeding conventional practice. For context, 2-3 times the 2020 stocking levels would rank among the highest of global wild herbivore densities (Fløjgaard et al., 2022; Manzano et al., 2023; Santini et al., 2022) and 15 times would surpass the maximum observed in conventional agriculture in Europe (Eurostat, 2020) (Supplementary Information). Generally, much smaller changes were required to shift to less extreme end states or to reduce the impact of a perturbation, particularly in the ABM, which had outputs of anywhere from 0-2.5 times 2020 densities.

Model results are not necessarily predictive of future states, but they can be used to assess scenarios and the sensitivity of the system to future stressors, i.e., how strong perturbations need to be to have significant ecosystem effects (Bailey & van der Grient, 2020). Results of the perturbation experiments demonstrate that with current stocking densities of reintroduced species, the Knepp ecosystem is generally resilient to shocks and changes in future environmental conditions. However, disturbances of sufficient size and duration can shift the end state in both the ODE and ABM, indicating a need for flexible and adaptive strategies in the face of novel future environmental conditions. Increasing adaptive capacity, or the ability of a system to cope with changes (Brooks & Adger, 2005), and practising adaptive management (Folke et al., 2004) are promising approaches for maintaining or creating desired states and ecosystem functions. Although some consider the ultimate goal of rewilding to be restoring self-sustaining ecosystems with minimal or no ongoing management (Carver et al., 2021), this finding suggests that, in the face of new environmental conditions, some ongoing monitoring and management may be needed to avoid ecosystem collapse.

The models can assist with adaptive management by optimising interventions for engineering the system towards desirable end states and increasing resilience. Outputs of the optimisation experiments were broadly intuitive: for example, in the ODE fallow and red deer – both large intermediate feeders who are known to impact woody vegetation (Knepp Estate, 2022a, 2022b) - were most successful at reducing woodland and thorny scrub, therefore steering the system towards higher amounts of grassland. The ABM outputs were likely more realistic than the ODE, in that they required less drastic changes in individual species' stocking densities to shift towards a new end state or minimise the impact of a perturbation (0-2.5 times current levels vs. 0-30 times in the ODE). However, the slower runtime of the ABM was a hinderance for the optimisation process as stocking densities had to be limited at 3 times their 2020 levels; some end states could only be reached with very high densities (**Error! Reference source not found.**), so this limited the range of end states that could be explored. In both models, optimising stocking densities could engineer resilience into the system by lessening the impacts of disturbances or facilitating the return of the system back towards its original stable state. Both models had similar trends in that increasing Exmoor ponies and Tamworth pigs, and decreasing fallow deer and Longhorn cattle, generally made the system more resilient to shocks. The optimised stocking densities presented here show one possible solution, but others may exist; future work could run the genetic algorithms many times to provide management with a range of possible outcomes.

When optimisation outputs are applied to all 100 accepted parameter sets, the end states are highly variable in the ABM whereas they are broadly similar in the ODE. The same is true of the 100 accepted parameter sets under current stocking densities: end states in the ABM range from

fully woodland, scrubland, or grassland, to mosaic ecosystems with various percentages of each habitat type, whereas the ODE remains predominantly woodland mosaic. This is likely due to the calibration process followed for each model, as the ODE utilised a single genetic algorithm output to inform the priors for the ABC. This was due to challenges with finding acceptable solutions in systems, like Knepp, that are not sufficiently data-limited for a simple random search with rejection, but not so data intensive that acceptable models can be found based solely on optimisation outputs (see Chapter 3: Neil et al., in prep). In contrast, the ABM used the outputs of 100 distinct genetic algorithms and therefore had a wider parametric spread. Future work could test this by applying the exact ODE calibration process to the ABM (i.e., picking just one ABM GA output and assuming, for each parameter, a uniform prior for the ABC process ranging ±10% of the GA values). The wider range of outputs suggests the ABM may be able to give a better idea of uncertainty in predictions. Instead of relying primarily on the 'best' parameter set, future work could organise the ABM end states into categories (i.e., woodland, scrubland, grassland-dominant, mosaic) and apply experiments to them separately, potentially giving a better understanding of risks and uncertainty. If data or expert opinion becomes available that can identify the most likely end state of the system, this could become an additional filter in future work.

Despite being more complex and passing nearly all filtering conditions, the ABM generated some unexpected outputs when applied to long-term dynamics. The best parameter set led to an extreme end state of nearly 100% woodland with zero thorny scrub plants, meaning scrubland could never naturally recover under any scenario. Running the system to its end state without any culling also showed that populations of Longhorn cattle could increase to unrealistically high

numbers. This may be a result of the system being so tightly controlled that realistic ecological and population dynamics are not observed, making it difficult to ensure the model is behaving sensibly. Sufficiently capturing realism may be easier in less intensively managed systems. Although both models incorporated long-term filters to help exclude unrealistic outcomes, this result suggests additional ones may be needed in the ABM. The existing long-term filters are somewhat subjective due to the absence of data about what will happen in the future at Knepp; these could be revisited as more information becomes available. Likewise, at very high stocking densities, localised mortality was observed to occur in the ABM, with impacts on ecosystem end states and potentially on model runtime. The assumption that agents of the same species would be reintroduced to the same general area was thought to be accurate since the animals typically live in herds. However, these and other spatial assumptions could be amended to assess their impacts on outcomes, for example incorporating more complex movements such as the avoidance of areas with high densities of competitors (Morales et al., 2010), different types of movements (i.e., migration, foraging) (Jeltsch et al., 2013; Schlägel et al., 2020), or more collective decision-making to better simulate the dynamics of herds (Morales et al., 2010) (see Chapter 4: Neil et al., in prep).

Both models had similar high-level insights, which suggests using the ODE – the 'simplest accurate model' – is adequate and preferable for exploring these questions when applied to moderately data-limited systems (i.e., those that have abundance data in addition to expert knowledge) like Knepp. The ODE model is faster and easier to work with, allowing it to explore a wider range of experiment scenarios than the ABM. However, it had a narrower range of end states due to calibration challenges, and it may therefore have captured less uncertainty in

predictions. Some unexpected experiment outputs likewise suggest it may be unable to capture essential aspects of the system's dynamics. Some results could be improved or contextualised with the inclusion of further data and expert knowledge; for example, the large changes in stocking density required to shift the system to a new end state may suggest that per capita herbivory parameters are not sufficiently high, or it could simply suggest that the chosen end state cannot feasibly be reached. However, especially given the challenges with identifying even a single acceptable parameter set in the ODE (see Chapter 3: Neil et al., in prep), it is also possible that the model needs additional mechanisms to fit the available data and constraints.

A benefit of exploring the same questions with multiple models, especially in situations where data is somewhat limited so that the models have some freedoms, is the ability to compare results and understand which elements are missing. There are several opportunities to incorporate more complexity into the ODE which could improve calibration and realism of results, especially when applied to systems with moderate data availability, like Knepp. This could involve adding more granularity to vegetation nodes, for example separating 'woodland' into age-dependent nodes of 'saplings' and 'trees' and adjusting their interactions as necessary. Another pathway could be to change the ODE from yearly to monthly time-steps, or make use of the discrete-time Lotka-Volterra equation (Bischi & Tramontana, 2010). Finally, incorporating heterogeneity (Poggiale & Auger, 2004), or spatial dynamics of herbivory, dispersal, habitat competition and facilitation could be interesting next steps (Neuhauser & Pacala, 1999; Wu et al., 2019). The ABM is shown to be sensitive to spatial assumptions in this paper, so future work would need to ensure that the implementation of space matches in the ODE for accurate comparison.

Incorporating these mechanisms into the ODE could generate more acceptable parameter sets and realistic outcomes, while still maintaining the benefits of a simpler model.

Summary: Paper 3

Paper 3 applies, for the first time, an ODE (as described in Paper 1) and a more complex ABM (as described in Paper 2) to questions of resilience at the Knepp Estate. Long-term filters were incorporated to the rejection sampling process following Paper 2's finding that some nodes, particularly roe deer, have wide posteriors and could experience unrealistically high population growth. Despite differing levels of complexity, both models produce similar and intuitive high-level insights. They demonstrate a series of end states which are largely dependent on stocking density and reveal a need for adaptive management in the face of potentially novel future conditions. The models can be used to assist adaptive management by, for example, optimising stocking densities for increasing resilience or engineering towards a desired end state.

By comparing model outputs and identifying advantages and disadvantages of each, this study can help guide inform model choice of future studies. There are several practical advantages and disadvantages to each model: the ABM had a wider range of end states which means it may be able to better capture uncertainty in predictions, but it generated some unrealistic outputs when applied to long-term dynamics, despite behaving sensibly in the short-term (Paper 2). It may therefore be best suited to exploring near-term dynamics in its current form, pending further data availability. The ODE, by comparison, was faster and easier to work with, but results suggest it may be too simplistic and potentially missing some important mechanisms. Overall, the models had similar high-level insights, indicating the simpler ODE can adequately capture the system and is therefore preferable. However, for case studies like Knepp which have a relatively high amount of data, further mechanisms may need to be added to the model to improve its calibration process and realism of some outputs.

A benefit of exploring the same questions with multiple models is the ability to compare results and understand which elements are missing. In this case, the inclusion of mechanisms in the ODE such as spatial dynamics of herbivory, vegetation facilitation, and competition, or increased granularity for habitat nodes (i.e., separating 'woodland' into 'saplings' and 'trees' and treating their interactions differently) could be valuable next steps, combining the relative speed and simplicity of the ODE with the realism of the more complex ABM.

5.5 Supporting Information

1. Version 2.0 of the ABM

There are two changes between v1.0 (as described in Neil et al., *in prep*) and an updated version of the ABM. First, the rejection rate for the roe deer criteria was high (>90%) during the GA process as populations tended to rise beyond 500 individuals using the first version; to increase the number of accepted runs, a probability chance of natural mortality for roe deer was added to each time-step based on their average lifespans in the new version (Neil et al., in prep).

Second, consumer energy levels are simplified: in the first version, consumer energy levels could residually decline so that after very long periods of time, their populations could fall to zero. Since the experiments in this paper require running the model for hundreds of years, the code was updated so that at each time-step, all consumers begin with 0 energy (as opposed to a losing -1 energy, as per the first version). All consumers are initialised with 0 energy, as are new offspring (as opposed to a random value between 0-1 or 0 and the parent's energy levels, respectively). If consumer energy stores do not reach 1 at each timestep (as opposed to their energy dipping below 0, as per the first version), they die and are removed from the system.

2. The GA process, and accepted parameters

In the ODE, 100% of the 100,000 runs passed the two ecological criteria, and 21% (20,656) passed all filters for habitat and roe deer conditions. The top 100 runs passed a total of 97-100% of filtering conditions. Correlation matrices and histograms for the accepted parameters in the ODE are shown in Figures A5.1 and A5.2 respectively.

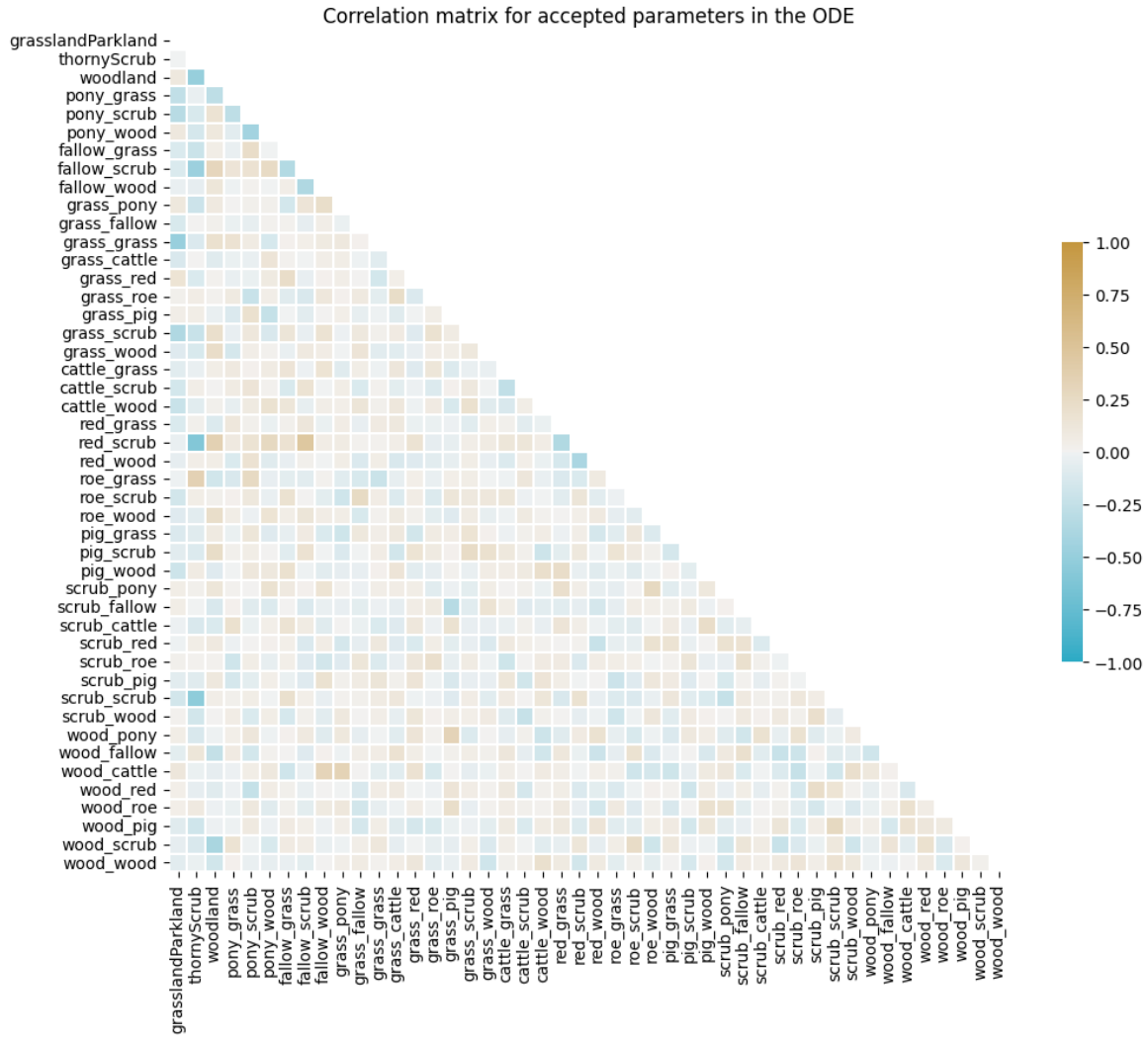


Figure A5.1: Correlation matrix for the accepted parameters in the ODE.

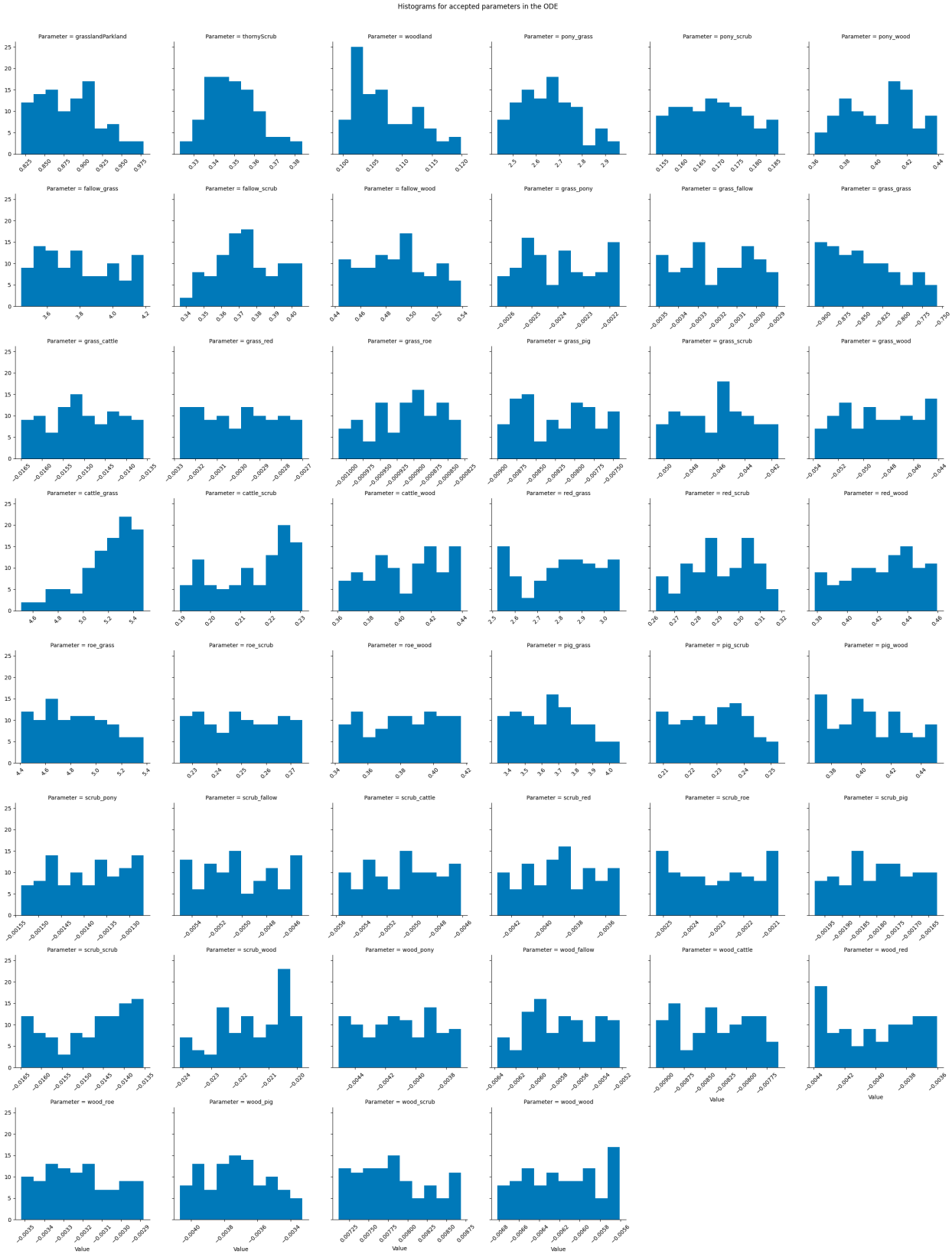


Figure A5.2: Histograms for the accepted parameters in the ODE.

Running each GA iteration to 500 years proved to be prohibitively time-consuming in the ABM, in part because roe deer populations often exploded in number. The model was therefore run ten years into the future and outputs rejected if roe deer populations exceeded 2x their maximum 2020 values (equivalent to 160 individuals; this value was arbitrary but thought to represent a realistic growth limit). Only the final GA outputs were passed through the two long-term ecological criteria in the ABM.

To save time and computational power, the 100k runs of the ABM are first run only to 2020 and filtered through the habitat and roe deer conditions. Those that pass are ordered by the number of filters passed and looped through, running 500 years into the future until 100 parameter sets are identified that pass all habitat, roe deer, and ecological criteria. Of the 100k runs, 2,245 (2.2%) pass the habitat and roe deer filters. The top 100 runs pass 79-95% of filtering conditions. Correlation matrices and histograms for the ABM are shown in Figures A5.3 and A5.4 respectively.



Figure A5.3: Histograms for the accepted parameters in the ABM.

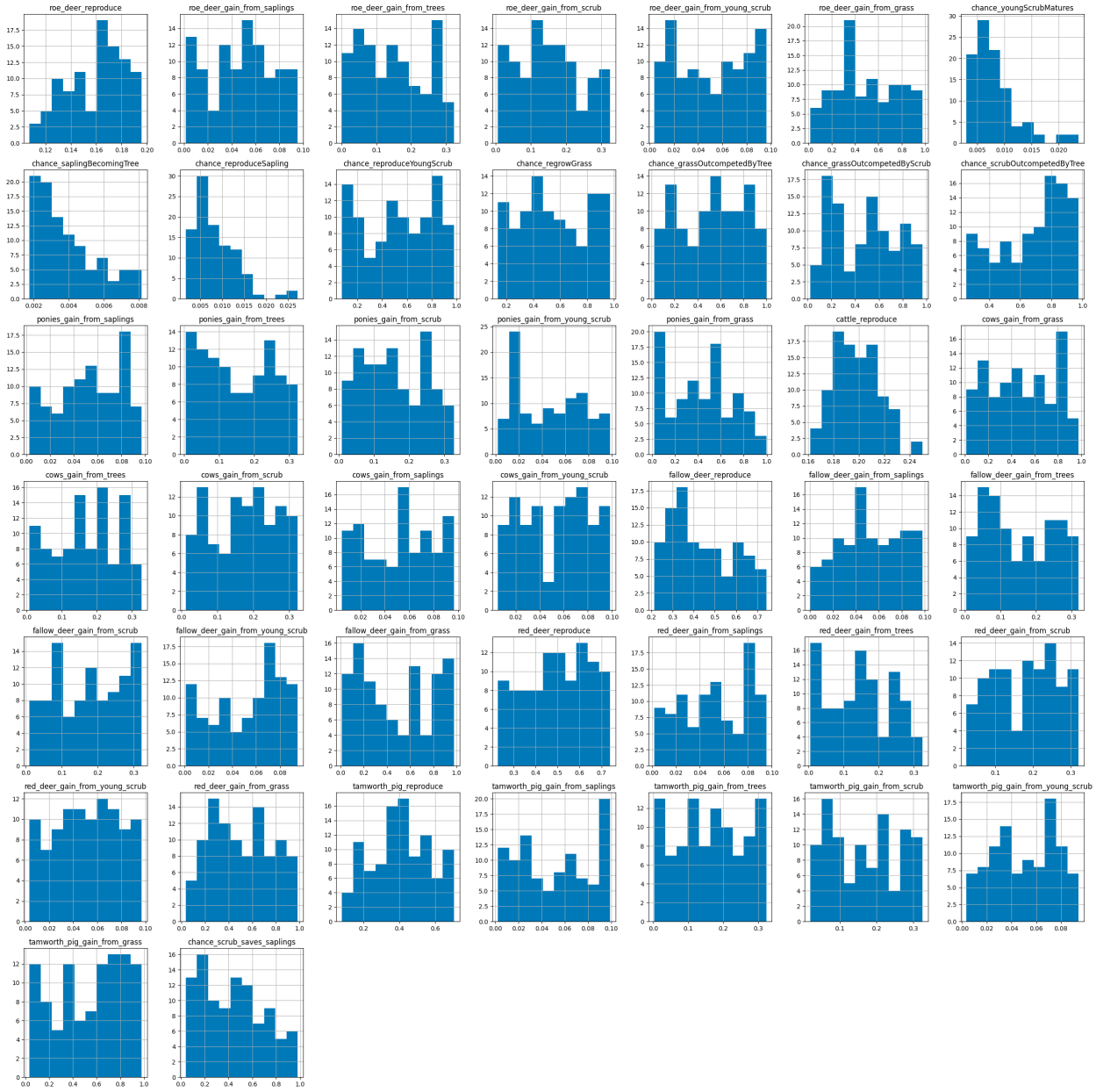


Figure A5.4: Histograms for the accepted runs in the ABM.

3. Details on the best parameter sets used

A parameter set was identified for the ODE which passes 100% of filtering conditions and the two ecological constraints. The outputs are as follows:

- Grassland growth rate: 0.91
- Thorny scrub growth rate: 0.35
- Woodland growth rate: 0.1

	Exmoor pony	**Fallow deer**	**Grassland**	**Longhorn cattle**	**Red deer**	**Roe deer**	**Tamworth pig**	**Thorny scrub**	**Woodland**
Exmoor pony	0	0	2.54	0	0	0	0	0.17	0.42
Fallow deer	0	0	3.87	0	0	0	0	0.39	0.46
Grassland	-0.0023	-0.0033	-0.91	-0.016	-0.0029	-0.001	-0.009	-0.05	-0.048
Longhorn cattle	0	0	5.3	0	0	0	0	0.23	0.42
Red deer	0	0	2.9	0	0	0	0	0.29	0.42
Roe deer	0	0	5	0	0	0	0	0.25	0.39
Tamworth pig	0	0	3.55	0	0	0	0	0.22	0.45
Thorny scrub	-0.0014	-0.0047	0	-0.0047	-0.0036	-0.0023	-0.0016	-0.014	-0.02
Woodland	-0.0045	-0.0063	0	-0.0089	-0.0041	-0.0035	-0.0038	0.0083	-0.006

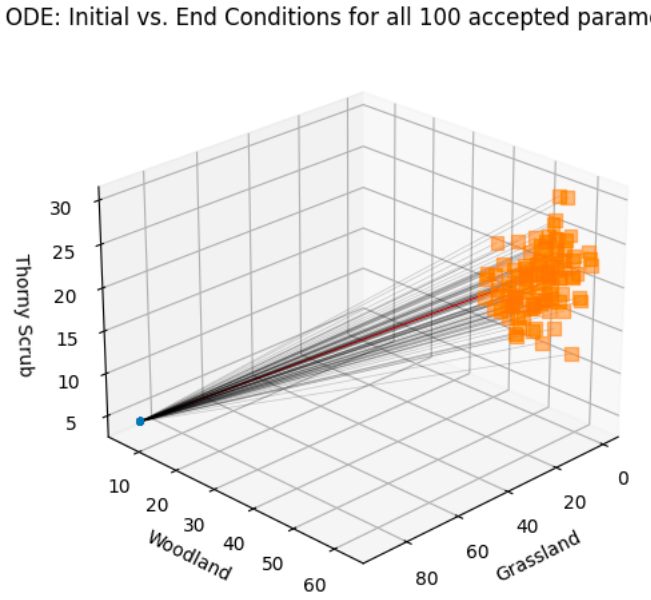
A parameter set was identified for the ABM which passes 95% of filtering conditions and the two ecological constraints. The outputs are as follows:

- Chance of reproducing sapling: 0.009
- Chance of reproducing young scrub: 0.96
- Change of regrowing grass: 0.38
- Chance of sapling becoming tree: 0.006
- Chance of young scrub becoming scrub: 0.009
- Chance of scrub being outcompeted by tree: 0.83
- Chance of grass being outcompeted by tree: 0.89
- Chance of grass being outcompeted by scrub: 0.54
- Roe deer reproduction: 0.17
- Energy roe deer gain from grass: 0.25
- Energy roe deer gain from trees: 0.14

- Energy roe deer gain from scrub: 0.04
- Energy roe deer gain from saplings: 0.09
- Energy roe deer gain from young scrub: 0.01
- Fallow deer reproduction: 0.48
- Energy fallow deer gain from grass: 0.33
- Energy fallow deer gain from trees: 0.13
- Energy fallow deer gain from scrub: 0.18
- Energy fallow deer gain from saplings: 0.09
- Energy fallow deer gain from young scrub: 0.01
- Red deer reproduction: 0.59
- Energy red deer gain from grass: 0.34
- Energy red deer gain from trees: 0.01
- Energy red deer gain from scrub: 0.32
- Energy red deer gain from saplings: 0.07
- Energy red deer gain from young scrub: 0.01
- Energy ponies gain from grass: 0.4
- Energy ponies gain from trees: 0.24
- Energy ponies gain from scrub: 0.2
- Energy ponies gain from saplings: 0.003
- Energy ponies gain from young scrub: 0.02
- Cattle reproduction: 0.21
- Energy cows gain from grass: 0.38
- Energy cows gain from trees: 0.07
- Energy cows gain from scrub: 0.01
- Energy cows gain from saplings: 0.07
- Energy cows gain from young scrub: 0.07
- Pig reproduction: 0.47
- Energy pigs gain from grass: 0.18
- Energy pigs gain from trees: 0.18
- Energy pigs gain from scrub: 0.24
- Energy pigs gain from saplings: 0.03
- Energy pigs gain from young scrub: 0.07
- Chance that scrub saves saplings from herbivory: 0.17

4. Landscape analysis

End states for each of the 100 accepted parameter sets in the ABM and the ODE are shown in Figure A5.5. The ODE end states are all similar, likely due to differences in the calibration process (only one acceptable GA output was identified versus 100 for the ABM).



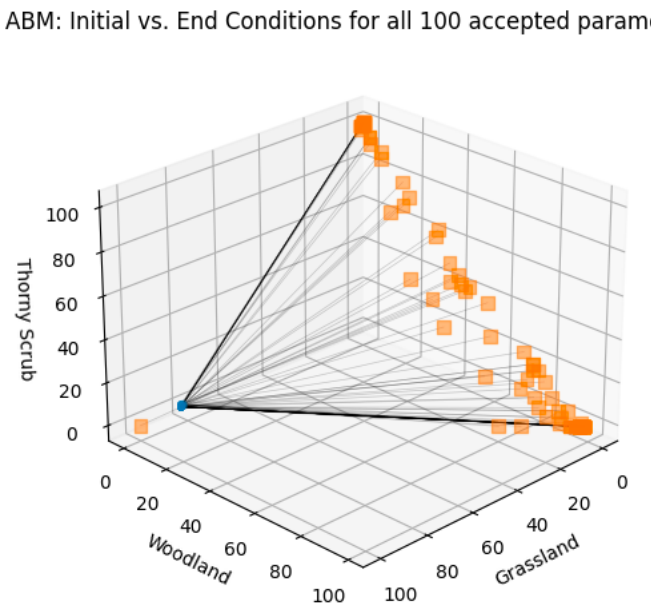


Figure A5.5: End states for all 100 accepted parameter sets in the ODE (top) and ABM (bottom). The blue dot shows the initial conditions, and orange squares show the range of possible end conditions.

In the ODE, every time a miniscule change to stocking densities is made, the trajectory of the ecosystem moves smoothly to a new end state (Figure A5.6). This is likely because the end state is not a 'true' equilibrium but instead dependent on management control.

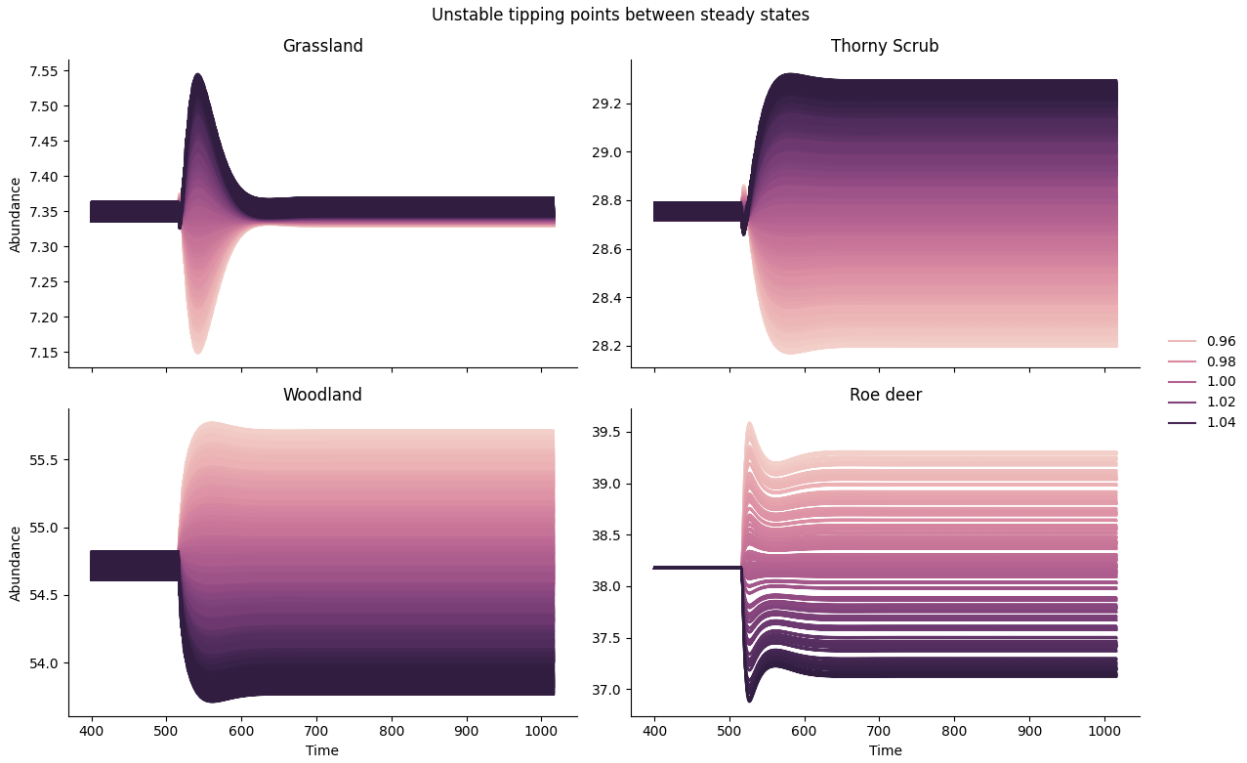


Figure A5.6: A time-series showing how the trajectory of end states in the ODE smoothly shifts when tiny changes to stocking densities are made. This graph shows only the 'unmanaged' ecosystem elements: habitats, and roe deer.

At very high stocking densities, spatial effects in the ABM prevent the system from going fully to bare ground (Figure A5.7). If consumers move randomly with no preference for any habitat type, the amount of bare ground in the end state was 27%, vs. 12% when consumers move preferentially (with stocking densities 50x their 2020 levels). The system end states are sensitive to these spatial decisions (Figure A5.8).

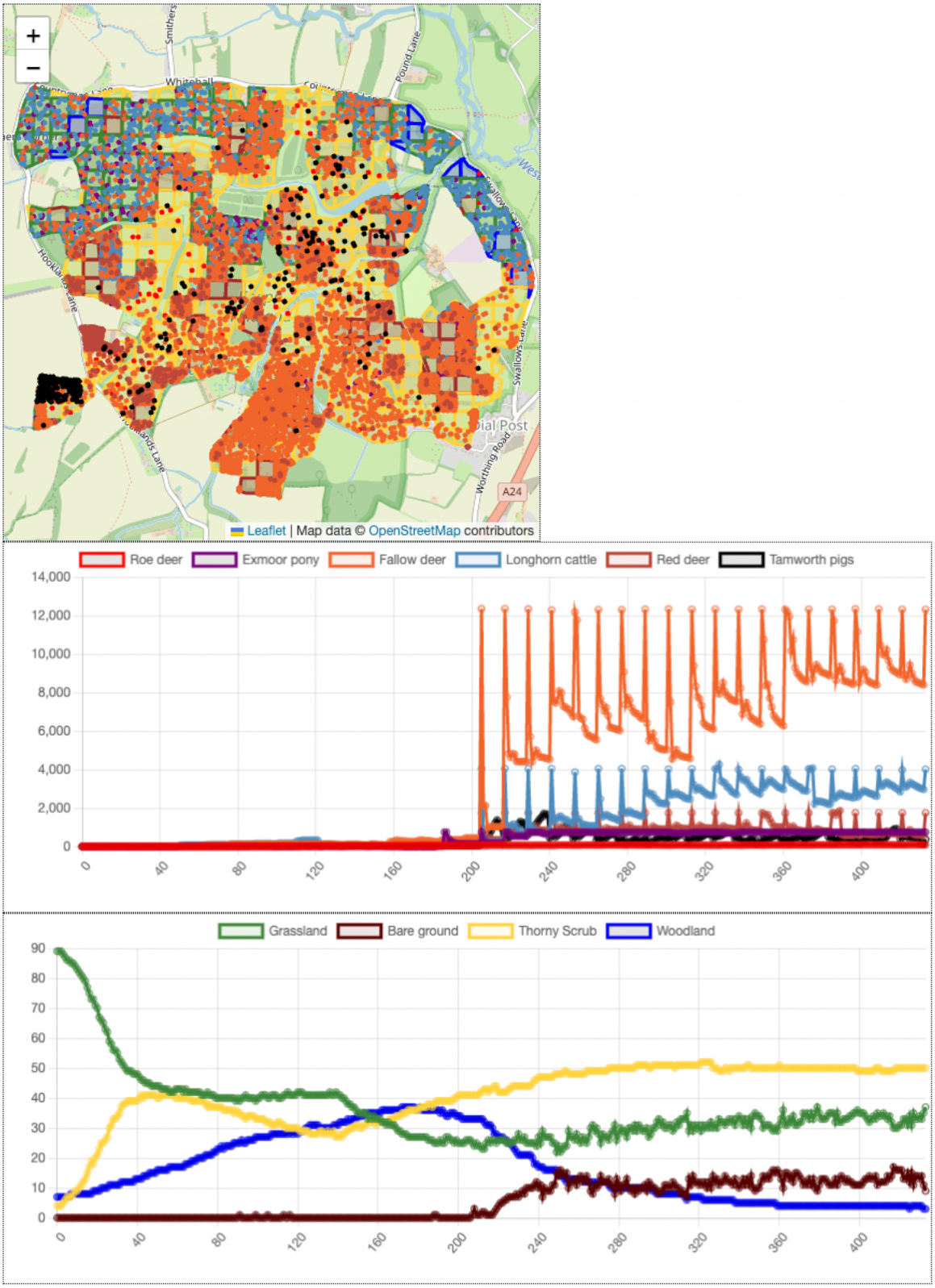


Figure A5.7: This figure shows the impacts of 50x 2020 stocking densities at time-step 500. Consumers can experience localised mass die-offs after each annual forcing as they consume resources faster than they can spread to new areas; this leaves some areas with relatively low enough herbivory levels for grassland maintenance. Tamworth pigs (black dots) and fallow deer (orange dots) are very concentrated in the southwest section of the estate following a recent annual forcing. Bare areas (brown)

are typically empty as they are not a preferred habitat type for any consumer species. Consumers instead congregate to grassland, woodland, or thorny scrubland, where their populations then rapidly plummet in the initial steps after annual forcings.

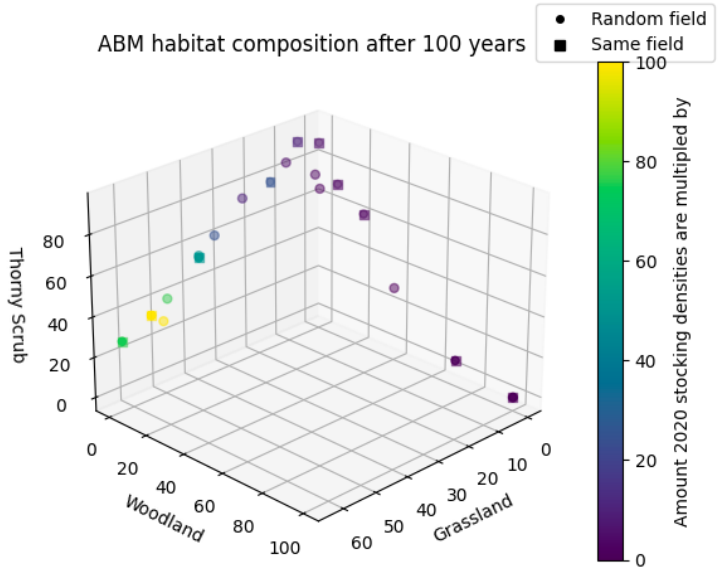


Figure A5.8: A landscape analysis for the ABM with different stocking densities at 100 years, showing the sensitivity of the system to two different spatial assumptions: all consumers are reintroduced to random fields, or consumers of the same species are reintroduced to the same field at each annual forcing.

5. Genetic algorithm experiment: altering the end state

Genetic algorithm outputs when collectively varying all reintroduced species' stocking densities to achieve a given end goal are shown in Table A5.1.

Table A5.1: The amount each 2020 stocking density needs to be multiplied by to achieve a given end goal.

Model	**Experiment**	**Exmoor pony**	**Fallow deer**	**Longhorn cattle**	**Red deer**	**Tamworth pigs**
ODE	45% grassland	26.2	26.7	0.55	29.8	5.7
ODE	50% thorny scrub	26.8	0.72	1.3	25.6	12.1
ODE	75% woodland	0.64	0.06	1.4	0.32	0.26
ABM	33% grassland	0.1	1.6	0.45	0.05	1.7

ABM	33% scrubland	1.8	0.95	0.23	2.3	0.56
ABM	Woodland mosaic	0.4	1	1	0.72	2

6. Long-term perturbation experiments

In the following experiments, the system is run to its end state before being perturbed (Figure A5.9). In the ODE, end states are the same compared to if the perturbations happened in the short-term. In the ABM, two end states would result if perturbations occurred in the long-term: a woodland-dominant one, or a grassland-dominant one with 0% woodland. The latter occurs with long durations (>37 years) of low to no vegetation growth (changes of 0-0.1x current values), and unlike in the short-term perturbations, does not become thorny scrubland as this node dropped to zero in the original end state.

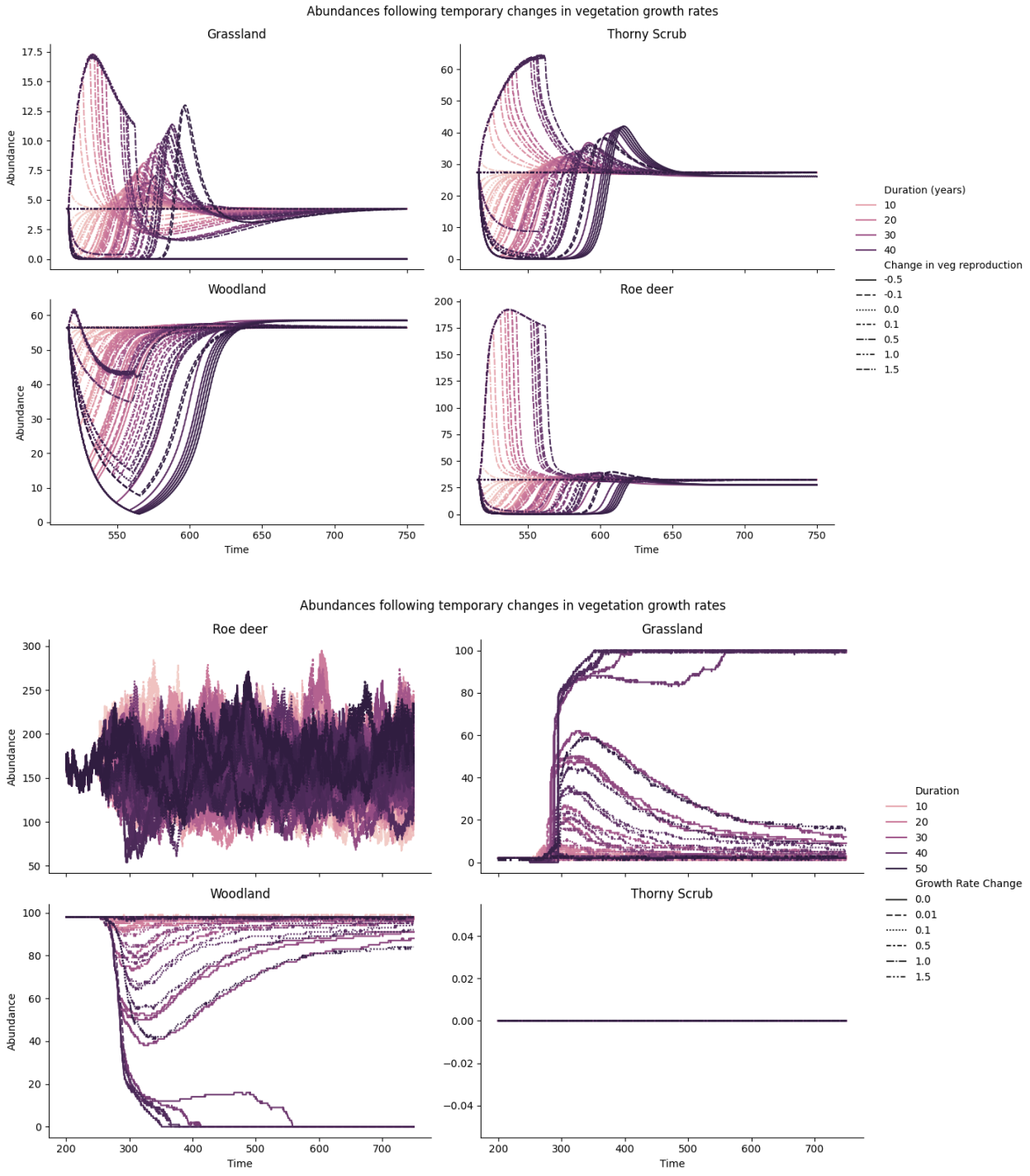
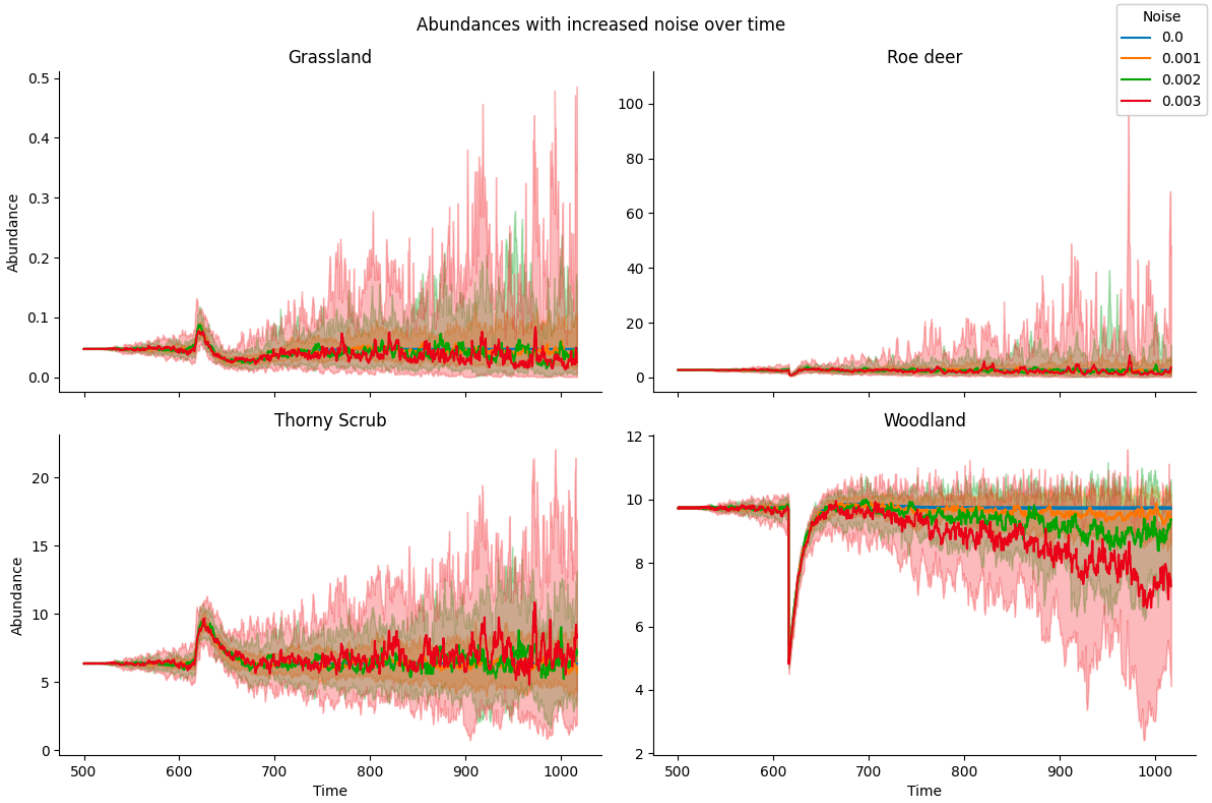


Figure A5.9: Results of the first perturbation experiment for the ODE (top) and ABM (bottom) when perturbations occur after the system has been run to its end state: the graphs begin at the end state and show the effects of changes to vegetation growth rates at different magnitudes and durations on abundance (percentage habitat type, or number of individuals for roe deer).

In the second perturbation experiment, the system is run to its end state before vegetation growth rates are subjected to increasing amounts of noise. After 100 years, 50% of woodland is lost to simulate an extreme event and assess the extent to which the ecosystem can recover (Figure A5.10). The end states are the same in the ODE as those outlined in the main text, but the ABM begins with an extreme end state of 0 thorny scrub plants which cannot recover.



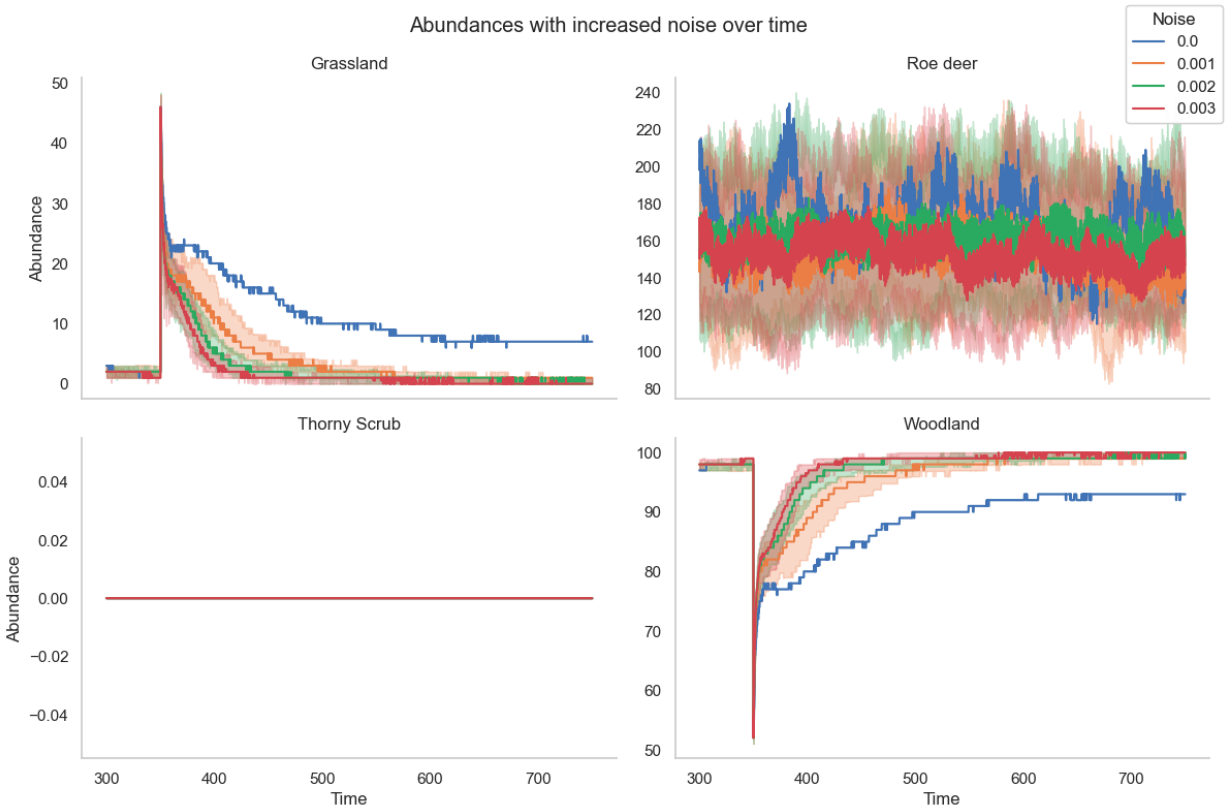


Figure A5.10: Results of the second perturbation experiment, in which the system is run to its end state before vegetation growth rates are subjected to increasing amounts of noise (ODE: top, ABM: bottom). Plots shown the median and 95th percentile.

If noise does not positively impact sapling growth rates in the ABM (i.e., growth rates at each time-step are bounded between chance_sapling_reproducing * noise, and chance_sapling_reproducing), woodland is much slower to regenerate and new end states can be achieved (Figure A5.11). This suggests that the positive impact of noise compensates for its negative impacts, allowing woodland to regenerate quickly.

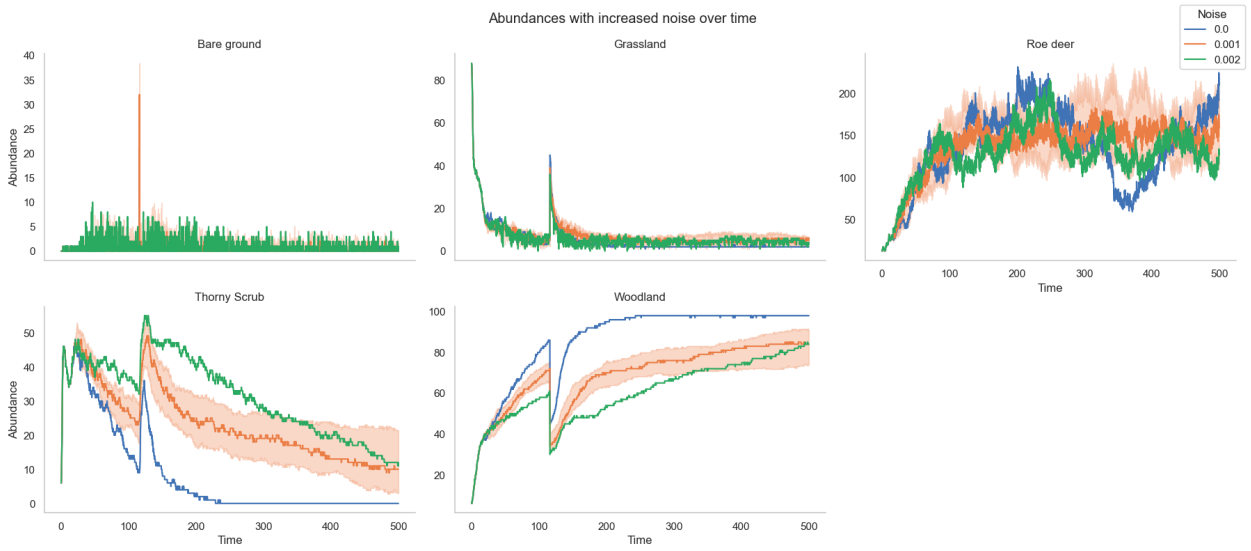


Figure A5.11: Ten example runs showing how the positive impacts of noise in the ABM allows woodland to regenerate quickly.

7. Livestock unit and biomass calculations

Livestock units (LU) were provided by Knepp (*2022, unpublished data)* and are calculated based on weight (kg) rather than fodder consumed. They are categorised by species, sex, and in some cases, age or additional impacts and behaviours (e.g., rootling). The averages of these LUs per species, and of the kgs (for biomass) were used in this paper (Table A5.2).

Table A5 2 Livestock units and biomass per species used in this paper.

Species	**Average Livestock Unit per individual**	**Average kg**	**2020 stocking levels (number of individuals)**
Fallow deer	0.1	44	247
Longhorn cattle	0.73	471	81
Red deer	0.13	86	35
Tamworth pigs	0.75	166	7
Exmoor ponies	0.5	300	15

CHAPER 6

Discussion and Conclusions

6 Discussion and Conclusions

The core question this thesis sought to address is how to provide a firm theoretical basis for recovering the health and resilience of degraded ecosystems. An ordinary differential equation (ODE) (Chapter 3) and a spatial agent-based model (ABM) (Chapter 4) were developed to explore questions related to rewilding, such as predicting the impacts of various management interventions and optimising approaches to attain a desired end state or avoid unintended consequences. The models were then applied to questions of resilience, and their outputs compared to assess the importance of model complexity (Chapter 5).

Key findings related to the thesis' two aims are outlined below. The significance of this research for the literature and wider rewilding field are discussed, as are opportunities for future research.

6.1 Summary of findings

6.1.1 **Aim 1:** Develop models that can inform rewilding decision-making at a case study in the UK by assessing the impacts of species reintroductions on ecosystem composition and resilience.

This aim was addressed by developing, testing, and validating two new ecological network models of varying complexity: an ordinary differential equation (ODE) and a spatial, more granular agent-

based model (ABM) **(Objective 1).** These were developed in collaboration with the Knepp Estate Rewilding Project in West Sussex, UK. The first paper (Chapter 3) presents the ODE, and the second (Chapter 4) the ABM. To the author's knowledge, this is the first time models have been applied to a dynamic rewilding system of interacting species, answering the call made by Delibes-Mateos et al., (2019) to use ecosystem models, in particular EEMs, for forecasting rewilding outcomes.

6.1.1.1 Model novelty and contributions

Both models represent valuable additions to the ecosystem network model literature. The model described in Chapter 3 represents the first use of EEMs in a moderately data-limited system (i.e., with time-series abundance data and expert knowledge available, rather than relying on stability or feasibility assumptions) to explore knock-on impacts of rewilding and management interventions on ecosystem dynamics and resilience. One emergent key finding of these constraints was that having positive intrinsic growth rates and negative diagonals of the α matrix for all ecosystem elements, as is standard in the EEM literature, is too unrealistic for this case (and potentially for most ecological systems), as it means consumer populations can continue growing even in the absence of any primary producers. Consumer diagonals and negative growth rates, totalling to twelve parameters in the ODE, could instead be set through logic via fixed parameters, rather than varied during optimisation. Updating the EEM framework to explicitly include such constraints could improve the accuracy of results, identifying simulations that are not fundamentally theoretically sound despite replicating the time-series data, while also simplifying the calibration process by narrowing the parameter space. However, the simplicity of the equation

is demonstrated to face challenges when applied to systems with abundance data and expert knowledge. Several potential ways forward are discussed.

The ABM presented in Chapter 4 represents an extension of the Lotka-Volterra EEM literature, in that both approaches involve generating many quantitative models, based on simple interaction networks, which are then filtered through plausible constraints to provide a range of future ecosystem states (Baker et al., 2016, 2019; Bode et al., 2017). However, the model presented in this thesis is the first time ABMs using rejection sampling, and additional complexities such as space and heterogeneity of individuals, have been used in this context. This methodology is demonstrated to be promising for projects interested in understanding emergent properties, the wood-pasture hypothesis, spatially dependent interactions such as vegetation competition and facilitation, or granular differences between the impacts of various candidate species for reintroduction. For systems like Knepp, which have relatively good data availability compared to other case studies in the EEM literature, simple random searches with rejection using the Lotka-Volterra-based approach can be difficult; ABMs are demonstrated to show potential for improving the calibration process and identifying a wider range of suitable parameter sets.

Chapter 5 uses, for the first time, an ODE and ABM to explore the impacts of rewilding and hypothetical management interventions on ecosystem resilience, and to assess what level of model complexity is necessary for answering these questions. This paper advances the rewilding and ecosystem modelling literature in two ways. First, it demonstrates the utility of these methods for assisting with adaptive management under changing environmental conditions. Second, by comparing model outputs and identifying advantages and disadvantages of each, it can help guide

future studies and inform model choice. In this case, the models had similar high-level insights, indicating the simpler ODE can adequately capture the system and is therefore preferable. However, for case studies like Knepp which have a relatively high amount of data, further mechanisms may need to be added to the model to improve its calibration process and realism of some outputs. Several potential next steps are discussed.

6.1.1.2 High-level insights and utility for rewilding management

In both papers, the models are used to assess the impacts of grazer reintroductions on the Knepp ecosystem, provide an understanding of possible outcomes resulting from different interventions **(Objective 2),** and predict how given end goals can be optimally achieved, for example through further species reintroductions or changes in grazer numbers **(Objective 3).** The ODE and the ABM had similar high-level insights into the system, notably that naturalistic grazing can drive the formation of mosaic wood-pasture habitats. Without species reintroductions, both models indicated the system would become woodland-dominant within several decades. This supports the literature which shows grazing can suppress tree regeneration (Kinnaird, 1974; Pollock et al., 2005), halt vegetation succession and maintain open habitats (Kowalczyk et al., 2021), and potentially support vegetation diversity (Sandom et al., 2014). Since habitat heterogeneity correlates with species richness (Bakker et al., 2016; Stein et al., 2014), this supports the idea that rewilding with large grazers can positively impact biodiversity.

Both the ODE and ABM produced acceptable dynamics based on simple interaction networks of species at Knepp, and therefore show promise as predictive support tools for assessing species

reintroductions and other decisions before implementation. Since both include uncertainty estimates, they can provide practitioners with quantitative estimates about the range of possible future system states, including any risks or potential unintended consequences of interventions. They can also be used to generate indicators for the state of the ecosystem, for example which parameter and timeframes will show whether the system will be maintained as a wood-pasture mosaic in the long-term. Sensitivity analyses of the models can assist with prioritising future research and data collection by identifying which observations will deliver the most benefit. Importantly, both methodologies can be flexibly and easily updated to incorporate both quantitative data and qualitative expert opinion. Most rewilding projects currently take a relatively subjective approach to management and decision-making, including at Knepp where decisions are often based on a 'feel for the land' (Dempsey, 2021). The models therefore have significant potential to complement this method by providing valuable information and support, while also facilitating ongoing collaboration, model improvement, and testing of expert assumptions.

In addition to providing an understanding of possible future ecosystem states, both models can be used to optimise management interventions towards a certain end goal. In this thesis, stocking densities of reintroduced grazers were optimised, as Knepp manages these at specific levels via annual culls. In some cases, the outputs of the optimisation process were intuitive, for example that a large browser or intermediate feeder would be the best candidate for reintroduction to reduce woodland cover (Figure 3.5, Figure 3.6). However, in other cases the results were unexpected: in the ABM, European elk were generally found to increase the risk of grassland and woodland collapsing in the long-term, whereas bison increased the risk for woodland but decreased grassland (Table 4.2). Likewise, increasing all stocking densities in the ABM did not consistently reduce the

risk of losing open areas in the long-term, nor did reintroducing any arbitrary large herbivore species (Table 4.2). This highlights the usefulness of predictive models for aiding decision-making: the ODE and ABM cannot make the decision, but they can provide managers with a holistic understanding of the range of possible outcomes, including any potential negative ones.

Both models are then applied to questions of ecosystem resilience (Chapter 5). They explore: 1) the existence of alternative end states at Knepp and possible transitions between them under future forcing scenarios **(Objective 4)**; 2) whether current management interventions are sufficient for maintaining desired states under novel future environmental conditions, and 3) the extent to which interventions can be optimised to build resilience into the system **(Objective 5)**.

The primary driver of the system end state is shown to be management decision-making regarding grazer stocking densities: any shift in their numbers changes the 'resilience landscape' and basins of attraction. Relative to the rewilding ideal of self-regulating ecosystems, Knepp is highly managed (i.e., with annual culls of reintroduced species, and temporary introductions of some male species to control reproduction). This level of control may help increase the resilience of the system to shocks, but large-magnitude or indefinite disturbances, such as increasing stochasticity in precipitation and temperatures due to climate change, can still lead to drastic shifts in end states. Results therefore demonstrate the importance of adaptive management in the face of changing environmental conditions, as adjustments to current management tactics may be required to build resilience into the system. It also suggests that, although some consider the ultimate goal of rewilding to be restoring self-sustaining ecosystems with minimal or no ongoing management (Carver et al., 2021), some ongoing monitoring and management may be needed to avoid

ecosystem collapses due to environmental change. Interventions could be relatively minimal: in this thesis, for example, the models could be used to optimise slight adjustments to stocking densities, with large impacts on the overall functioning and composition of the system. These results align with the resilience literature related to adaptive capacity, which emphasises the importance of focussing on an ecosystem's ability to cope with changes (Brooks & Adger, 2005), and with adaptive ecosystem management for helping maintain or create the desired states (Folke et al., 2004).

Although the thesis focussed specifically on the Southern Block of the Knepp Estate, the models were built with broader applicability in mind. Both the Lotka-Volterra equation and ABM frameworks used here have strong foundations in the ecological literature and have been applied across diverse settings (see Baker et al., 2016, 2019; Flores et al., 2019; Philips, 2020). The fundamental structures, species interactions, and management questions asked of the models are representative of common themes in rewilding projects, both in the UK and further afield. This theoretical foundation and methodological flexibility give them considerable potential for generating generalisable insights and for wider application. Managers at different sites could therefore adapt these models and use them as "what if" tools to explore scenarios relevant to their context, such as: "how many of *x* species should I reintroduce to achieve *y*?" or "what might be the ecological impact of *x* proposed management intervention?"

6.1.2 **Aim 2:** Analyse the significance of model complexity for answering questions related to rewilding and ecosystem resilience.

This aim was addressed by applying, for the first time, both models to questions of resilience, assessing the benefits and drawbacks of the simpler ODE versus the more complex ABM **(Objective 6)**, and comparing their outputs to identify under what conditions they were meaningfully different **(Objective 7).**

These questions were explored due to uncertainties around whether a simpler or more complex model can better capture moderately data-limited ecological systems. Existing literature suggests the simpler ODE (Chapter 3) could fit the data more easily due to a smaller parameter space; however, the more complex ABM (Chapter 4) could incorporate more priors, expert knowledge, and 'realism constraints,' potentially using the limited data more efficiently (Evans, 2012; Parunak et al., 1998). As discussed above, the models produced reasonable results and had some similar insights: both found, for example, that grazing with large herbivores can facilitate habitat heterogeneity, and management decisions regarding stocking densities can affect ecosystem end states and overall resilience. This finding supports Colon et al. (2015) who found that an ODE and ABM of a hypothetical predator-prey system exhibit similar qualitative behaviours, patterns and dynamics. However, there were several differences and practical benefits/drawbacks to the ODE and the ABM for exploring ecological questions. These can be broadly categorised into the following: a) speed and computational efficiency; b) ease of calibration; c) types of questions that could be explored, and d) realism of outputs. Each of these will be discussed in further detail below.

The relative simplicity of the ODE meant that it was much faster and less computationally intensive to run and analyse than the ABM. This aligns with Colon et al. (2015) who likewise found that "running ABM simulations [of a predator-prey system] and analysing their outputs were computationally intensive and time consuming tasks" compared to a simpler ODE. The faster runtime had several benefits for the calibration process as well as the experiments explored; for example, the genetic algorithm had significantly more iterations in the ODE than the ABM, which is likely a factor in the better fit of the ODE to the data (in Chapter 5, the top 100 parameter sets passed 97-100% of filtering conditions in the ODE vs. 79-95% in the ABM). The faster speed also made it easier to explore questions related to long-term dynamics like resilience. In Chapter 5, this allowed for a wider view of the system than the ABM: significantly more landscape analysis assessments for the ODE could be run (1,000 vs. 150 in the ABM) and bounds for stocking densities in the optimisation experiments could be much wider (0-100x current levels vs. 0-3x in the ABM), giving more opportunities to explore model boundaries and a richer variety of scenarios.

However, the simplicity of the equation-based approach may have contributed to challenges with calibration and rejection sampling in the ODE, as identified in Chapter 3. In both the ODE and ABM, simple 'reality check' constraints were used in addition to filtering conditions based on the empirical time-series data at Knepp. These were helpful for narrowing down the range of accepted parameters and improving the realism of outputs, and could in some cases improve calibration by setting fixed parameters. However, in our case it also made the rejection sampling process more difficult as many more runs were rejected. Optimisation using genetic algorithms assisted with narrowing the search within the parameter space, but ultimately in the ODE, manual searching

(i.e., manually removing nonsensical options from the parameter space) was also necessary. Arguably, the advantages of the simpler model regarding speed and computational power were outweighed by this time-consuming process. This also meant that uncertainty in predictions was reduced in the ODE, as only one genetic algorithm solution could be found that replicated the data while also passing the constraints. By comparison, the 'if-then' statements driving the ABM provided more freedom to write reasonable rules than the equation. The calibration process was much easier; no manual searching was necessary, and 100 distinct genetic algorithm outputs could be generated, providing a diversity of solutions and helping prevent collapse on a single local minimum. These calibration challenges may be unique to case studies, like Knepp, that are not sufficiently data-limited for a simple random search with rejection, but not so data intensive that acceptable models can be found based solely on optimisation outputs. In these cases, the Lotka-Volterra approach may be too simplistic to provide adequate outputs which fit the data while also passing constraints.

As mentioned above, the relative speed of the ODE enabled it to explore, in some situations, a wider range of long-term scenarios than the ABM. However, there were several questions that the ABM was better suited to answering. By incorporating spatial dynamics, the model could be used to assess interesting spatial dynamics relevant to rewilding, such as under what conditions the wood-pasture hypothesis and thorny scrub facilitation of saplings holds true. Emergent properties could also be explored in the ABM: in Chapter 4, the inclusion of spatial interactions between woodland and thorny scrub revealed an emergent behaviour in which, with large herbivores present, woodland regenerated more frequently in thorny scrubland than grassland or bare ground, likely due to the protection that scrub provides saplings. Without large herbivores present,

woodland regenerated more frequently in grassland and bare ground. The spatial ABM is therefore especially promising for rewilding projects which are interested in spatially dependent interactions and dynamics, such as the wood-pasture hypothesis and formation of mosaic ecosystems, or spatial experiments such as the importance of grazing refuges for wood-pasture formation (Smit et al., 2015). The inclusion of heterogeneity and additional granularity around herbivore movement and dietary preferences in the ABM was also useful for understanding the impacts of future reintroductions. Consumers have different movement patterns and habitat preferences in the model, and therefore differing impacts on vegetation. In some cases, these differences required species-specific management interventions. For example, in Chapter 4, European elk increased the risk of grassland and woodland collapsing, whereas European bison increased the risk for woodland but decreased grassland. This additional complexity made it easier to assess subtleties around which species – and why - would need to be reintroduced to achieve end goals.

However, despite being more complex, producing sensible outputs in the relative near term (Chapter 4), and passing a high percentage of filtering conditions (Chapters 4 and 5), the ABM still generated some unexpected outputs when applied to long-term dynamics. Roe deer populations were observed to have wide posteriors in Chapter 4, and therefore additional long-term filters were added in Chapter 5 to ensure this node could not explode to unrealistically high numbers. Despite these additional filters, some underlying dynamics were still fundamentally counterintuitive. The 'best' parameter set in Chapter 5 had an extreme end state of 100% woodland and zero thorny scrub plants, for example, and Longhorn cattle populations could increase to several thousand if culling did not occur. In the short-term (Chapter 4), the rejection sampling outputs appeared sound; these issues were not revealed until the model was applied to long-term

questions of resilience. The existing mechanisms, filters, and assumptions can be revisited and added to with more data and expert knowledge to enhance the ABM's ability to explore long-term dynamics, but in its current form, the model may be best suited to exploring near-term questions.

A benefit of applying multiple models to the same questions (especially in systems like Knepp where data is relatively limited, allowing the models to have some freedoms), is their outputs can be compared to understand which important mechanisms and processes may be missing. Colon et al. (2015), in their comparison of an ODE and ABM of a predator-prey system, recommended that "ABMs should, as much as possible, be developed in conjunction with simpler 'toy' models. Doing so facilitates the analysis, allows one to compare results, and finally to draw robust conclusions." Likewise, Parunak et al. (1998) encourages "explicit case comparisons of their ABMs with existing or potential EBMs [equation-based models, like ODEs] where relevant. Such comparisons are particularly valuable in simple systems in which one can trace the causes of divergence between the models." These comparisons can then guide further research and model improvements.

The ABM and ODE were found to have similar high-level insights in this thesis, indicating the ODE, as the 'simplest accurate model,' may be preferable for exploring many questions about this system (Hunter-Ayad et al., 2020). However, results of the landscape and experiment outputs in Chapter 5, in addition to the calibration challenges outlined above, suggest the ODE may be too simplistic to capture system dynamics at Knepp, and could benefit from the inclusion of further complexity. Several potential improvements are outlined in Chapters 3 and 5, such as the addition of noise, spatial dynamics of herbivory, dispersal, habitat competition and facilitation (Neuhauser & Pacala, 1999; Wu et al., 2019), and more granular vegetation components (e.g., separating

'woodland' into age-dependent nodes of 'saplings' and 'trees' and adjusting their interactions as necessary). Another potential avenue for model improvement could be changing the ODE from yearly to monthly time-steps, making use of the discrete-time Lotka-Volterra equation (Bischi & Tramontana, 2010), incorporating heterogeneity (Poggiale & Auger, 2004) or more complex interactions such as nonlinear Type II functional responses, which have been frequently observed in herbivores (Gross et al., 1993). Including some of these mechanisms into the ODE could generate more realistic outcomes, while still maintaining the benefits of a more simplistic model. However, as previously discussed, Knepp has a relatively high amount of data, expert knowledge, and constraints compared to other rewilding projects. It is therefore possible that the simpler model would be entirely sufficient and more widely applicable to other sites, potentially avoiding some of the unexpected outcomes observed in this thesis.

Exploring models with intermediate levels of complexity may also reveal a solution which is simpler and requires less computational power than the ABM but captures more processes than the ODE. Partial differential equations, for example, could incorporate the temporal and spatial processes of the ABM while maintaining the equation-based approach of the ODE, potentially making them a useful 'middle ground' for understanding spatial dynamics, like the wood-pasture hypothesis, in ecosystems (Holmes et al., 1994; Parunak et al., 1998). Likewise, stochastic differential equations could combine some of the noisy features of the ABM with the more deterministic features of the ODE (Colon et al., 2015; Kemeth et al., 2022). These have been used to model questions related to coevolution, extinction and coexistence in ecological communities, and transitions between stable states (Boettiger, 2018; Jeltsch et al., 2019). They could better

capture the effect of random environmental fluctuations on the ecosystem and improve the shortcomings of the ODE.

6.2 Opportunities for future research

6.2.1.1 Model improvements: processes, structures, and applications

The models presented in this thesis can be continuously improved with the addition of more expert knowledge and empirical data. There is therefore considerable potential for iterative stakeholder engagement and collaboration around fine-tuning model behaviours, structures, and parametric assumptions. For example, although both model methodologies are well-suited to deriving insights from limited ecological data, it is possible that some outputs are overly simplistic due to the relatively few time-series points, particularly for habitat nodes. The inclusion of further information could reveal interesting dynamics such as non-linear, more complex trends in the abundance of woodland and thorny scrubland over time. Revisiting the parametric bound assumptions could likewise potentially improve some of the unexpected results observed in Chapter 5, particularly the system requiring very high changes in stocking densities to shift to extreme end states. This could clarify, for example, whether the per capita herbivory parameters are not sufficiently high, or whether the new end states simply cannot be feasibly reached.

In addition to the model improvements discussed in the previous section, there are several areas which may be valuable to discuss with management and potentially include in the models. These

include exploring additional processes beyond predator-prey dynamics, for example the Allee effect (positive density dependence), which can have significant implications for population dynamics, including feedback loops of how much of a vegetation component - and what type, in the ABM - is eaten (Terry, 2015). Additional nuance in consumption and population dynamics could also impact results; for example, changes in herbivory pressure can alter vegetation palatability with cascading impacts in the system (Augustine & McNaughton, 1998).

As discussed in Chapters 3-5, spatial assumptions around consumer movements could be made more complex in the ABM, and both models could incorporate consumer vegetation consumption and metabolic rates, for example to inform parameter bounds or act as a filter on model runs. This could give a more nuanced and comprehensive look into how different herbivores impact habitats, potentially better informing management decisions regarding which species to reintroduce, and how many. Chapters 4 and 5 also identified a need for additional long-term filters, particularly for roe deer and Longhorn cattle. Gaining a better understanding of what factor(s) limit their populations and adding these components to the models could improve both the calibration process and overall speed of the model.

Exploring alternative model structures could be another interesting avenue for future research. For example, subsequent discussions with experts at Knepp identified sallow scrub as an important subcomponent of the 'scrub' node. Unlike thorny scrub, it is not believed to facilitate saplings, but instead acts as a temporary copse and often collapses at a young age, allowing the habitat to open again (Penny Green, *pers comm.,* 2023). It therefore behaves differently to both woodland and thorny scrubland and is said to have a fair amount of coverage in the Southern Block of Knepp

(Penny Green, *pers comm.,* 2023). Sallow scrub was not explicitly included in this thesis due to a lack of time-series data, but as more studies become available, adjusting the model structure to incorporate it could yield interesting results. Likewise, the network models in this thesis are based on the wood-pasture hypothesis, but alternatives exist which could influence interaction assumptions, such as the traditional 'closed canopy' theory (Iversen, 1960; Peterken, 1996). Other researchers have pointed out that disturbance factors, such as fires and storms, may have also been integral in creating open landscapes and allowing sapling regeneration (Bradshaw et al., 2003) – these natural disturbance regimes could be considered in future iterations of the models. Certain nodes, such as soil microbiome and nutrient cycling, may also be important for system dynamics and could be added to the models; these were not included in this thesis due to lack of data, and since they are outside the focus of the wood-pasture hypothesis. If additional nodes and complexities are added, improving computational efficiency, for example by using a sequential Monte Carlo sampling approach for ensemble generation (Vollert et al., 2024), could be a valuable next step and potentially identify more acceptable parameter sets.

Other model questions have been identified as useful for rewilding management and decision-making. Exploring the impact of rewilding on ecosystem services, such as carbon sequestration, is one potential avenue. Knepp is undertaking ongoing field work related to measuring carbon sequestration, so a "carbon" node could be added to the model and validated using this data (Penny Green, *pers comm.,* 2022). Of relevance to other rewilding projects are questions such as: how quickly do you build up the reintroduced species' numbers at the onset, and in what order should species be reintroduced to achieve an end goal (Jepson & Blythe, 2020)? Investigating the knock-on impacts of different functional groups if reintroduced to rewilding sites, such as beavers or lynx,

would also be of potentially significant interest not only to practitioners but also to policymakers and the wider public. Beavers have been reintroduced to Knepp and could therefore be a suitable candidate for further investigation, but lynx would require application to a new case study due to insufficient space at Knepp for accommodating their large ranges.

Incorporating the broader, peopled landscape may also be a valuable next step, as decision-making is rarely solely determined by ideal ecological outcomes. Examples could include adapting the models to incorporate human-wildlife conflict or the spread of 'injurious weeds', as Knepp currently has a management-intensive weed control policy to reduce the negative impact of unwanted plants to neighbouring land areas (Tree, 2018). Coupling these models with, for example, flood or wildfire models could also allow a greater understanding of how changes in the vegetation composition may reduce the risk of extreme events to neighbouring communities under future forcing scenarios.

Neither model captured the cyclical vegetation turnover expected under the wood-pasture hypothesis (section 2.2.2). Rather than oscillating between closed-canopy woodland, grazer-maintained grasslands, and thorny scrubland, both the ODE and ABM move towards an end state and remained stable upon arrival (see Chapter 5). Future work could explore why this was the case: for example, model structure, the priors used, and lack of long-term data for calibration may have all played a role. Another possibility is that wood-pasture oscillations are driven in part by consumer population fluctuations, and these dynamics were therefore not observed as grazer numbers are tightly controlled at Knepp. The wood-pasture hypothesis is under debate and the traditional view is the 'closed canopy' theory (section 2.2.2) (Iversen, 1960; Peterken, 1996). It

may therefore be possible that the hypothesis itself is missing a key process; further model assessment could advance our understanding by revealing whether there are any conditions that can lead to the emergence of these cyclical systems.

As discussed in Chapter 2, there is a wide breadth of rewilding approaches which vary in the level of ongoing management. An interesting next step would be to apply the models to less intensively managed case studies, for example those having complete trophic food webs (i.e., those with apex predators present, which may not need grazer population control), and comparing their outputs to see whether findings are different to the ones presented here. The managed nature of Knepp could be a factor in the unrealistic long-term model dynamics observed in Chapter 5 (e.g., Longhorn cattle populations in the ABM exploding to unrealistically high numbers in the absence of culling), as the system is so tightly controlled that realistic ecological and population dynamics are not controlled. Some of these challenges with sufficiently capturing realism may therefore be avoided in less managed systems.

6.2.1.2 Addressing model implementation and barriers to use

The majority of conservation decision-making is currently driven by experience or "common sense" (Cook et al., 2010; Pullin et al., 2004; Sutherland et al., 2004), and examples of models influencing ecological decisions are rare (Rapacciuolo, 2019). However, the current lack of reliance on evidence-based information could compromise outcomes, and a rich literature shows that models can be successfully used to inform and generate effective management interventions (DeAngelis et al., 2021; García-Díaz et al., 2019).

There are several barriers hampering the wider uptake of ecosystem models on the ground. The first is that practical usage of models requires trust in the reliability and value of their outputs. Many ecological managers are sceptical of their value (Lester, 2020), in part because of many failures of models to provide useful information, or in some cases providing incorrect inferences which led to serious unintended consequences (Sofaer et al., 2018; Walters & Maguire, 1996). As the statistician George Box once said: "all models are wrong, but some are useful." Iterative stakeholder engagement and collaboration around model structural and parametric assumptions, as well as open discussions about uncertainty and outcomes – especially if results are not expected or intuitive - could reduce these risks while building trust (DeAngelis et al., 2021), and help to maintain model utility despite its 'wrongness' (Weiskopf et al., 2022). Modellers and ecosystem decision-makers have largely operated separately to-date (DeAngelis et al., 2021), but the methodologies in this thesis can help to bridge this gap, as well as the gap between 'common sense' versus empirical analyses, as they can easily be updated to incorporate both expert knowledge and empirical data. This gives them considerable potential for practical 'on the ground' use and ongoing collaborative refinement. Such an integrated approach has additional benefits in that it could assist with grant applications and raising project funding, and, by making assumptions explicit, addressing concerns from policymakers or the wider public about any potential negative impacts of rewilding.

A second barrier relates to accessibility. Models which require technical expertise to run and interpret outputs can discourage practitioner uptake (Weiskopf et al., 2022). There are examples of nature-related models being developed and run via consultancies, with results provided in an

easy-to-read format to clients, although these are often geared towards corporates and financial institutions with potentially prohibitively high costs for many rewilding projects. Collaborating with a university, wherein students and researchers adapt and run the models in exchange for rewilding data, could be an option with benefits for both researchers and rewilding management. Ecopath with Ecosim, a well-known ecological modelling software (Polovina, 1984), is open access and offers relatively affordable professional licenses and packages with technical support included. The Madingley model (Purves et al., 2013) is likewise open access but takes another approach by working to enhance its accessibility and ease-of-use. User-friendly modelling frameworks, simplified programming languages (e.g., Netlogo for agent-based models), and ready-to-use packages and programs all make models more easily accessible. The models in this thesis are open access, but at this stage, they require some understanding of coding to run; a next step could therefore be to explore creating a more accessible user interface for encouraging engagement from both technical and non-technical audiences, and for facilitating a stronger link between modelling and management decision-making.

6.3 Summary and overall conclusions

In the face of the biodiversity and climate crises, gaining a robust understanding of how to recover the health of degraded ecosystems is more urgent than ever. This thesis presents two new models, an ODE and a spatial ABM of the Knepp Estate, which are used explore questions related to restoring ecosystems via rewilding, such as optimising the number and functional traits of

reintroduced species, improving resilience, and informing how a given end goal can be achieved. The ODE represents the first use of this methodology in a system with relatively good data availability (i.e., incorporating time-series data, expert knowledge, and 'reality check' constraints) to explore knock-on impacts of rewilding on ecosystem dynamics and resilience. Results advance the ecosystem modelling literature by revealing how the constraints can be used to narrow the parameter space, therefore simplifying the calibration process, and to identify simulations that are not fundamentally theoretically sound despite replicating the time-series data. They also suggest that in sites like Knepp, which have relatively high amounts of data availability, the EEM approach may be too simplistic. The ABM uses, for the first time in this context, rejection sampling, and additional complexities such as space and heterogeneity of individuals to model rewilding outcomes. These were useful for improving the ease of calibration and capturing certain interactions - such as the facilitation of saplings by thorny scrub - and revealing emergent behaviours.

The models are shown to produce acceptable dynamics based on simple interaction networks. They can be used to understand the ecosystem-wide impacts of species reintroductions and inform decision-making, providing practitioners with quantitative estimates about the range of possible future system states. Results support the idea that rewilding with naturalistic grazing can drive the formation of mosaic wood-pasture habitats and positively impact overall biodiversity. Adaptive management may be needed to maintain desired ecosystem states under novel future environmental conditions. The models can assist with this by assessing the risk of ecosystem collapse towards undesirable states, and optimising interventions for moving towards healthy equilibriums or enhancing resilience. Importantly, both the ODE and ABM can be flexibly and

easily updated to incorporate both empirical data and qualitative expert opinion. This gives them considerable potential for complementing the more subjective decision-making process used by most rewilding projects, providing valuable information and support while also facilitating ongoing collaboration and model improvement.

Direct comparisons between different modelling methodologies are uncommon, but invaluable for identifying the 'simplest accurate model,' understanding missing elements, and guiding future improvements (Colon et al., 2015; Hunter-Ayad et al., 2020). In this thesis, the ODE and ABM are demonstrated to have similar high-level insights, but the ODE may benefit from additional complexity when applied to systems with decent data availability. The ABM is used as an uncertainty analysis to guide further research and improvements to the ODE, with the goal of identifying a 'middle ground' wherein the benefits of the simpler ODE can be maintained while enhancing the ease of calibration, realism of its outputs and range of questions it can explore. Other practical benefits and drawbacks to each model are discussed, such as model runtime, computational intensity, and the types of questions they are best suited to answering. This thesis therefore helps to provide some clarity on which model methodology is best suited to a given case study, ensuring it is as simple as possible while also capturing key ecosystem components and processes.

Several possible model improvements are suggested in the respective papers (Chapters 3-5) and Discussion. Despite these, the approaches outlined here are demonstrated to have potential for capturing the underlying dynamics of ecosystems such as that at Knepp, informing future system states based on current trajectories, and advising on new interventions aimed at achieving desired

future system states. The models could therefore act as predictive management support tools, providing practitioners with a means of assessing species reintroductions before their implementation, informing management decisions, optimising resilience in the face of the biodiversity and climate crises, and constraining possible outcomes. Although only applied to one case study in this thesis, it is hoped the models can be adapted and applied to other sites, including to related sectors such as invasive species management, regenerative agriculture, and ecosystem restoration more generally. Key strategies for enhancing model implementation and uptake on the ground are discussed. By helping practitioners make scientifically informed decisions while considering risks and uncertainties in a systematic manner, the methodologies presented here can help address some of the key criticisms of rewilding, namely that a more robust appraisal is required of its potential as a policy and management technique (Pettorelli et al., 2018; Rubenstein & Rubenstein, 2016; Torres et al., 2018).

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