Rewilding complex ecosystems
–
a theoretical framework and empirical contributions

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Entrance to Peneda-Gerês National Park

Abstract

Rewilding is a novel approach to ecosystem and biodiversity restoration. While the potential risks and benefits of rewilding are hotly debated in the scientific community and in society, a unifying definition of the term “rewilding” is lacking and empirical evidence about the outcomes is poor. I provide a unifying framework that is based on long-standing ecological theory and provides guidance for the design, implementation, monitoring and evaluation of rewilding projects across spatial scales and societal circumstances from urban spaces to abandoned landscapes. It accommodates for different approaches to rewilding and accounts for ecological and societal risks and benefits associated with rewilding actions. I further present two examples of how rewilding can be empirically studied using camera traps and multispecies occupancy models. These studies test and support some of the framework’s statements and provide important contributions to the much-needed evidence base on rewilding.

Keywords: rewilding, restoration, resilience, camera trapping, landscape abandonment, herbivores, mammals, multispecies occupancy model, biodiversity, ecosystem

Rewilding ist ein Ansatz zur Renaturierung von Ökosystemen dessen mögliche Risiken und Nutzen in Wissenschaft und Gesellschaft umstritten sind. Bislang fehlt eine einheitliche Definition für „Rewilding“ und es gibt nur wenige empirische Untersuchungen seiner Effekte. Ich lege ein theoretisches Rahmenwerk vor, das verschiedene Rewildingansätze vereint und deren ökologische und gesellschaftliche Risiken und Nutzen erfasst. Dieses bietet einen Leitfaden für die Entwicklung, Umsetzung, Überwachung und Bewertung von Rewildingprojekten auf verschiedenen räumlichen Skalen und unter verschiedenen sozio-ökologischen Voraussetzungen von urbanen Räumen bis hin zu Wildnisgebieten. Des Weiteren präsentiere ich zwei Beispiele, wie Rewilding mithilfe von Wildtierkameras und *multispecies-occupancy*-Modellierungen empirisch untersucht werden kann. Die vorliegenden Studien testen die Annahmen des theoretischen Rahmenwerks und liefern einen wichtigen Beitrag zu den empirischen Grundlagen für Rewilding.

Schlagworte: Rewilding, Renaturierung, Resilienz, Kamerafallen, Herbivoren, Säugetiere, Biodiversität, Ökosysteme

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Summary

Rapid global change is creating fundamental challenges for the persistence of natural ecosystems and their biodiversity. Conservation through the protection of landscapes has had mixed success, and there is an increasing awareness that the long-term protection of biodiversity requires inclusion of flexible restoration along with protection. Rewilding is one such approach that has been both promoted and criticized in recent years. Criticisms include the lack of a clear conceptualization of rewilding, insufficient knowledge about the possible outcomes, and the perception that rewilding excludes people from landscapes. The three studies presented in this dissertation aim at contributing to overcoming these criticisms by providing a synthesis of ecological theory and empirical studies to further understanding of rewilding actions.

The concept of rewilding has evolved from its initial emphasis on protecting large, connected areas for large carnivore conservation to a process-oriented, dynamic approach. In Chapter 2, I present a definition of rewilding that encompasses the variety of approaches to rewilding. Based on a review of theories on ecosystem resilience, natural disturbance regimes and ecosystem complexity, I identified three ecosystem processes, namely habitat connectivity, integrity of trophic networks, and natural disturbance regimes, that should be targeted in rewilding. I developed a framework that conceptualizes the interactions among the three ecosystem processes, while considering the societal dimensions of rewilding. The framework aims at providing useful guidance for the design and implementation of rewilding projects across spatial scales and societal circumstances from urban spaces to abandoned landscapes.

In Chapters 3 and 4, I present two empirical studies conducted in the Peneda-Gerês National Park, in northwestern Portugal. Using camera trap data from one sampling season, in Chapter 3, I disentangled the effects of man-made infrastructure, vegetation cover, and interspecific interactions among wild and semi-domestic herbivores and predators. I tested which habitat characteristics determine occupancy probability of roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and three ancient domestic breeds, the Barrosã and the Cachena cattle (*Bos taurus*) and the Garrano horses (*Equus caballus*). I tested whether ungulate species occupancy is influenced by human infrastructure, and whether occupancy probability of wild ungulates is impacted by the presence or absence of predators or of domestic ungulates. The results of this chapter contribute to a better understanding of trophic processes and how these are influenced by internal (i.e. species interactions) and external (i.e. environmental) factors.

Chapter 4 expands the research question of Chapter 3 and tests parts of the framework developed in Chapter 2. I hypothesized that fire events would influence habitat use of both domestic and feral ungulates. To test this hypothesis, I studied how interspecific interaction processes coupled with wildfires as a source of natural disturbance influence habitat choice of wild and domestic ungulates. This study can serve as an example of how the interaction of several ecosystem processes can be studied. The results of this work contribute to a more nuanced understanding of the processes and spatio-temporal dynamics that influence habitat choice.

Rewilding aims at combining thorough, scientifically sound and empirically tested actions with an emotional narrative that can contribute to a positive, hopeful notion of conservation and can engage people to care and act for their environment. For rewilding to be successful, it needs to fulfill certain standards, for example comparability, transparent goals and methods, measurements of progress, options to adapt original plans, and generation of societal benefits. Given the dynamic nature of ecosystems, the rapid global change and the multiplicity of legislative frameworks across countries, this endeavor remains a challenge. This thesis contributes to fulfilling these mentioned standards, as it provides a flexible framework, offers guidance for the development and evaluation of management plans, and offers two examples of studies that assess the effects of rewilding.

Chapter 1

Introduction

For millennia, humans have altered the Earth’s surface in a variety of ways. First, we altered vegetation cover and animal species composition through hunting and fire. With the onset of agriculture, large areas were deforested to be used as cropland, and habitats such as grasslands, shrublands and savannas were turned into pastures (Ramankutty et al. 2018). Rapid human population growth and associated demand for agricultural and forest products, as well as the increased use of fossil fuels led to unprecedented impacts of humans on nature (Steffen 2004). Those changes even led to the proposal of a new geological epoch termed the “Anthropocene” (Crutzen 2002).

The conversion of land, led by processes such as agricultural expansion (van Vuuren et al. 2006; Ellis et al. 2010; Foley et al. 2011), is currently the main driver of biodiversity and ecosystem change (van Vuuren et al. 2006; Leadley et al. 2010; Pereira et al. 2012). Such shifts in societal and environmental conditions have severe impacts on the world’s ecosystems. The rates of habitat loss and ecosystem degradation are increasing (Dirzo and Raven 2003; MA 2005; J. A. Foley 2005; Barnosky et al. 2017), and most large bodied animals have disappeared from their natural habitats (Dirzo et al. 2014). The absence of these species has led to the loss of many important ecological processes (for example, natural grazing, predation, stochastic disturbance events or nutrient cycling; (Cardinale et al. 2012; Pettorelli et al. 2017)). These processes are thought to be critical for the resilience of ecosystems, i.e. the ability of ecosystems to recover from environmental perturbations (Perino et al., *in press*; Holling 1973; Scheffer et al. 2001; Oliver et al. 2015).

While the amount of agricultural land continues to increase globally (Rey Benayas 2007; Ramankutty et al. 2018), large regions in the Northern Hemisphere are experiencing the abandonment of agricultural areas (Ramankutty et al. 2018). Thousands of square kilometers have already been released from anthropogenic pressure (Ramankutty and Foley 1999).

Farmland abandonment is characterized by decreases in the size of areas used as pastures or for crop production (Brown et al. 2005), and by a regeneration of successional native vegetation (Kammesheidt 2002), and often occurs in areas with low productivity of marginal agricultural land. It is often caused by socio-economic shifts, for example ageing populations (MacDonald et al. 2000; Rey Benayas 2007) and slow population growth (Keenleyside and Tucker 2010), or the intensification of agricultural practices (Russo 2007; Keenleyside and Tucker 2010). This trend is expected to lead to the abandonment of up to 29 million hectares of agricultural land in Europe by 2030 (Navarro and Pereira 2012).

The abandonment of agricultural practices leads to a transition from agricultural land to semi-natural vegetation and eventually forest (Verburg and Overmars 2009). On the one hand, this may encompass the risk of habitat homogenization and the loss of high-nature-value farmland (Verburg and Overmars 2009), resulting in habitat loss for species adapted to agricultural landscapes, and a conversion of landscapes that are part of the cultural heritage of a region (Van Eetvelde and Antrop 2004). On the other hand, agricultural abandonment may benefit ecosystems. For instance, the expansion of shrub land and forests will likely lead to reduced fragmentation and increased habitat size and connectivity (Bodin and Saura 2010; Hernández et al. 2015). The recovery and expansion of semi-natural vegetation and forests may improve habitat quality (Bowen et al. 2007) and benefit biodiversity by providing habitats for species that have declined due to the loss of large natural areas (Queiroz et al. 2014). As human impacts, such as hunting (Breitenmoser 1998; Chapron et al. 2014) decrease with continuing land abandonment, opportunities open for recolonization by species that have suffered from those pressures, thus improving the trophic complexity of degraded ecosystems (Ripple and Beschta 2012; Deinet et al. 2013). For these reasons, the abandonment of agricultural land offers unique opportunities for large scale ecological restoration (Navarro and Pereira 2012).

1.1 The need to rethink restoration

The urgency and importance of restoration is widely acknowledged and has just recently been underpinned by the UN General Assembly declaring 2021 to 2030 the UN decade of ecosystem restoration (UN General Assembly 2019).

Traditionally, conservation actions have often sought to halt ecosystem degradation by aiming at preserving a static ecosystem condition represented by a specific species composition and the delivery of particular ecosystem functions and services. These goals are often achieved by the implementation of protected areas. Although such approaches can be a powerful way to reduce or slow down biodiversity loss (Chape et al. 2005; Gray et al. 2016; Pringle 2017), reported population declines inside protected areas (Hallmann et al. 2017) show that conservation efforts need to go one step further in order to tackle the current biodiversity crisis (Pimm and Raven 2000; Koh 2004). This insight is reflected by a shift in the view on conservation and restoration. Ecosystems are increasingly recognized as dynamic systems whose future development cannot always be predicted (Thomas and Middleton 2003; Lindenmayer et al. 2017). Shifting societal and environmental conditions, including climate change, land-use change and increasing demand for resources amplify this unpredictability, making it difficult to anticipate the response of ecosystems (Thomas and Middleton 2003; Turner and McCandless 2004; Lindenmayer et al. 2017) and the outcomes of restoration efforts. In light of this, there is growing recognition that conservation in the Anthropocene needs to encompass process-oriented and dynamic approaches that focus more broadly on the adaptive capacity of ecosystems (Barnosky et al. 2017) and on the restoration of ecosystem processes (Thomas and Middleton 2003; Valiente-Banuet et al. 2015; Corlett 2016a; Barnosky et al. 2017; Cantrell et al. 2017).

1.2 Rewilding as an alternative approach to restoration

Rewilding is one such approach to dynamic restoration that has been pointed out as a possible avenue towards a sustainable use of our planet’s resources (Ripple et al. 2017). Originally introduced as a concept to restore habitats for large carnivores (Soulé and Noss 1998), the term is now used for a wide variety of restoration approaches. Rewilding ranges from passive approaches that focus mainly on removing regeneration obstacles (e.g. removal of dams, hunting bans) to enable the autonomous re-establishment of ecosystem dynamics (Navarro and Pereira 2012; Cantrell et al. 2017; Fernández et al. 2017), to introductions of non-native species as ecological proxies for species that became extinct centuries or millennia ago (Svenning et al. 2016; Fernández et al. 2017). Despite the marked differences among those approaches, the aim to restore self-organizing and complex ecosystems, with a number of interlinked processes that promote and support each other is common to all rewilding approaches (Chapter 2).

Many scientists and practitioners consider some level of continuing management as critical to replace ecosystem processes that have been lost due to human activities (Queiroz et al. 2014), whereas rewilding aims to assist the restoration and regeneration of degraded ecosystems to a level where human management is no longer needed or reduced to a minimum (Seddon et al. 2014; Lorimer et al. 2015; Fernández et al. 2017). While this requires a solid understanding of the ecosystem processes and the interactions among them, the low intervention goal of rewilding makes it an attractive alternative for the restoration of large or remote areas where active management can be costly or logistically challenging (Navarro and Pereira 2012).

Importantly, rewilding cannot be discussed without considering its societal dimension (Berkes and Folke 1998). Almost all areas that are candidates for rewilding are either in close vicinity to human settlements or have been used by people in the (recent) past. In consequence, rewilding actions will affect local people. Many of these effects will be beneficial for humans (Navarro and Pereira 2012). Exposure to green or natural spaces, for example, lowers stress levels, increases positive emotions and cognitive function, encourages physical activity and facilitates social cohesion (Markevych et al. 2017). Wilderness experiences, in particular, promote psychological resilience in children and adolescents (Masten and Reed 2005), and personal transformation and self-fulfillment in adults (Naor and Mayseless 2017).

Rewilding lays particular emphasis on the emotional experience and perception of wild nature (Jepson 2016; zu Ermgassen et al. 2018). How societies want to experience nature (Rosa et al. 2017; Díaz et al. 2018) and to what degree society can accept the autonomy of natural processes are important factors that can determine the choice and success of rewilding actions (Chapter 2). Such considerations may also determine the extent to which rewilded ecosystems can be used as a potential source of alternative income (for example nature-based tourism), and basis for livelihood for people who formerly relied on incomes generated from agriculture (Jobse et al. 2015; Corlett 2016b).

1.3 Criticism of rewilding

Despite its potential as a novel approach to restoration, rewilding research and practice are facing draw-backs that have hampered the common use of rewilding principles for restoration. Although rewilding is receiving considerable attention and interest both in the scientific community and in society, empirical studies that test the outcomes of rewilding actions are still rare (Svenning et al. 2016; zu Ermgassen et al. 2018; Pettorelli et al. 2018), yielding only insufficient knowledge about the possible outcomes of rewilding endeavors (Rubenstein and Rubenstein 2016). Moreover, rewilding researchers have so far failed to agree on a consistent definition of rewilding (Nogués-Bravo et al. 2016; Hayward 2019), and the multiplicity of interpretations make it difficult to identify and compare different rewilding projects (Seddon et al. 2014; Jepson 2016; Hayward 2019).

Finally, societal concerns and undesired consequences for people can prevent the application of rewilding. For instance, natural disturbances like fires or floods may threaten humans or human infrastructure (Turner 2010). Crop damage by ungulates or predation of livestock by large predators (Bauer et al. 2009) are becoming more frequent and more severe where animals are brought back or their populations recover (Treves 2009), often sparking conflicts with local communities. Additionally, concerns have been raised that rewilding projects are designed to exclude people from landscapes (Jørgensen 2015), or that culturally and traditionally important landscapes, including the unique heritage and biodiversity they contain are lost with continuing abandonment and succession of natural vegetation (Fischer et al. 2012; Plieninger et al. 2014; Corlett 2016b). Particular concerns have been expressed regarding impacts on cultural ecosystem services, for example aesthetic values (Schirpke et al. 2016), sense of place (Höchtl et al. 2005), and a general “erasure” of human history and involvement with the land and its flora and fauna (Jørgensen 2015). Such concerns have to be taken seriously and the impacts of rewilding on society should be treated with high priority in rewilding research.

1.4 The potential of camera trapping studies to monitor rewilding trajectories

Rewilding is a long-term endeavor. Some ecological processes may take decades to recover, making the monitoring and detection of change difficult and expensive. Consequently, research on rewilding requires long term data to assess its outcomes and success.

Camera trapping is an attractive approach to long-term monitoring as it is non-invasive, relatively inexpensive in terms of equipment and labor (O’Connell and Nichols 2010), and can be used to answer a wide variety of research and management questions on large geographic scales (Nichols et al. 2011). Camera trap analyses can range from estimates of abundance and population density over records of species occurrences to the studies on spatial and temporal dynamics of single or multiple species (Nichols et al. 2011).

The probability of species occurrence in certain sites can be determined by occupancy modelling (MacKenzie et al. 2002). This method extends traditional presence/absence surveys by accounting for imperfect detection (MacKenzie et al. 2002) and, since its introduction, has been expanded to applications appropriate for multiple species or sampling seasons (MacKenzie 2006; O’Connell and Nichols 2011).

In the empirical work of this dissertation, I used an innovative approach to occupancy modelling that allows to study the effects of interspecific interactions between more than two species while accounting for imperfect detection (Rota et al. 2016). With this model, it is possible to study how interspecific interactions alter the occupancy probability of species in response to changes in predictor variables. This feature makes the model particularly suitable to test interactions among aspects of trophic complexity (here, interspecific interactions) and other ecosystem processes important to support resilience in ecosystems (Chapter 2) and is therefore well-suited for the study of rewilding trajectories.

1.5 Objectives of the thesis

The first aim of this dissertation was to provide a theory-driven, unifying framework for rewilding, providing a basis for the choice of rewilding targets and actions. The second aim of this work was to conduct field studies that exemplarily test components, identify potential weaknesses of the framework and serve as examples for studies that contribute to the necessary empirical underpinnings for rewilding (Figure 1.1).

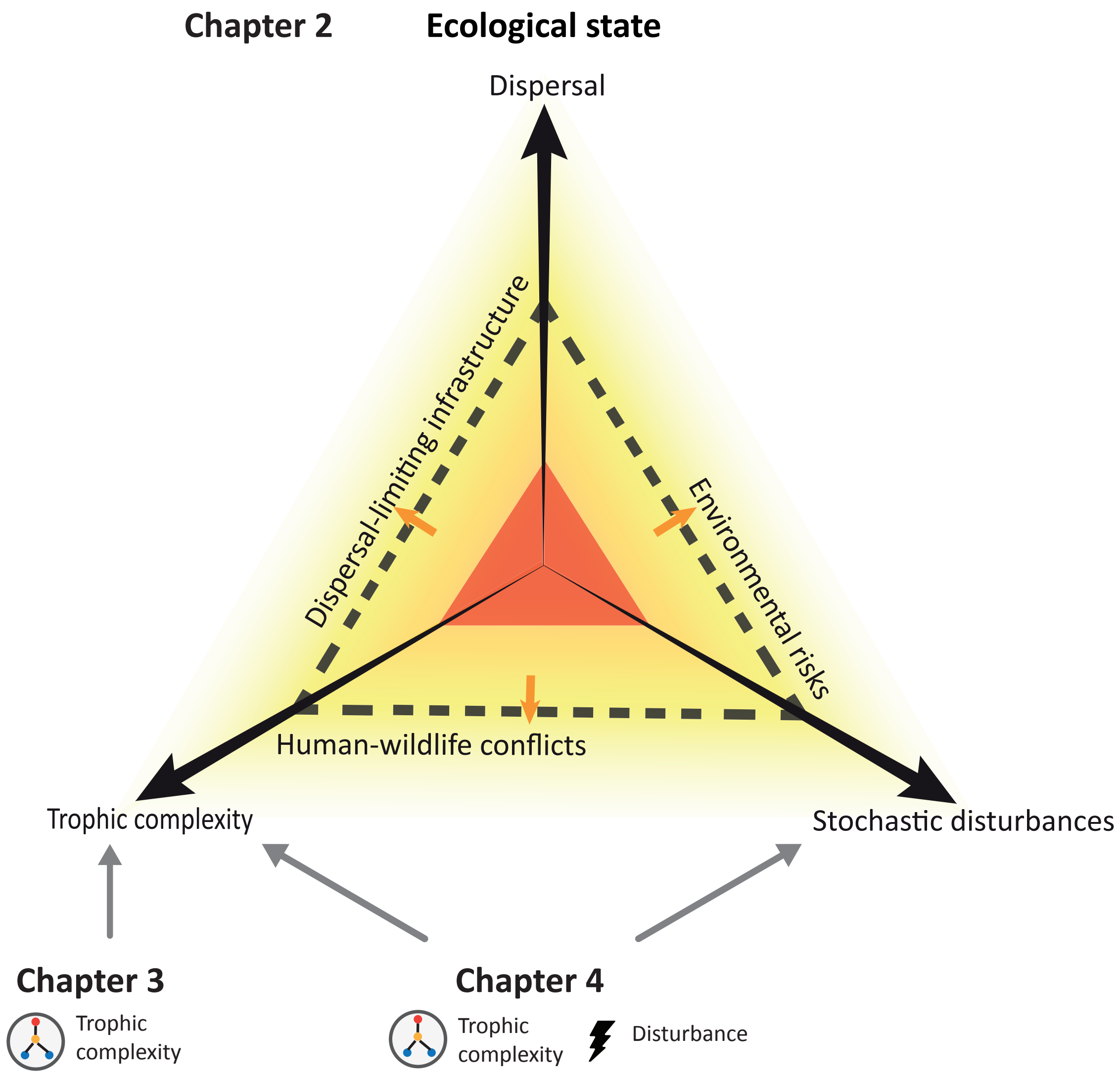

Figure 1.1. Conceptual interlinkage of the chapters of this dissertation. Chapter 2 presents a conceptual framework for rewilding, focusing on dispersal, trophic complexity and stochastic disturbances as key ecological processes contributing to resilience in ecosystems. The field study presented in Chapter 3 investigated aspects of trophic complexity. The field study presented in Chapter 4 investigated interactions between aspects of trophic complexity and natural disturbances. Aspects of dispersal were not covered in the case studies. (Figure adapted from Figures 2.1 and 2.2, Chapter 2).

In **Chapter 2**, I present a definition of rewilding that encompasses the variety of approaches to rewilding. Based on a review of theories on ecosystem resilience, natural disturbance regimes and ecosystem complexity, I identified three ecosystem processes, namely habitat connectivity, integrity of trophic networks, and natural disturbance regimes, that should be targeted in rewilding. I then developed a framework that conceptualizes the interactions among the three ecosystem processes, while considering the societal dimensions of rewilding. The framework aims at providing useful guidance for the design and implementation of rewilding projects across spatial scales and societal circumstances from urban spaces to abandoned landscapes.

To complement and test some components of the theoretical framework developed in Chapter 2, I conducted two empirical studies (**Chapters 3 and 4**) in the Peneda-Gerês National Park, in northwestern Portugal (Figure 1.1). The region is facing a marked rural exodus since the mid-20th century, that triggered large-scale agricultural abandonment and natural vegetation regeneration. With increasing populations of wild herbivores and carnivores, and largely undisturbed natural succession processes, the area constitutes an interesting study case for passive rewilding. Moreover, it offers opportunities to study societal effects associated with agricultural abandonment, for example, human-wildlife conflicts or shifts in economic activities (but note, that the empirical study of societal effects was not part of this dissertation!). The trajectories that can be observed in Peneda-Gerês are common to many Mediterranean systems (Plieninger et al. 2014) and results from studies could inform management actions in other regions facing landscape abandonment and offering opportunities for rewilding.

In 2015, I initiated a monitoring project using camera trapping that will serve for monitoring long-term ecological effects of landscape abandonment and passive rewilding. Using camera trap data from one sampling season, in **Chapter 3**, I disentangled the effects of man-made infrastructure, vegetation cover and interspecific interactions among wild and semi-domestic herbivores, and predators. I tested which habitat characteristics determine occupancy probability of roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and three ancient domestic breeds, the Barrosã and the Cachena cattle (*Bos taurus*), and the Garrano horses (*Equus caballus*). I tested whether ungulate species occupancy is influenced by human infrastructure, and whether occupancy probability of wild ungulates is impacted by the presence or absence of predators and of domestic ungulates. The results of this chapter contribute to a better understanding of trophic processes and how those are influenced by internal (i.e. species interactions) and external (i.e. environmental) factors.

Using data from three consecutive years of camera trapping, the work presented in **Chapter 4** expands the research question of Chapter 3 and tests parts of the framework developed in Chapter 2. I hypothesized that fire events would influence habitat use of both domestic and feral ungulates. To test this hypothesis, I studied how interspecific interaction processes coupled with wildfires as a source of natural disturbance influence habitat choice of wild and domestic ungulates. This study can serve as an example of how the interaction of several ecosystem processes can be studied (as proposed in Chapter 2). The results of this work contribute to a more nuanced understanding of the processes and spatio-temporal dynamics that influence habitat choice.

Chapter 5 synthesizes the findings of Chapters 2 through 4 and integrates the theoretical basis with the findings of the empirical research. I discuss further recommendations for the planning of rewilding projects to address the challenges of global change, and provide suggestions on how to better anticipate the outcomes of rewilding projects through empirical studies. Finally, I discuss remaining challenges and limitations, and suggest future research to contribute to successful and socially acceptable rewilding plans.

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Chapter 2

Rewilding complex ecosystems

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Rewilding complex ecosystems

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Enhanced abstract

Background: Rapid global change is creating fundamental challenges for the persistence of natural ecosystems and their biodiversity. Conservation through the protection of landscapes has had mixed success, and there is an increasing awareness that the long-term protection of biodiversity requires inclusion of flexible restoration along with protection. Rewilding is one such approach that has been both promoted and criticized in recent years. Proponents emphasize the potential of rewilding to tap opportunities for restoration while creating benefits for both ecosystems and societies. Critics discuss the lack of a consistent definition of rewilding and insufficient knowledge about its potential outcomes. Other criticisms arise from the mistaken notion that rewilding actions are planned without considering societal acceptability and benefits. Here, we present a framework for rewilding actions that can serve as a guideline for researchers and managers. The framework is applicable to a wide range of rewilding approaches ranging from passive to trophic rewilding and aims to promote beneficial interactions between society and nature.

Advances: The concept of rewilding has evolved from its initial emphasis on protecting large, connected areas for large carnivore conservation to a process-oriented, dynamic approach. Based on concepts from resilience and complexity theory of social-ecological systems, we identify trophic complexity, stochastic disturbances, and dispersal as three critical components of dynamics of natural ecosystems. We propose that the restoration of these processes, and their interactions, can lead to increased self-sustainability of ecosystems and should be at the core of rewilding actions. Building on these concepts, we develop a framework to design and evaluate rewilding plans. Alongside ecological restoration goals, our framework emphasizes people's perceptions and experiences of wildness and the regulating and material contributions from restoring nature. These societal aspects are important outcomes and can be critical factors for the success of rewilding initiatives (Figure 2.1). We further identify current societal constraints on rewilding and suggest actions that can mitigate them.

Outlook: Rewilding challenges us to rethink the way we manage nature and it invites us to broaden our vision about how nature will respond to changes that society brings, both intentionally and unintentionally. The effects of rewilding actions will be particular for each ecosystem, and thus a deep understanding of the processes that shape ecosystems is critical to anticipate these effects and to take appropriate management actions. In addition, the decision

whether a rewilding approach is desirable, should consider stakeholders' needs and expectations. To this end, structured restoration planning based on participatory processes involving researchers, managers and stakeholders, that includes monitoring and adaptive management, can be used. With recent calls to designate 2021-2030 as the decade of ecological restoration, rewilding could be pushed to the forefront of discussions by policy and decision-makers on how to reach post-2020 biodiversity goals.

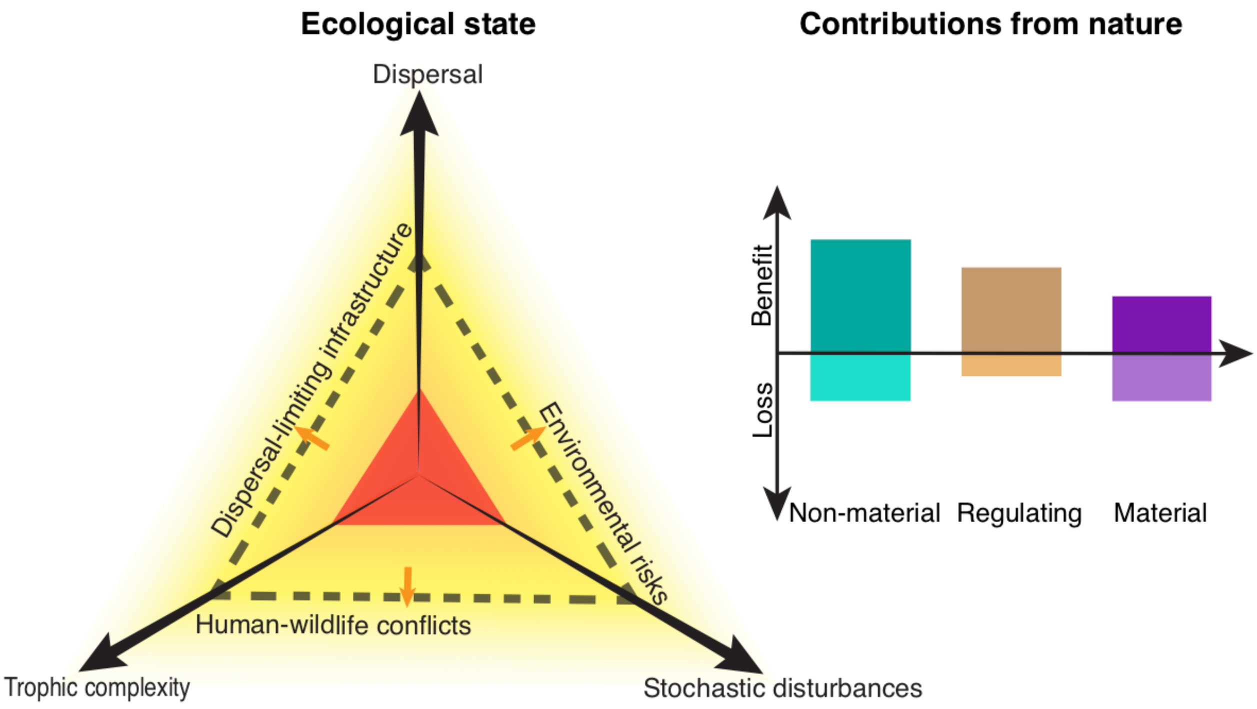

Figure 2.1: Rewilding actions and outcomes are framed by the societal and the ecological context. Rewilding can be assessed by representing the state of ecosystems in a three-dimensional space where each dimension corresponds to an ecological process. Restoration of these processes can positively influence their interactions, e.g., species diversity and trophic complexity can be increased if dispersal to new ecosystems is possible. The difference in volume between the restored (yellow pyramid) and the degraded ecosystem (red pyramid) is a proxy for the effects of rewilding on the self-sustainability of the ecosystem. The dashed line around the yellow pyramid represents the societal boundaries that determine to what extent ecological processes can be restored. Rewilding actions can help to push the societal boundaries further towards the ecological potential (orange arrows), by promoting societal support and opportunities for people to experience the autonomy of ecological processes in enjoyable ways. Societal outcomes can be assessed by mapping positive and negative impacts on non-material, regulating and material contributions from nature (bar plot, right panel).

Abstract

Rewilding has been both promoted and criticized in recent years. Benefits include flexibility to react to environmental change and the promotion of opportunities for society to re-connect with nature. Criticisms include the lack of a clear conceptualization of rewilding, insufficient knowledge about the possible outcomes, and the perception that rewilding excludes people from landscapes. Here, we present a framework for rewilding that addresses these criticisms. We suggest rewilding should target trophic complexity, natural disturbances, and dispersal, as interacting ecosystem processes that can improve ecosystem resilience and maintain biodiversity. We propose a structured approach to rewilding projects that include assessment of the contributions of nature to people and the social-ecological constraints on restoration.

One Sentence Summary: Rewilding can increase ecosystem resilience by promoting interactions among ecological processes, and aims to reconnect people with nature.

Shifting societal and environmental conditions, including land-use change and increasing demand for resources, are accelerating biodiversity loss and ecosystem degradation (Dirzo and Raven 2003; Millenium Ecosystem Assessment. Ecosystems and human well-being: Biodiversity synthesis. 2005; Foley 2005; Barnosky *et al.* 2017). The associated loss of many important ecological processes (Cardinale *et al.* 2012; Pettorelli *et al.* 2017) can decrease the complexity and resilience of ecosystems by hampering their capacity to recover from perturbations (Holling 1973; Scheffer *et al.* 2001; Oliver *et al.* 2015). Although responses to the biodiversity crisis, especially the establishment of protected areas, have reduced biodiversity loss in some instances (Chape *et al.* 2005; Gray *et al.* 2016; Pringle 2017), reports of ineffective protected areas (Laurance *et al.* 2012) and on-going declines of threatened species (Hallmann *et al.* 2017) show that conservation needs to go beyond current efforts (Pimm and Raven 2000; Koh 2004).

A growing body of literature emphasizes the need for novel, process-oriented approaches to restoring ecosystems in our rapidly changing world (Thomas and Middleton 2003; Valiente-Banuet *et al.* 2015; Barnosky *et al.* 2017; Higgs *et al.* 2018). Dynamic and process-oriented approaches focus on the adaptive capacity of ecosystems (Barnosky *et al.* 2017) and on the restoration of ecosystem processes promoting biodiversity, rather than aiming to maintain or restore particular ecosystem states characterized by predefined species compositions or particular bundles of ecosystem services. Such approaches recognize ecosystems as dynamic systems (Lindenmayer *et al.* 2007) whose future development cannot always be predicted (Corlett 2016a; Cantrell *et al.* 2017).

Rewilding is one such approach to restoration. It aims at restoring self-sustaining and complex ecosystems, with interlinked ecological processes that promote and support each other while minimizing or gradually reducing human interventions (Lorimer *et al.* 2015; Jepson 2016; Fernández *et al.* 2017). Rewilding also emphasizes the emotional experience and perception of wild nature and wild ecosystems without human intervention (Monbiot 2013). Although conventional restoration projects often aim to minimize human intervention, many scientists and practitioners consider some level of management as critical to replace ecosystem processes that have been lost due to human activities or to maintain important aspects of cultural landscapes (Queiroz *et al.* 2014). Such management often focuses on selected processes via precisely defined actions aiming at rather concrete end states (e.g., management of Satoyama landscapes in Japan (Katoh *et al.* 2009)). Rewilding, on the contrary, recognizes and works with complexity and autonomy as ecosystem-inherent characteristics and acknowledges their dynamic, unpredictable nature (Prior and Brady 2017).

Despite its potential to address pressing challenges in restoration, critics of rewilding have pointed out several shortcomings that have as yet hampered the application of rewilding principles. Criticism includes a lack of a consistent definition of rewilding (Nogués-Bravo *et al.* 2016) and insufficient knowledge about the possible outcomes of rewilding endeavors (Rubenstein and Rubenstein 2016). In addition, concerns have been raised about rewilding activities being planned in a manner that excludes people from landscapes rather than designing rewilding projects with local support (Jørgensen 2015).

Here, we articulate a conceptual framework for rewilding projects that addresses the above-mentioned criticisms. We start by briefly reviewing the history of the rewilding concept, from its initial emphasis on protecting large connected areas for carnivore conservation (Soulé and Noss 1998a) to the diversity of rewilding concepts today (Fernández *et al.* 2017). We propose a framework to design and evaluate rewilding plans that integrate the current diversity of rewilding approaches. Our framework draws on ecological theory to identify three interacting ecological processes that promote the self-organization of ecosystems and, therefore, should be the focus of rewilding actions. For each of these processes, we review ecological knowledge and identify rewilding actions that can assist the restoration of self-sustaining, resilient ecosystems. Importantly, these actions will vary depending on the societal context. Rewilding can happen spontaneously if humans withdraw from landscapes, for example after agricultural abandonment

(Navarro and Pereira 2012; Estel *et al.* 2015; Meyfroidt *et al.* 2016) or in areas that have become inhospitable due to armed conflict (Baumann *et al.* 2015; Baumann and Kuemmerle 2016; Hanson 2018) or environmental catastrophes such as Chernobyl (Hostert *et al.* 2011; Deryabina *et al.* 2015). In other cases, rewilding projects are driven by active choices about how societies want to experience nature (Díaz *et al.* 2018) and to which degree society can accept an autonomy of natural processes. In these cases, the feasibility of rewilding projects also depends on the material, non-material and regulating contributions from nature that emerge from rewilding (Figure 2.3). We discuss how rewilding projects need to account for social-ecological dynamics, from the point of view of both addressing people's preferences and the effects that humans have on ecosystems. Finally, we apply our framework to a set of on-going rewilding projects and illustrate how interactions among the key processes can be promoted to increase both ecosystem resilience and societal benefits.

A brief history of the rewilding concept

Rewilding, as it was originally conceived 20 years ago (Soulé and Noss 1998a), referred to "the scientific argument for restoring big wilderness based on the regulatory roles of large predators" (Soulé and Noss 1998a) that could act as keystone species and maintain the resilience and diversity of terrestrial ecosystems through top-down control (Soulé and Noss 1998a; Terborgh *et al.* 1999). The protection and restoration of "large, strictly protected core reserves, connectivity and keystone species" (Soulé and Noss 1998b) were the central characteristics of this first definition of rewilding. Although the conservation of large carnivores and their habitats is still an important aspect of rewilding (Svenning *et al.* 2016; Fernández *et al.* 2017), the concept has evolved from this original idea to include a range of diverse approaches (Fernández *et al.* 2017). Trophic rewilding, perhaps the closest to the original concept, advocates the reintroduction of missing keystone species, such as large carnivores and large herbivores. Trophic rewilding often advocates the use of functional replacements, i.e. the introduction of non-native species as ecological proxies for species that became extinct centuries or millennia ago (Jørgensen 2015; Svenning *et al.* 2016; Fernández *et al.* 2017). A particular type of trophic rewilding is Pleistocene rewilding, which aims at the restoration of ecosystems that include and are shaped by populations of megafauna extirpated since the Late Pleistocene, taking a long-term evolutionary perspective on ecosystems (Svenning *et al.* 2016). In contrast, ecological or passive rewilding emphasizes the passive management of ecological succession in abandoned landscapes. Passive rewilding actions include the creation of no-hunting areas, low-intervention forestry management, set-aside agricultural land, the removal of dispersal barriers, or the restoration of natural flood regimes (Navarro and Pereira 2012; Cantrell *et al.* 2017; Fernández *et al.* 2017). The ecosystem features that rewilding aims to restore are characteristic of wilderness areas ("wilderness | Definition of wilderness in English by Oxford Dictionaries"; Chapman 2006), but importantly, they are not restricted to those. Instead we refer to wildness, which is the autonomy of natural processes ("wildness | Definition of wildness in English by Oxford Dictionaries"; Chapman 2006) that can occur in a variety of settings and across spatial scales. The restoration of wildness, rather than wilderness, is thus the goal of rewilding. Broadening the original definition of rewilding and articulating the restoration of wildness rather than wilderness as its central goal makes rewilding applicable across spatial scales and adaptable to a wide range of societal and landscape contexts, from urban green spaces to abandoned agricultural landscapes (Prior and Brady 2017).

A theoretical framework for rewilding

In many ecosystems, complexity and resilience are maintained by trophic complexity, natural disturbances, and dispersal (Bengtsson et al. 2003; Elmqvist et al. 2003) (Figure 2.2). Human activities often lead to degradation in one or more of these ecological processes. Rewilding aims to restore these three ecological processes to foster complex and self-organizing ecosystems that require minimum human management in the long run (Suding et al. 2004). If missing or degraded ecosystem processes are not expected to recover (on policy relevant time scales) without assistance, rewilding may encompass initial interventions, sometimes followed by continuous minimal management. In the following, we explain each of the processes in detail, elaborate how interactions among them can promote ecosystem resilience, and illustrate how rewilding can be used to restore and promote such interactions.

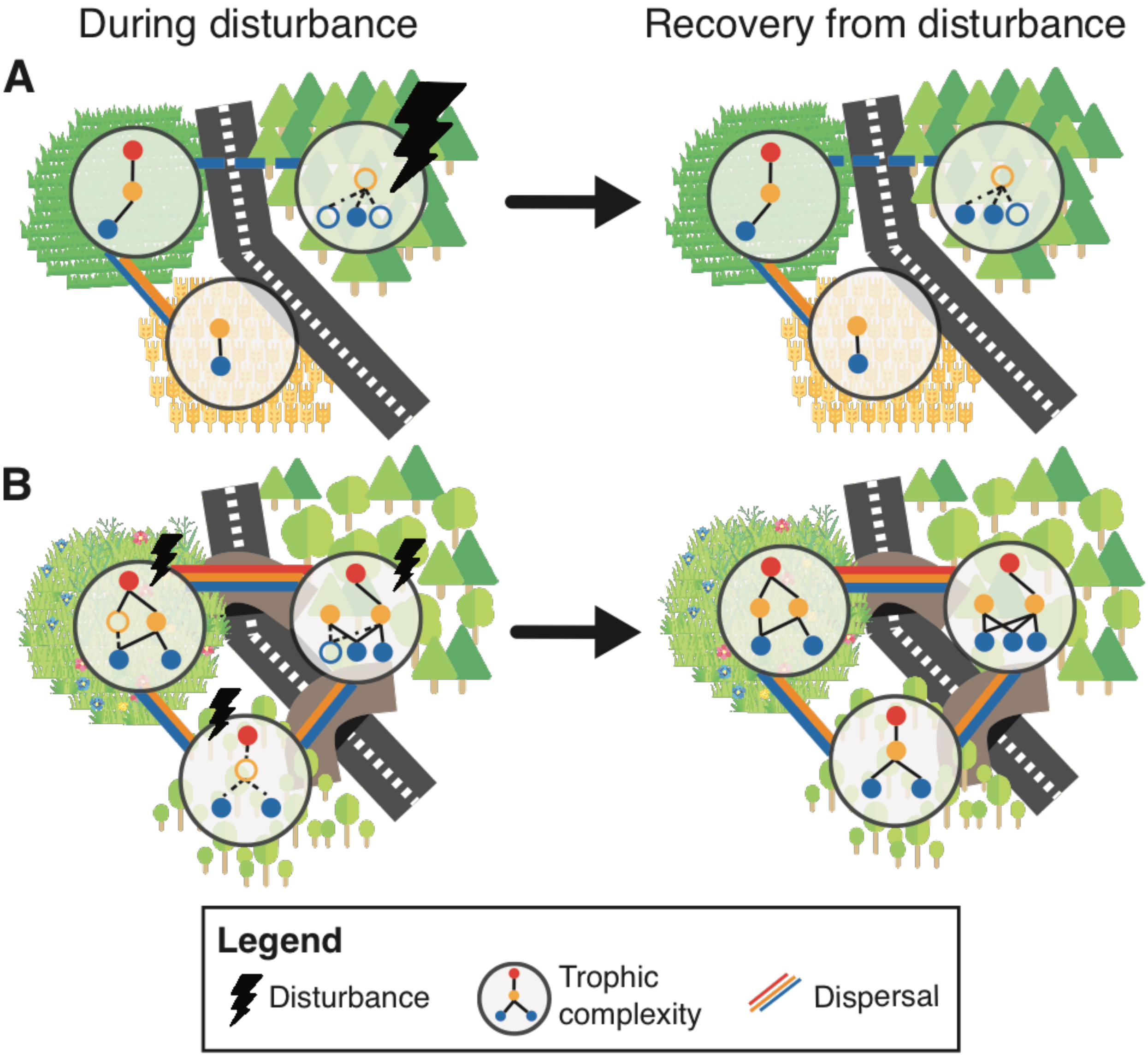

Figure 2.2: Promoting interactions among ecosystem processes enhances resilience of rewilding areas. A) Intensively managed areas, are often characterized by decreased trophic complexity. Dispersal barriers between ecosystems impede the movement of individuals, particularly at higher trophic levels. Natural disturbances are often suppressed or altered in their magnitude and frequency, potentially leading to even larger disturbance events. Impoverished trophic networks, dispersal barriers and deterministic disturbances can hamper recovery of depressed populations (open nodes in the trophic webs) after major disturbance events. B) Rewilded areas have restored complex trophic webs, with functional roles of top predators (red nodes) and herbivores (yellow nodes). Improved connectivity among habitats allows for dispersal of species at all trophic levels. Frequent disturbance events occur in the landscape. Dispersal among habitats aids recovery of ecosystems after disturbance events by allowing recolonization and recovery of populations of affected species. Large vertebrates present in complex ecosystems often act as dispersal agents for plants and can introduce stochasticity into a system, e.g. through predation or grazing.

Trophic complexity

Species at higher trophic levels are often highly connected and functionally important to ecosystems (Figure 2.2) (Sole and Montoya 2001). Large-bodied herbivores exert strong influences on the diversity and abundance of other taxa such as birds, small mammals, insects (Foster *et al.* 2014; van Klink *et al.* 2015) and plants (Janzen 1984; Bello *et al.* 2015). These effects occur through direct pathways, such as the provisioning of dung and carrion (Barton *et al.* 2013) or facilitation of dispersal (Janzen 1984; Bello *et al.* 2015), but also through the modification of the physical environment by grazing and trampling, or the building of dams by beavers (van Klink *et al.* 2015; van Klink and WallisDeVries 2018). Large carnivores can, through predation, affect population sizes and behavior of herbivores and create spatio-temporal heterogeneity in these processes. In the absence of top-down control by carnivores, high densities of large herbivores can have detrimental effects on the abundance and diversity of other species groups (Foster *et al.* 2014; van Klink *et al.* 2015).

Humans cause changes in species composition and alter species interactions through hunting, harvesting or planting selected species in agriculture and forestry (Figure 2.2a). Especially large vertebrates are susceptible to human-driven defaunation due to their body size, long reproductive cycles, and high metabolic demands leading to the need for large foraging ranges (Cardillo 2005; Ripple *et al.* 2014, 2015; Dirzo *et al.* 2014; Bakker *et al.* 2016). Thus, even where large vertebrates are still present in human-dominated landscapes, they might not be able to exert the top-down control they have in wild ecosystems due to their reduced densities (Dorresteijn *et al.* 2015; Kuijper *et al.* 2016). Selective defaunation of top predators and large herbivores can result in trophic cascading effects and higher susceptibility of ecosystems to collapse (Sole and Montoya 2001; Dunne *et al.* 2002).

Rewilding can enhance trophic complexity through a variety of actions that depend on the characteristics of the ecosystem. Passive rewilding measures can, for example include the creation of no-hunting areas. Where spontaneous recolonization is unlikely, the restoration of trophic complexity might also be achieved by translocating species. Introductions of ecological replacements can be an option if species have gone extinct globally (Svenning *et al.* 2016). However, such replacements can entail unforeseeable uncertainties and ecological risks and should be assessed with caution (Fernández *et al.* 2017). Rewilding can also be supported by activities to promote coexistence between people and wildlife, e.g., through compensation schemes for crop- or livestock damage (Persson *et al.* 2015; Ceaușu *et al.* 2019).

Stochastic disturbances

Natural disturbances often occur in a stochastic manner at different locations, magnitudes and frequencies, enhancing spatial and temporal heterogeneity in ecosystems (Bengtsson *et al.* 2003). They can trigger reorganization and reconfiguration of ecosystems (Franklin *et al.* 2000) and can lead to increased ecosystem complexity. They promote co-existence as often there is a trade-off in species' competitive abilities and resilience to events like fires, floods or pest outbreaks (Franklin *et al.* 2000). Species that are able to survive disturbances act as biological legacies that promote recovery and reorganization (e.g., seed banks or small mammals surviving a fire) (Bengtsson *et al.* 2003).

In human-dominated landscapes, natural disturbances are often suppressed (e.g., fire suppression or flood regulation) or altered in their magnitude and frequency (Figure 2.2a), which may lead to even larger and potentially devastating disturbance events (e.g., large wildfires rather than smaller and more frequent ones). Instead, stochastic disturbances are replaced by predictable and constant disturbances (e.g., use of fertilizers and irrigation to maintain constant inputs to ecosystems, or annual soil mobilization to weed out competing species (Bengtsson *et al.* 2003)). These deterministic disturbances often act in the same place over a long period of time without a chance for the affected ecosystem to recover and reorganize (Franklin *et al.* 2000) and may lead to the loss of sensitive species (1). Moreover, human efforts to repair damage after natural disturbance events can remove biological legacies (Franklin *et al.* 2000; Bengtsson *et al.* 2003) and lead to additional perturbations that hinder natural regeneration and reorganization processes (Lindenmayer *et al.* 2017). For example, salvage logging to remove dead trees after wind throw or pest outbreaks often removes important resources and habitats for saproxylic beetles or cavity-nesting species (Thorn *et al.* 2018).

Rewilding actions aim to release ecosystems from continued and controlled anthropogenic disturbances to allow for natural variability and sources of stochasticity (Kulakowski *et al.* 2017) (Figure 2.2b). Mowing of grassland can be reduced or replaced by natural grazing. Dams can be removed or their management modified to restore natural flood regimes (Putkunz 2011). Logging can be replaced by allowing natural fire and pest regimes.

Dispersal

Populations depend on dispersal among habitats to avoid overcrowding (Moseby *et al.* 2018), intraspecific competition and loss of genetic diversity (Wasserman *et al.* 2012). The exchange of individuals from different populations can increase gene flow, mitigate inbreeding and hence lead to more viable populations (Lacy 1997). Habitat degradation or anthropogenic dispersal barriers reduce habitat connectivity and dispersal ability (Figure 2.2a).

A rewilding approach includes the improvement of connectivity within and among ecosystems to promote dispersal. While connectivity efforts often focus on corridors alone, a multi-scale approach should seek to identify and link opportunities, ranging from local features such as hedgerows to support birds or insects (Rey Benayas and Bullock 2015), to large-scale corridors which allow recolonization by large mammals over long distances. Connectivity can also be improved by removing or increasing the permeability of dispersal barriers (Figure 2.2b) such as roads, dams or fences. The permeability of unsuitable habitat, particularly homogeneous agricultural areas, can be improved by the introduction of natural landscape elements (Merckx and Pereira 2015).

Integrating across ecological processes

The three ecological processes can influence and promote one another (Figure 2.2). Disturbances can, for example, promote habitat heterogeneity and increase resource availability for less competitive species and may therefore lead to an increase in species diversity (Cortés-Avizanda *et al.* 2012). High dispersal among habitats aids recovery of ecosystems after (major) disturbance events by allowing recolonization and recovery of populations of affected species (Figure 2.2b). Large vertebrates present in complex ecosystems often act as dispersal agents for plants (Janzen 1984; Bello *et al.* 2015), and can introduce stochasticity into a system, e.g., through predation or grazing (Estes *et al.* 2011). Therefore, the restoration of one of these processes may positively influence the functionality levels of the two other processes (Figure 2.2b). Interactions among the processes can increase ecosystem resilience by jointly promoting, for example, functional redundancy or recolonization.

Rewilding efforts can be assessed by representing ecosystems in their degraded and restored states in a three-dimensional, pyramid-shaped space where each axis corresponds to an ecological process, and the faces represent the interaction between processes (Figure 2.1). During the restoration of a process, the respective vertice of the pyramid moves further away from the origin and the volume of the pyramid increases. The difference in volume between the restored and degraded ecosystem is thus a proxy for the effect of rewilding on the resilience of the ecosystem. Note that because the processes interact, it is expected that restoring only one dimension but leaving the other two unaddressed often corresponds to a smaller improvement than restoring the three dimensions simultaneously, e.g., the change in the volume of the pyramid is very small when one of the axis is fully restored but the other two axes remain highly degraded.

Rewilding as a societal choice

Ecosystems cannot be assessed separately from human societies (Berkes and Folke 1998). All areas that are candidates for rewilding are influenced by people and/or have a history of use. Consequently, any rewilding project can affect local livelihoods and wellbeing. Societal changes can influence ecosystems in positive or negative ways and vice versa, and the trajectories of ecosystems are often defined by human decisions that focus on the delivery of certain resources and ecosystem services (Daily 1997; Ceaușu *et al.* 2019). Considering and managing for interactions between ecosystems and people while assessing and communicating the benefits of rewilding for society (Figure 2.3) can incentivize actions that benefit both ecosystems and society (Ceaușu *et al.* 2019) and, therefore, increase the acceptance and success of rewilding endeavors. The restoration of the three ecosystem processes can positively impact people's lives in various ways. Rewilding plays an important role for non-material contributions of nature and relational values of biodiversity (Díaz *et al.* 2015). A growing body of literature concludes that exposure to green or natural spaces can reduce stress levels, increase positive emotions and cognitive function, encourage physical activity, and facilitate social cohesion in humans (Fredrickson and Anderson 1999; Markevych *et al.* 2017; Engemann *et al.* 2018). Especially wilderness experiences provide an opportunity for eco-therapy to promote psychological resilience in children and adolescents (Masten and Reed 2005), and personal transformation and self-fulfillment in adults (Naor and Mayseless 2017). Moreover, the satisfaction that certain people perceive if species or ecosystems exist and thrive (Krutilla 1967; Alexander 2000) can reach societies in great geographical distance to an actual rewilding site. The presence of charismatic or symbolic species or landscapes can inspire spiritual, artistic and technological development (Díaz *et al.* 2018). Far-ranging and migrating species travelling on dispersal pathways may motivate nature-based activities such as birdwatching (Díaz *et al.* 2018). Being able to witness natural processes associated with childhood experiences, like the migration of swallows or cranes, can promote a sense of place and rootedness and be the basis for narratives, rituals and celebrations that form the core of the cultural identity of a place (Díaz *et al.* 2018).

Economic benefits of rewilding may arise from opportunities for nature-based economies and alternative sources of income based on non-material contributions from nature (e.g., recreational activities (Jobse *et al.* 2015; Corlett 2016b; Díaz *et al.* 2018)). Furthermore, natural disturbance events can trigger innovation and change in social-ecological systems (Gunderson 2003). Rewilding promotes other regulating services and nature-based solutions such as regulation of climate, air quality, pollination and dispersal of seeds (IUCN 2012; Díaz *et al.* 2018). Improved dispersal potential and trophic complexity may prevent the depletion of material contributions from nature (Díaz *et al.* 2018) such as economically relevant natural resources (e.g., wildlife game), not only in the areas undergoing rewilding but also in surrounding areas.

However, rewilding can also have undesired consequences for people. Natural disturbances like fires or floods may threaten humans and human infrastructure (Turner 2010). Human-wildlife conflicts, for example crops damaged by large herbivores or livestock killed by large predators (Bauer *et al.* 2009), are becoming more frequent and more severe where these animals are reintroduced or their populations recover (Treves 2009). Additionally, concerns over the loss of traditional, cultural landscapes, including their unique natural and cultural heritage, are growing in Europe and other regions (Fischer *et al.* 2012; Plieninger *et al.* 2015; Corlett 2016b). Particular unease has been expressed regarding impacts on farmland biodiversity and on cultural ecosystem services, for example aesthetic values (Schirpke *et al.* 2016), sense of place (Höchtl *et al.* 2005), and a general "erasure" of human history and involvement with the land and its flora and fauna (Jørgensen 2015).

In sum, the relationship of people with wildness in nature is and has always been characterized by sets of paradoxes (Arts *et al.* 2012). These range from contradictory views of wildness in nature ascribed to prehistoric peoples as a "constant threat to [human] life and livelihood" vs. the "primary source of life and livelihood" to contemporary, contradictory perceptions as "a potentially dangerous, alienating and challenging place" vs. "a potentially peaceful refuge to relax and conveniently enjoy" (Arts *et al.* 2012). This range of emotions highlights that well-planned rewilding projects that mitigate possible conflicts have higher potential to maximize the positive experiences and beneficial contributions from nature.

Applying the framework

A structured and participatory approach to rewilding is important to ensure that all stakeholders have a clear understanding of the goals, the management options, the desirable outcomes, and the associated risks (Margules and Pressey 2000). The first step of a rewilding project should be an analysis of the ecological status of the focus area, by identifying missing and/or degraded components. Paleo-ecological data, for example on past vegetation change, megafauna presence, or fire dynamics, as well as past information on land-use histories should be considered in such analyses (Barnosky *et al.* 2017).

In the second step, managers should assess the ecological viability of different management options and potential synergies among those. Together with key stakeholders (e.g., conservationists, farmers, hunters, general public), managers should identify social-ecological constraints (e.g., infrastructure hindering dispersal, emerging human-wildlife conflicts or risks associated with the restoration of natural disturbances), and evaluate benefits and disadvantages associated with the rewilding intervention.

The third step is the implementation of the rewilding actions using an adaptive management approach. This includes the monitoring of the different interventions, ideally using a before-after-control-impact (BACI) approach (Green 1979), that considers both the ecological and the societal outcomes. Results of this monitoring may lead to adjustments in ongoing rewilding interventions or raise the need for further management actions and decisions. The implementation phase should be accompanied by a communication strategy that involves affected communities in decisions, and outreach activities that inform the wider public about the outcomes of rewilding. These should be offered via a broad array of opportunities for nature experiences (e.g., guided tours through the rewilding area, nature education tools, opportunities for leisure activities). Additionally, managers may seek to develop opportunities for sustainable business opportunities to increase the acceptance of rewilding among stakeholders.

Our stepwise approach can also be applied for passive rewilding projects. In that case, there is no deliberate decision to initiate a project, but instead managers can take advantage of ongoing social-ecological dynamics (e.g., farmland abandonment). If this opportunity is identified, the first step will involve an assessment of the already ongoing passive rewilding dynamics, associated risks and benefits, and potential impediments to those dynamics. The second step will focus on identifying options to support those dynamics and mitigate threats. This will often involve the consolidation of ongoing non-intervention (e.g., establishment of no-hunting arrangements, or protected areas), or the mitigation of emerging conflicts. Similar to active rewilding projects, the third step involves adaptive management, monitoring and outreach activities.

We now demonstrate the stepwise application of our framework with four rewilding case studies, spanning a range of scales, ecosystem types, and degrees of intervention (Figure 2.3). As it will become apparent, the development of a rewilding project is rarely a linear process. Due to the adaptive nature of our approach, some of the steps will be carried out repeatedly and/or in parallel.

Restoration of the natural flood regime in the Leipziger Auwald City Forest, Germany

The Leipziger Auwald is an alluvial forest surrounding and crossing the city of Leipzig in Germany. Since the middle of the 19th Century, flood suppression and changes have led to a well-documented change in tree community composition with increasing dominance of sycamore (*Acer pseudoplatanus*), Norway maple (*Acer platanoides*) and common ash (*Fraxinus excelsior*), mainly at the expense of hornbeam (*Carpinus betulus*) and oak (*Quercus robur*) (Haase and Gläser

2009). In its current state, connectivity between the waterbodies in the Auwald is severely diminished, and active management is necessary to restore this process (Figure 2.3a).

After identifying the flood disturbance as a major missing component of this ecosystem, city managers have started yearly experimental flooding of a pilot area in the early 1990s (Richter and Teubert 2011). Results of concomitant monitoring confirmed the effectiveness and suitability of this management action. Flooding lead to an increase of flood-tolerant species like oak and hornbeam and a decrease or local extinction of some plant species that are intolerant to flooding but had become dominant after flooding had been suppressed (e.g., sycamore and Norway maple) (Richter and Teubert 2011). At the same time, colonization by moisture-tolerant slug species and (re-)colonization by several ground beetle species associated with alluvial forest systems was observed (Richter and Teubert 2011). The findings of this long-term experiment inform the implementation phase where the natural flood regime is restored in several drained branches of the river (Lebendige Luppe project) (Putkunz 2011) (Figure 2.3a).

The implementation phase is accompanied by an extensive outreach strategy that offers several opportunities for the public to engage with the ecosystem in the Auwald. It provides multimedia teaching material to support environmental education, and tools for interactive experiments (e.g., magnifying glasses, landing nets and maps) that allow children to learn about the ecology and topography of the alluvial forest and explore its flora and fauna. A local conservation NGO organizes excursions to inform about ongoing activities and regular public discussion forums offer the opportunity to engage actively in the project. Two concomitant research programs evaluate the ecological outcomes of the project and monitor and evaluate the acceptance and perception of natural processes in the Auwald, respectively (“Lebendige Luppe - Sozialwissenschaftliche Begleitung”).

Non-intervention policy in the Swiss National Park

Established in 1914, the Swiss National Park is the oldest National Park in Europe and the largest protected area in Switzerland (“1904-1914 - Swiss National Parc”). Already in 1909, its founders, both botanists and naturalists, who were concerned with the widespread development of touristic infrastructure threatening the region’s unique flora and fauna, identified the region around the Pass dal Fuorn as a suitable target area owing to its remoteness and species richness (“1904-1914 - Swiss National Parc”).

Making space for natural processes and conducting research on how these develop are central missions of the park management (“1904-1914 - Swiss National Parc”). The establishment of the park and management decisions were advised by cartographers and naturalists who had extensive knowledge about the area and its ecosystems (Lozza 2014). The protection status of the area was secured by a lease agreement that was negotiated with the local municipalities, and was financed through the foundation of the Swiss Federation of Nature Conservation.

Since its establishment, the National Park has been subject to a strict non-management approach and has been fully protected from human activities such as hunting, agriculture or forestry.

Trophic complexity was promoted through targeted reintroductions of ibex (*Capra ibex*) in 1920, 1923 and 1926, and bearded vultures (*Gypaetus barbatus*; 1991 - 2007) (Bundesversammlung der Schweizerischen Eidgenossenschaft 1980). Natural disturbances are not managed and dispersal potential is high for most species (Figure 2.3b). The development of the ecosystem has been monitored continuously, and many of the monitoring schemes have been in place for decades (Lozza 2014). Conflicts with local communities were mitigated via selected active management measures. For example, public discontent over sapling damage caused by red deer (*Cervus elaphus*) was mitigated by organizing hunting events outside the borders of the park (Lozza 2014). The non-management approach has resulted in the recovery of large populations of red deer, chamois (*Rupicapra rupicapra*), ibex, and roe deer (*Capreolus capreolus*), species that were nearly extinct or very rare in Switzerland when the park was established (Senn and Suter 2003). The increased red deer density has resulted in higher plant species richness in subalpine grassland (Schütz *et al.* 2003). Additionally, wolves (*Canis lupus)* and brown bears (*Ursus arctos*) have recently been sighted, suggesting the imminent recolonization of the area by large predators. Socio-economic studies show that the park attracts around 150,000 visitors per year, contributing significantly to the economic prosperity of the region (Backhaus *et al.* 2013; Knaus and Backhaus 2014; Lozza 2014).

Restoring ecological interactions in the Tijuca National Park, Rio de Janeiro City, Brazil

The Atlantic Forest of Brazil is a globally important biodiversity hotspot. However, most of the protected areas containing Atlantic Forest remnants have been defaunated (Galetti *et al.* 2017). One of these remnants is the Tijuca National Park in Rio de Janeiro. During the 17th and 18th century, deforestation for agricultural purposes and hunting pressure have led to severe losses of its native fauna. Since the forest is completely surrounded by urban infrastructure, the animal species community could not fully recover after the area was reforested in the 19th century (Fernandez *et al.* 2017), and dispersal of mammal species to other ecosystems is still inhibited.

The REFAUNA project was established in 2012 to restore the mammal community via gradual reintroductions of species that have disappeared from the Atlantic Forest (Fernandez *et al.* 2017). Tijuca was considered suitable for first reintroductions because its relatively small size and its location in an urban area would allow for easy monitoring and control of the released animals (Fernandez *et al.* 2017). Researchers identified two native, locally extinct candidate species, the red-humped agouti (*Dasyprocta leporina)* and the howler monkey (*Alouatta guariba*), both of which were expected to promote ecological interactions in the National Park. Agoutis are important dispersers of large seeded plants (Jansen *et al.* 2012) and increase seed survival by transporting them to locations with lower densities of conspecific tree species. Howler monkeys influence dung beetle abundances and the decomposition of howler dung by the beetles can enhance nutrient cycling and soil fertilization (Nichols *et al.* 2008).

Concomitant monitoring revealed that the presence of agoutis and howler monkeys enhanced ecological interactions in the park. Agoutis broadened their diet and improved the dispersal and germination success of several large-seeded plants. By interacting with the dung-beetle community, howler monkeys promoted the dispersal of large seeds and with likely positive effects on forest regeneration (Fernandez *et al.* 2017) (Figure 2.3c). Although Tijuca is Brazil's most popular National Park (Viveiros de Castro *et al.* 2015), there is little emotional connection between the park and people living in adjacent communities (Carreiro and Zipperer 2011). To improve the linkage between the park and local communities, the management has installed a park council where representatives of governmental institutions, non-governmental organizations and of the private sector, aim to reach satisfactory management decisions for all stakeholders (Briot *et al.* 2007). A community based, cooperative project has trained locals as tourist guides and offers tours through the park and a neighboring favela. Additionally, the cooperation runs a restaurant that offers products of local cuisine prepared with products growing in the forest and in community gardens (Barros and Melo 2011; Nidumolu 2015).

Ecosystem and wildlife recovery in the Chernobyl exclusion zone

The meltdown of the nuclear reactor in Chernobyl on 26th April 1986 resulted in massive contamination, especially in the immediate surrounding of the reactor (Baverstock 2003; Environmental Consequences of the Chernobyl Accident and Their Remediation: Twenty Years of Experience 2006; Moller and Mousseau 2006). The evacuation of the entire local population within a 30km exclusion zone around the reactor, and the most strongly contaminated areas outside this zone resulted in the abandonment of about 1,400km^2 of agricultural land (Hostert *et al.* 2011; Deryabina *et al.* 2015). The breakdown of the Soviet Union, with widespread outmigration and an additional 36% of all farmland abandoned in Belarus and Ukraine, further lowered human pressure in the surrounding of the Chernobyl site (Hostert *et al.* 2011).

Two years after the meltdown, the Belarusian part of the exclusion zone and adjacent areas were turned into the strictly protected 1,300km^2 Polesie State Radioecological Reserve. In 1993, the reserve was extended by 850km^2, making it the largest nature reserve in Belarus ("http://www.zapovednik.by/en/about/"). Management of the exclusion zone on both sides of the border has since followed a paradigm of minimum to no intervention. Targeted reintroductions of European bison (*Bison bonasus*) in the Polesie State Radioecological Reserve and of Przewalski's horses (*Equus ferus przewalskii*) to the Ukrainian exclusion zone to restore trophic interactions in the Chernobyl area were exceptions to this passive approach. Recognizing the growing ecological and conservation value of the Chernobyl area, the Ukrainian government has recently established the 2,300km² Chornobyl Radiation and Ecological Biosphere Reserve in 2016 ("http://chornobyl-gef.com/en/tasks-of-the-reserve.html"), establishing an almost 500km², contiguous rewilding area in the heart of Eastern Europe. Management activities in the biosphere reserve aim at the recovery of biodiversity and ecosystem resilience and include monitoring of the ecological, medical and radiation status of the area as well as educational activities ("http://chornobyl-gef.com/en/tasks-of-the-reserve.html").

The region now harbors the entire portfolio of extant European large carnivores (i.e., wolf, lynx (*Lynx lynx*), and brown bear), large herbivores (European bison, wild horse, moose (*Alces alces*), red deer, roe deer, and wild boar (*Sus scrofa*), a rich meso-predator community (e.g., European badger (*Meles meles*), raccoon dog (*Nyctereutes procyonoides*), red fox (*Vulpes vulpes*)) and key ecosystem engineers, such as the Eurasian beaver (*Castor fiber*) (Figure 2.3d). The Chernobyl exclusion zone is the only area where these species interact in sizeable numbers with one another in a large wilderness complex and can thus be considered one of the most iconic natural experiments on rewilding in recent history.

The way forward

Rewilding directly targets restoring ecological functions instead of particular biodiversity compositional states. Therefore, the effects of rewilding may be indirect and unexpected. Consequently, the development of sound rewilding plans requires a deep understanding of interacting ecosystem processes leading to resilience, and of the socio-economic context in which rewilding takes place. Interdisciplinary training of scientists and practitioners is required to develop such understanding. Moreover, objective, evidence-based assessments of rewilding initiatives are needed to make rewilding projects fully accountable to funders, the public and the research community. A recently proposed method to assess progress of rewilding projects using a combination of expert-opinion and monitoring data (Torres *et al.* 2018) is a step towards this goal.

Unfortunately, current landscape management and conservation policies do not provide sufficient opportunities for rewilding to be implemented on a broader scale. For instance, the common agricultural policy (CAP) incentivizes agricultural activities in low production areas, impeding opportunities for rewilding in such areas (Pettorelli *et al.* 2018). Restoration policies often focus on the safeguarding of current or historical conditions (Pettorelli *et al.* 2018) and the protection of certain species and habitats (Navarro and Pereira 2015; Jepson 2016; Pettorelli *et al.* 2018). Therefore, the successful contribution of rewilding to national and international biodiversity goals depends on policy changes that shift the conservation focus towards restoring the ecological processes identified in our framework (Navarro and Pereira 2015).

Discussions on post-2020 biodiversity strategies by the signatory countries of the Convention on Biological Diversity (CBD) are currently being initiated, and several parties support El Salvador's proposal to declare the next decade a "decade of restoration" (Ministerio de Medio Ambiente y Recursos Naturales (MARN) 2018). We believe that rewilding provides one of the possible pathways towards the vision where "By 2050 biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people" (CBD 2010). Perhaps innovative policy changes favoring rewilding can add to the current momentum for novel approaches to restoration (Higgs *et al.* 2018; Mace *et al.* 2018). For instance, Aichi Target 15, which aimed at restoring 15% of degraded ecosystems by 2020, could be revised to recognize rewilding as a major approach to ecological restoration. An ambitious positive target of increasing wildness across the globe by 2030 could be a truly inspiring goal, infusing new energy and public support into global biodiversity policies.

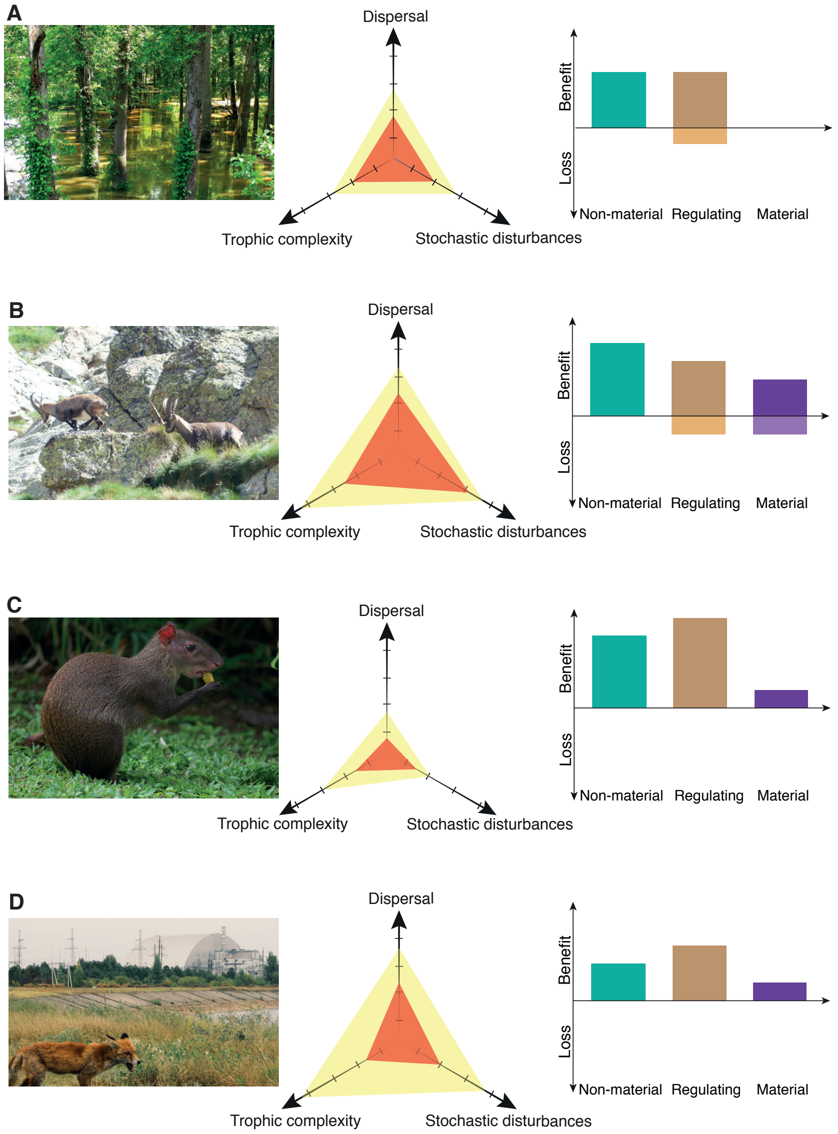

Figure 2.3: Restored ecological processes and their influence on contributions from nature. The ecological state of each case study is represented in a three-dimensional space with one axis for each ecological process of our framework (trophic complexity, dispersal, and stochastic disturbances). The initial ecological state is represented by the red pyramids while the yellow pyramids represent the ecological state after the rewilding actions. The barplots indicate the number of contributions to people (*42*) that are positively or negatively affected by rewilding actions. (A) Rewetting of a river branch in the Leipziger Auwald led to increases in flood-tolerant species and an overall increase in species richness in several taxa. Management actions increased the provision of non-material (e.g., opportunities for learning and inspiration) and regulating services (e.g., habitat creation and maintenance). Impacts on material services are negligible as the project neither affects large agricultural areas nor significantly improves nature-based income opportunities. (B) Non-management, a hunting-ban and reintroductions improved trophic complexity and stochastic disturbance in the Swiss National Park. Management actions promoted economic prosperity of the region (positive material contributions) and agricultural abandonment (negative material contributions). The park provides non-material and regulating contributions, e.g., opportunities for nature experiences, and habitat creation and maintenance. (C) Reintroductions of mammals to Tijuca National Park improved ecological interactions. Restoration potential of all three processes is limited due to the urban location of the park. Management actions may increase material contributions (i.e. income generation through ecotourism). Non-material contributions, e.g., supporting identities or maintenance of options can potentially emerge from community based projects. (D) Land abandonment, protection and reintroductions led to the recovery of the large mammal community in the Chernobyl exclusion zone. Positive regulating, non-material and material contributions include habitat creation and maintenance, opportunities for learning and inspiration, and for wildlife tourism. (Picture credits: A) pxhere creative commons license CC00, B) pxhere creative commons license CC00, C) Brian Gratwicke/Wikimedia Commons, D) Max/Adobe Stock)

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Chapter 3

Habitat choice and coexistence of free-ranging livestock and wild ungulates in an area facing rapid land abandonment

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Habitat choice and coexistence of free-ranging livestock and wild ungulates in an area facing rapid land abandonment

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Abstract

Large scale land abandonment in Europe has the potential to benefit biodiversity by providing habitats for species that have declined due to the loss of large natural areas and provides opportunities for large-scale restoration via passive rewilding. The expected recovery and range expansion of wild mammal species has implications for farming practices and human wildlife conflicts but also for the conservation of biodiversity and the restoration of ecosystem processes. However, there is to date little evidence about the interactions and possible competition between livestock and wild ungulates in European landscapes. Using a novel approach to multispecies occupancy modeling, we investigated habitat choice and patterns of interspecific interactions between livestock and wild ungulates in a marginal agricultural landscape in Northern Portugal. We tested whether the presence of livestock, predators or human infrastructure has negative impacts on the occupancy probability of wild ungulates. Our results showed strong habitat overlap of ungulate species. We found no evidence for negative interactions among free-ranging livestock and wild ungulates or for negative impacts of human infrastructure on the habitat choice of wild ungulates.

3.1 Introduction

About 40 % of the Earth’s ice-free terrestrial areas are currently used for agriculture (Foley et al. 2011) and the resulting loss of natural ecosystems and the associated biodiversity change are recognized as major global concerns (Navarro and Pereira 2012). However, although trends of deforestation and habitat loss are expected to continue in tropical areas, we observe the opposite trend in large parts of the Northern Hemisphere (Pereira et al. 2010). High-income countries are facing reductions in the amount of agricultural land, due to commercialization and industrialization of agricultural practices and slow population growth at regional scales (Keenleyside and Tucker 2010), and low productivity of marginal agricultural land and ageing populations at local scales (MacDonald et al. 2000). The contraction of cultivated land and the decline of rural populations are leading to large-scale land abandonment in Europe. Especially in the Mediterranean basin where limited soil productivity, topography, and accessibility limit the potential for agricultural intensification, land abandonment is a common phenomenon (Plieninger et al. 2014).

Agricultural abandonment is associated with the transition from open areas to shrub-land and forest. Although this may carry the risk of habitat homogenization, the release of marginal agricultural land from anthropogenic pressure has the potential to benefit biodiversity by providing habitats for species that have declined due to the loss of large natural areas (Queiroz et al. 2014). The transformation of open areas to shrubland and forest is likely to reduce fragmentation and increase habitat size and –connectivity (Bodin and Saura 2010; Hernández et al. 2015), and may therefore improve habitat quality (Bowen et al. 2007) and provide opportunities for large scale restoration via passive rewilding (Navarro and Pereira 2012). Rewilding is a flexible approach to restoration and aims to promote trophic integrity, natural disturbance regimes and dispersal potential to restore self-sustaining, resilient ecosystems while largely reducing human management (Chapter 2).

In many cases, the restoration of ecological processes through rewilding may result in the recolonization by large mammals or may trigger increases in their populations. This has implications for farming practices and human wildlife conflicts but also for the conservation of biodiversity and the restoration of ecosystem processes. It has been hypothesized, that, especially in forest habitats, livestock poses a threat to wildlife, e.g. through degradation of habitat, removal and destruction of seedlings and understory vegetation, and resource competition (e.g. Carter et al. 2014; Zhang et al. 2017). Free ranging livestock may compete with wild ungulates for habitat and resources, and can alter habitat use patterns of wildlife (Chirichella, Apollonio, and Putman 2014; Rebollo, Robles, and Gómez Sal 1993). However, there is little knowledge about the interactions and possible competition between livestock and wild ungulates in European landscapes. Although it has been shown that livestock can have strong negative impacts on wildlife in regions where free ranging livestock is still a major agricultural practice (Chirichella, Apollonio, and Putman 2014; Gordon and Illius 1989; Acevedo, Cassinello, and Gortazar 2008), patterns of species distribution and habitat partition between domesticated and wild ungulate species in abandoned landscapes in Europe are not well understood (Apollonio, Andersen, and Putman 2010). Especially in areas that continue to experience marginal extensive farming, population increases of wild species may lead to unexpected patterns of habitat use and species interaction in both domestic and wild species.

Here, we address this gap by investigating the impacts of free ranging horses (*Equus ferus caballus*) and cattle (*Bos taurus*) and the two largest predators in the region (wolves, *Canis lupus signatus*, and red foxes, *Vulpes vulpes*) on the occurrence and habitat use of wild ungulates (wild boar, *Sus scrofa* and roe deer, *Capreolus capreolus*). We studied habitat preferences of the free ranging livestock species, of the wild ungulates, and of the predator species. We tested the hypotheses that (H1) habitat characteristics determining occupancy probability would be unique for each species, that (H2) ungulate species occupancy would be lower in locations close to human infrastructure, and that (H3) occupancy probability of wild ungulates would be impacted by the presence or absence of predators and (H4) by the presence or absence of domestic species. Understanding such interactions between domestic and wild species and the consequence of changing land-use practices on habitat use is important to guide and inform passive restoration approaches like rewilding.

3.2 Material and methods

3.2.1 Study system

Our study was conducted in the Peneda-Gêres National Park in North Western Portugal (42°N, 8°W). The study area was located in the Peneda mountain range that constitutes the northwestern part of the park and ranges in elevation between 300 m and 1340 m above sea level (Rodrigues 2010).

The area has a long-standing agricultural tradition that is based on the common use of lands (Sousa and Correira 2014) but since decades is facing agricultural abandonment (van der Zanden, Carvalho-Ribeiro, and Verburg 2018). The parish of Castro Laboreiro has about 500 inhabitants (census 2011) and large parts of the villages in the area are abandoned (Rodrigues 2010). Today, the main agricultural activity is the extensive breeding of cattle, sheep (*Ovies gmelini aries*), domestic goats (*Capra aegagrus hircus*) and horses. Cattle and horses are free ranging but while cattle are kept in stables at night during winter and receive supplementary feeding, horses are largely unmanaged. The area hosts a diverse mammal community with (large) predators such as Iberian wolf, red fox, and common genet (*Genetta genetta*), and large herbivores such as roe deer, red deer (*Cervus elaphus*), wild boar and Iberian ibex (*Capra pyrenaica*). Some of these species, i.e. the Iberian ibex, the Iberian wolf and - living at the edge of its distribution and being an important prey species - the roe deer are of high conservation concern to this region (Torres Tinoco, Virgós, Panzacchi, et al. 2012).

Currently, traditional farming practices are disappearing in this marginal agricultural region. The decrease in agricultural activity and the associated increase in habitat connectivity is likely to lead to increasing population densities and range expansions of wild ungulates (Acevedo et al. 2010). The region therefore provides an interesting study model to investigate the patterns of species interaction between extensively managed, free-roaming livestock and wild mammals in the face of landscape abandonment.

The National Park covers an area of approx. 703km^2 with elevations ranging from 50m to 1,548m above sea level. The region is influenced by Atlantic, Mediterranean and Continental climate with a mean temperature of 9.6°C and an annual precipitation of up to 2,800mm with a peak in December (433mm) and a drop to 36mm in August (Honrado 2003) with frequent wildfires during summer. Due to its large elevation range and its rugged terrain, the area is exposed to a wide range of microclimates and hosts a great diversity of habitats. Main habitat types include Galicio-Portuguese oak forests (mainly *Quercus robur* and *Q. pyrenaica* (Proença et al. 2010), shrublands dominated by gorse (*Ulex minor, U. europaeus*), heather (*Erica umbellata, E. arborea, E. australis, E. cinerea, E. tetralix, E. ciliaris, Calluna vulgaris, Daboecia cantabrica*) and broom (*Cytisus striatus*) and large rocky areas (Honrado 2003). Pine forests (*Pinus pinaster*) and agricultural fields are found to a lesser extent.

3.2.2 Large mammal species

The community of wild mammalian ungulates is composed of roe deer, red deer, wild boar and Iberian ibex. Domestic and semi-domestic ungulates include the Cachena and Barrosã cattle breeds and the Garrano horse, all local breeds which are listed by the FAO as endangered (FAO 2016), as well as sheep and goats. The cattle are used for meat production and are managed, whereas the Garrano horses are largely unmanaged and freely roam the area throughout the year. Sheep and goats are usually guarded by a shepherd and guarding dogs. They are led to pastures for feeding and are kept in barns at night to prevent predation by wolves (own observation).

The European roe deer is the most common cervid species in Europe (Apollonio, Andersen, and Putman 2010) and the habitat requirements for central and northern European populations are well studied (Torres Tinoco et al. 2011). The population in Peneda-Gerês lives at the southwestern edge of the species' distribution where it only occurs in low densities and is thought to be more susceptible to local extinction due to potential environmental changes (Torres Tinoco et al. 2011; Torres Tinoco, Virgós, Panzacchi, et al. 2012). As an important prey species for the endangered Iberian wolf, it is of high ecological value and conservation concern in this region (Torres Tinoco et al. 2015). Nevertheless, these marginal populations are not well studied to date, and information on habitat use and the reaction to predators or anthropogenic influences, including livestock management remain scarce (but see Torres Tinoco et al. 2011, 2012; Valente et al. 2014).

Wild boar are able to exploit a wide range of resources: They occur in a large variety of habitat types, feed opportunistically on plants, small mammals and invertebrates, and frequently exploit agricultural crops (Massei and Genov 2004). In areas where predators are present, they are often an important prey species (Meriggi and Lovari 1996). Wild boar prefer habitats that provide high-energy food and cover from predators (Massei and Genov 2004). Although habitat requirements of wild boar are well studied, there are, to the best of our knowledge, no studies investigating patterns of interspecific competition between livestock and wild boar.

This study focused on the habitat use and possible interactions between semi-wild livestock (free-ranging horses and cattle) and the main wild ungulates roe deer and wild boar. We also studied interspecific interactions of ungulates with foxes and wolves to test for potential interactions of domestic and wild ungulates with predators. Since sheep and goats are guarded and therefore prevented from exhibiting natural habitat choice, these species were not included in the analysis. Although red deer and Iberian ibex were recorded by camera traps in previous years, they were not recorded during the study period and could therefore not be included in this analysis.

3.2.3 Camera trapping

We deployed 64 cameras (Reconyx HC 600 Hyperfire HD) in a grid of approx. 16km^2 with one camera per 0.25ha grid cell (approx. 500 m spacing between each camera, Figure 3.1). We used a land cover map of the study area (Rodrigues 2010) to choose camera locations in advance and distributed them as uniformly as possible across the different habitat types (Figure 3.2).

In most cases, the actual camera location deviated from the originally chosen one due to topographical barriers, but we aimed to not deviate from the original camera locations by more than 50m. Cameras were attached to trees or rocks at a height of approx. 80cm above the ground. Cameras were facing random directions to avoid detection biases (e.g. by directing cameras at animal trails). Cameras were triggered by movement. We set cameras to take pictures 24 hours a day and took a set of three pictures per trigger with no delay after trigger to increase the probability of obtaining identifiable images. The camera sensor was set to medium sensitivity and the flash was set to be balanced optimally between maximum flash range and shutter speed. We used camera trapping data collected between April 13th 2016 and August 22nd 2016. Due to theft or camera failure, we obtained data from a total of 60 cameras. We processed all images manually and built a matrix of presence/absence records, using one record per species, camera location and day.

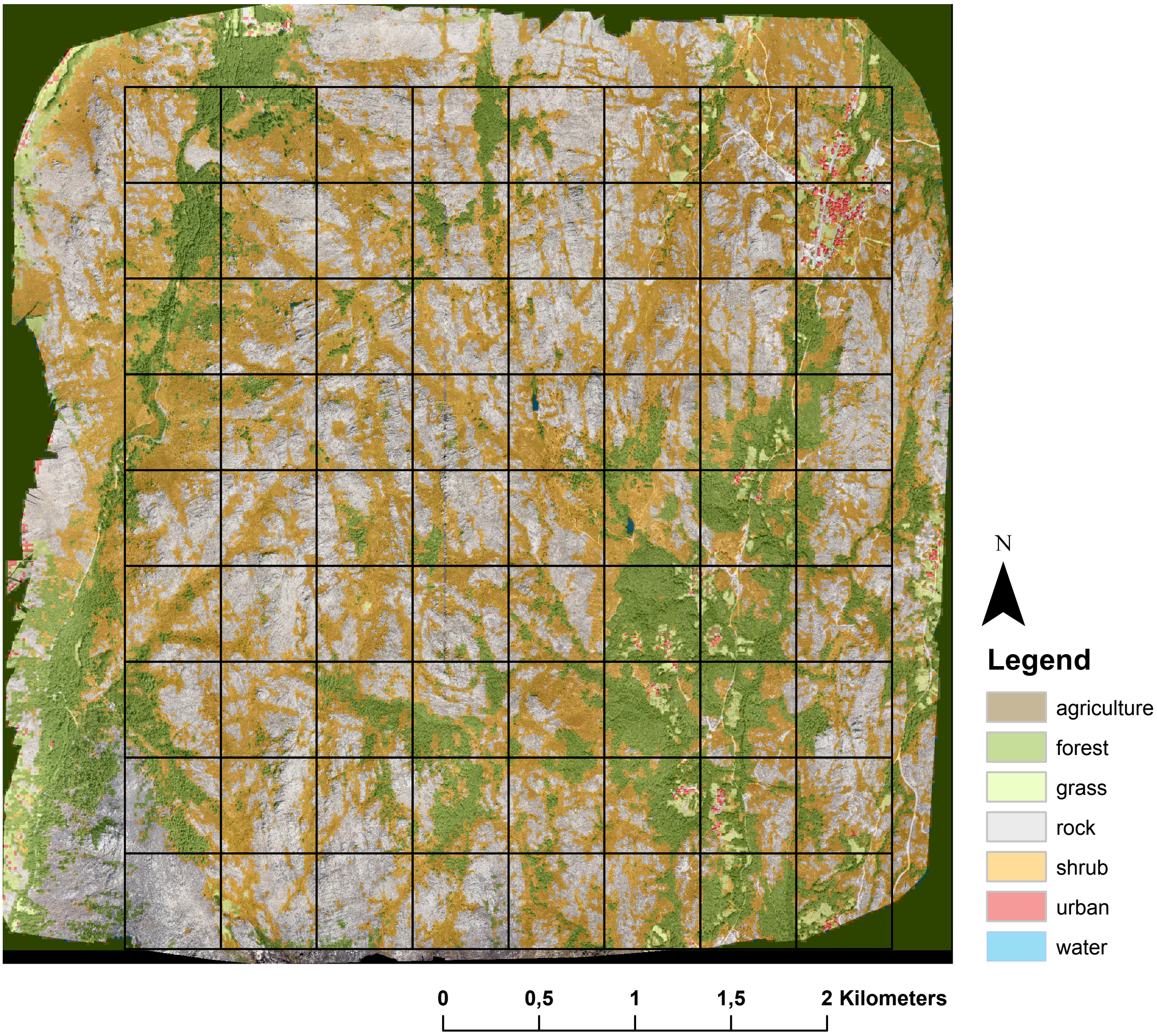

Figure 3.1: Aerial image of the study area in Peneda-Gerês National Park (42°N, 8°W) with land cover classification. Cameras were distributed uniformly across different habitat types with one camera per grid cell.

3.2.4 Modelling framework

We adapted and used a multispecies occupancy model (Rota *et al.* 2016) that generalizes the single species-model developed by MacKenzie et al. (2002) to more than one species, using a multivariate Bernoulli distribution (MVB). Similar to the single-species model, a detection model is linked with a partially observed, latent process model.

In single-species occupancy models, the probability of presence of species *i* in site *s*, Ψ_{is} follows a univariate Bernoulli distribution $z \sim Bernoulli(\Psi)$, with the corresponding probability mass function

$$F(z|\Psi) = \Psi^{z}(1\text{-}\Psi)^{z\text{-}1} = \exp(z \log\left(\frac{\Psi}{1-\Psi)}\right) + \log(1-\Psi)). \tag{1}$$

From this probability mass function, we can derive the log odds a species occupies a site, the so-called natural parameter, that can be modelled as a function of covariates, assuming a logit link:

$$\mathrm{f} = \log\left(\frac{\Psi}{1-\Psi}\right) = \mathrm{x}'\beta\ . \tag{2}$$

where *x* is a vector of occupancy covariates and β is a vector of slope parameters, i.e. the log odds ratio of occupancy probability resulting from a 1-unit change in *x* (Rota *et al.* 2016).

Expanding the univariate Bernoulli distribution to more than one dimensions, the multispecies occupancy model estimates the occupancy probability Ψ of species *i* conditional on the presence or absence of another species *j*, while accounting for non-detections (Rota *et al.* 2016). We extended the model to four species. Including four species into the model results in 16 combinations of 1's (species present) and 0's (species absent) following a multivariate Bernoulli distribution

$$Z \sim MVB(\Psi_{1111}, \Psi_{1110}, \Psi_{0111}, \Psi_{1011}, \Psi_{1101}, \Psi_{1100}, \Psi_{1010}, \Psi_{1001}, \Psi_{0110}, \Psi_{0011}, \Psi_{0101}, \Psi_{1000}, \Psi_{0100}, \Psi_{0010}, \Psi_{0001}, \Psi_{0000})$$

where Z is a two-dimensional vector of 1's and 0's indicating a latent occupancy state for all four species, and Ψ is the probability of all possible sequences of 1's and 0's (Rota *et al.* 2016). For example, Ψ_{1111} represents the case where species all four species are present, $\Psi_{1000}, \Psi_{0100}, \Psi_{0010}$ and Ψ_{0001} represent the cases where each of the species occurs alone, Ψ_{0000} represents the case where none of the species are present, and so on.

In a four-species model the natural parameters $f_1, f_2, f_3, f_4$are defined as:

$$f_1 = \log\left(\frac{\Psi_{1000}}{\Psi_{0000}}\right) = x_{\alpha}{}'\alpha, \tag{3}$$

$$f_2 = \log\left(\frac{\Psi_{0100}}{\Psi_{0000}}\right) = x_{\beta}{}'\beta, \tag{4}$$

$$f_3 = \log\left(\frac{\Psi_{0010}}{\Psi_{0000}}\right) = x'_{\lambda}\lambda, \tag{5}$$

$$f_4 = \log\left(\frac{\Psi_{0001}}{\Psi_{0000}}\right) = x'_{\mu}\ . \tag{6}$$

The natural parameters for the co-occurrence of two species, e.g. species *i* and *j* are defined as:

$$f_{12} = \log\left(\frac{\Psi_{1100}\Psi_{0000}}{\Psi_{0100}\Psi_{1000}}\right) = x'_{\gamma}\gamma, \tag{7}$$

where *x* is a vector of occupancy covariates and α, β and γ are vectors of slope parameters. γ can be interpreted as an interaction factor, that defines the difference in log odds ratios of occupancy probability of one species resulting from a 1-unit change in *x* when the other species is present or absent (Rota *et al.* 2016).

Importantly, we assume that higher order interactions (i.e. the probability that more than two species co-occur) are a function of marginal occupancy of one species and pairwise interactions of two species, e.g.

$$f_{123} = \log\left(\frac{\Psi_{1110}\Psi_{1000}\ \Psi_{0100}\Psi_{0010}}{\Psi_{1100}\Psi_{1010}\Psi_{0110}\Psi_{0000}}\right) = 0. \tag{8}$$

(See Supplementary Information for derivation of all natural parameters from the probability mass function for four species).

The probability of co-occurrence of each species pair can then be expressed via the multinomial logit link, e.g.

$$\Psi 1000 = \frac{\exp(\mathrm{f1})}{\left(\begin{array}{c} 1+\exp(\mathrm{f1})+\exp(\mathrm{f2})+\exp(\mathrm{f3})+\exp(\mathrm{f4}) \\ +\exp(\mathrm{f1}+\mathrm{f2}+\mathrm{f12})+\exp(\mathrm{f1}+\mathrm{f3}+\mathrm{f13})+\exp(\mathrm{f1}+\mathrm{f4}+\mathrm{f14}) \\ +\exp(\mathrm{f2}+\mathrm{f3}+\mathrm{f23})+\exp(\mathrm{f2}+\mathrm{f4}+\mathrm{f24})+\exp(\mathrm{f3}+\mathrm{f4}+\mathrm{f34}) \\ +\exp(\mathrm{f1}+\mathrm{f2}+\mathrm{f3}+\mathrm{f12}+\mathrm{f13}+\mathrm{f23}) \\ +\exp(\mathrm{f1}+\mathrm{f2}+\mathrm{f4}+\mathrm{f12}+\mathrm{f14}+\mathrm{f24}) \\ +\exp(\mathrm{f1}+\mathrm{f3}+\mathrm{f4}+\mathrm{f13}+\mathrm{f14}+\mathrm{f34}) \\ +\exp(\mathrm{f2}+\mathrm{f3}+\mathrm{f4}+\mathrm{f23}+\mathrm{f24}+\mathrm{f34}) \\ +\exp(\mathrm{f1}+\mathrm{f2}+\mathrm{f3}+\mathrm{f4}+\mathrm{f12}+\mathrm{f13}+\mathrm{f14}+\mathrm{f23}+\mathrm{f24}+\mathrm{f34}) \end{array}\right)} \tag{9}$$

(See Supplementary Information for more examples).

Marginal occupancy

Assuming that species occurrences are not influenced by the presence or absence of another species (i.e. γ=0), we can model their *marginal occupancy* (*P*) in response to environmental variables by summing all cases where the focus species is present regardless of whether any of the other species are present or absent. For example, the marginal occupancy of species *i* can be modelled as:

$$P(z_1 = 1) = \Psi_{1111} + \Psi_{1110} + \Psi_{1100} + \Psi_{1000} + \Psi_{1011} + \Psi_{1001} + \Psi_{1101} + \Psi_{1010}. \qquad (10)$$

Conditional occupancy

Assuming that the occurrence of a species *i* is dependent on the presence or absence of a second species *j*, we can model the *conditional occupancy* of both species:

$$P(z_1 = 1|z_2 = 0) = \frac{\Psi_{1000}+\Psi_{1011}+\Psi_{1001}+\Psi_{1010}}{\Psi_{1000}+\Psi_{1011}+\Psi_{1001}+\Psi_{1010}+\Psi_{0001}\Psi_{0010}+\Psi_{0011}+\Psi_{0000}}, \qquad (11)$$

$$P(z_1 = 1|z_2 = 1) = \frac{\Psi_{1111}+\Psi_{1110}+\Psi_{1100}+\Psi_{1101}}{\Psi_{1111}+\Psi_{1110}+\Psi_{1100}+\Psi_{1101}+\Psi_{0111}+\Psi_{0110}+\Psi_{0101}+\Psi_{0100}}, \qquad (12)$$

$$P(z_2 = 1|z_1 = 0) = \frac{\Psi_{0111}+\Psi_{0110}+\Psi_{0100}+\Psi_{0101}}{\Psi_{0111}+\Psi_{0110}+\Psi_{0100}+\Psi_{0101}+\Psi_{0001}\Psi_{0010}+\Psi_{0011}+\Psi_{0000}}, \qquad (13)$$

$$P(z_2 = 1|z_1 = 1) = \frac{\Psi_{1111}+\Psi_{1110}+\Psi_{1100}+\Psi_{1101}}{\Psi_{1111}+\Psi_{1110}+\Psi_{1100}+\Psi_{1101}+\Psi_{1000}+\Psi_{1011}+\Psi_{1001}+\Psi_{1010}}. \qquad (14)$$

Evidence for species interactions while accounting for environmental variables can be explored by comparing a model assuming that species occur independently to one that assumes species interaction. An advantage of the MVB model compared to other joint distribution models is that it allows the influence of environmental variables on one species to differ in the presence and absence of another species (Rota et al. 2016).

3.2.5 Detection probability

Trigger reach of the cameras varied across sites due to differences in vegetation cover and topography. We modelled detection probability for species *i* at site *s* in survey *t* as a function of the maximum distance d_{ist} at which the camera would still detect movement and trigger.

p_{ist}= logit^{-1} (d'_{ist} α_i), where α_i is a slope parameter that defines the change in detection probability with a 1-unit change in detection distance.

3.2.6 Occupancy covariates

We included the proportion of the main habitat types oak forest, shrubland and grassland as occupancy covariates in the model. We extracted the proportion of each land cover type in a 50m buffer around each camera locations from land cover maps. During camera setup, we confirmed and corrected land cover types if necessary. We included cost-distance (i.e. the distance weighted by the effort it requires to move between two points) to settlements and cost-distance to roads in the model, because we hypothesized that human disturbance may impact the habitat choice and occurrence of the different species. Cost-distance values were obtained using a digital elevation model and calculated in ArcGIS (version 10.2.1). We checked for collinearity between occupancy covariates using Spearman rank correlation and found all covariates to be uncorrelated (Correlation coefficients below 0.7, data not shown).

For each study species, we calculated marginal occupancy probability across changes in the five covariates. To test for interspecific competition, we calculated conditional occupancies for each species pair and tested whether the presence or absence of a species influenced the occupancy probability of a second species in response to changes in the habitat covariates. Note, that we did not include higher order interactions, i.e. we assumed that the probability of three or more species occurring together was a function of marginal and pairwise conditional occupancy probabilities.

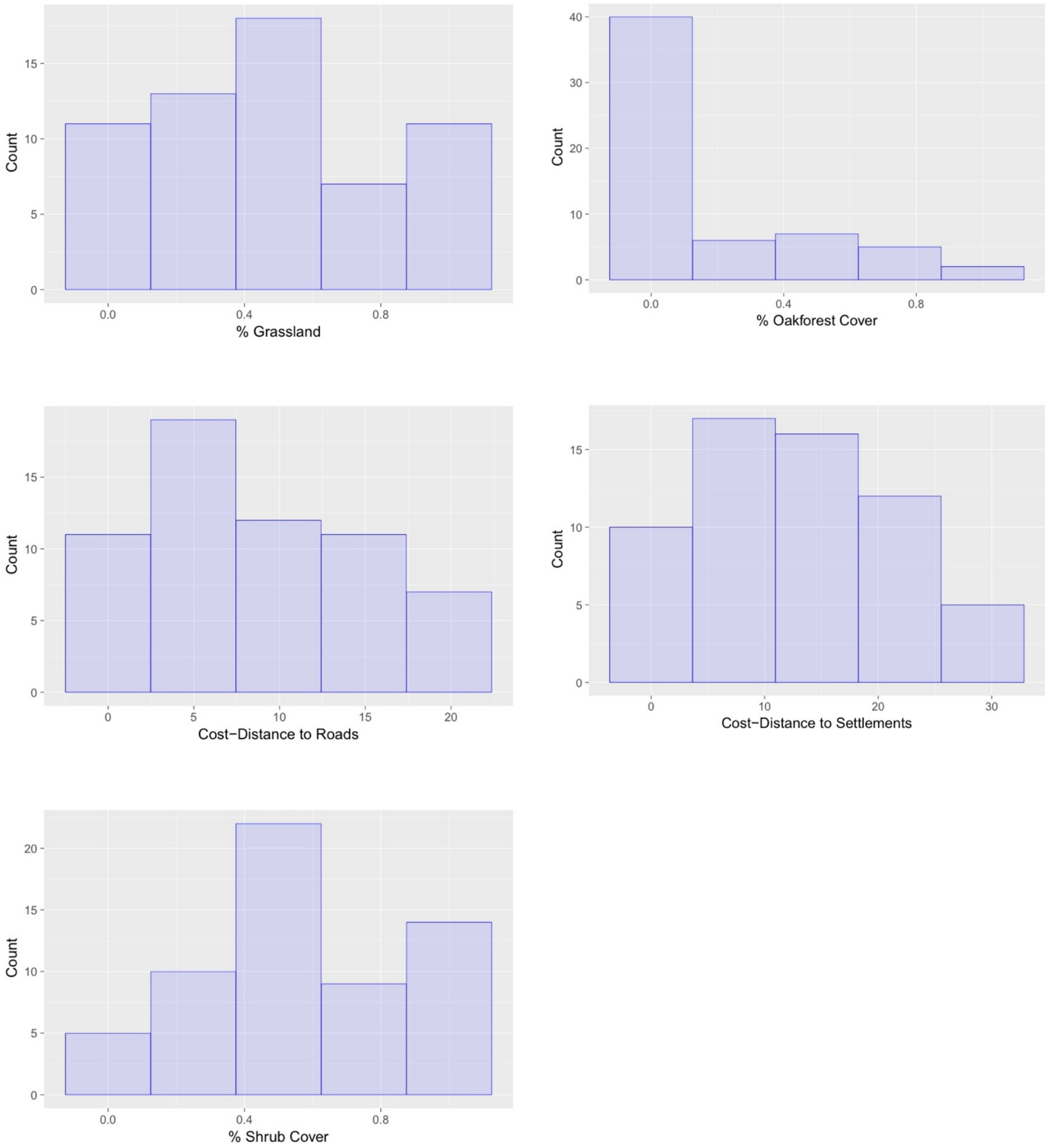

Figure 3.2: Distribution of cameras across occupancy covariates.

3.2.7 Modeling framework

We used rStan version 2.18.2 (Stan Development Team 2018) to run all models. We ran 15 models with five covariates included to explain marginal occupancy and to explain pairwise interspecific interactions as a function of each of the variables.

For each model, we ran four chains with 2,500 iterations after a burn-in phase of 500 iterations each. Convergence of chains was inspected visually using trace plots and adequate convergence was determined using the Brooks-Gelman-Rubin convergence diagnostic (Rhat<1.1, Gelman et al. 2014). All models achieved adequate convergence after 2,500 iterations. We chose a logistic prior distribution for all parameters because this results in a uniform distribution when assuming a logit link (Rota et al. 2016). For all estimates, we calculated 95% credible intervals (on the logit scale). Estimates where the limits of the credible intervals overlapped zero were defined insignificant.

3.3 Results

Cameras were recording between 13th April and 22nd August 2016, totaling to 6,409 days across 60 sites. Per site, camera working days ranged from 30 to 134 days.

Roe deer were the most widespread species. They were recorded in 51 out of 60 camera locations in 428 occasions (naïve occurrence 0.85). Horses were the most frequently recorded species and were observed in 41 camera locations on 435 occasions (naïve occurrence 0.68). Cattle were recorded in 38 camera locations on 417 occasions (naïve occurrence 0.63). Wild boar were recorded in 35 camera locations on 179 occasions (naïve occurrence 58%). Foxes were recorded in 28 camera locations on 84 occasions (naïve occurrence 0.47) and wolves were recorded in six camera locations on 32 occasions (naïve occurrence 0.10). In one of the camera locations all target species were recorded. None of the target species were recorded in five of the camera locations. One or more ungulate species co-occurred with foxes in 26 sites and co-occurred with wolves in six sites.

3.3.1 Detection probability

We modelled detection probability as a function of detection distance, i.e. the distance at which the camera would still detect movement and trigger. Detection probability was generally low, but was higher for ungulate species than for predator species (Table 3.1). Detection probability of cattle and horses increased significantly with an increase in detection distance. Detection probability of foxes decreased significantly with an increase of the distance a camera would still trigger. Detection probability of the other species did not vary significantly with changes in the maximum detection distance (Figure 3.3, Table 3.2).

Table 3.1: Summary detection probabilities.

	Wild boar	Roe deer	Cattle	Horse	Red fox	Wolf
Mean detection probability	0.105	0.116	0.105	0.116	0.022	0.041
Standard deviation	0.023	0.042	0.023	0.042	0.007	0.004

Table 3.2: Change in detection probability p per 1-unit change in detection distance. 2.5% CI and 97.5% CI values indicate thresholds of 95% credible intervals. Estimates where credible intervals overlapped zero were defined as insignificant. Asterisks indicate the species whose detection probability was significantly influenced by changes in detection distance.

	Wild boar	Roe deer	Cattle*	Horse*	Red fox*	Wolf
2.5% CI	-0.276	-0.022	0.149	0.318	-0.591	-0.564
Mean	-0.129	0.075	0.240	0.417	-0.322	-0.133
97.5% CI	0.016	0.169	0.333	0.514	-0.062	0.254

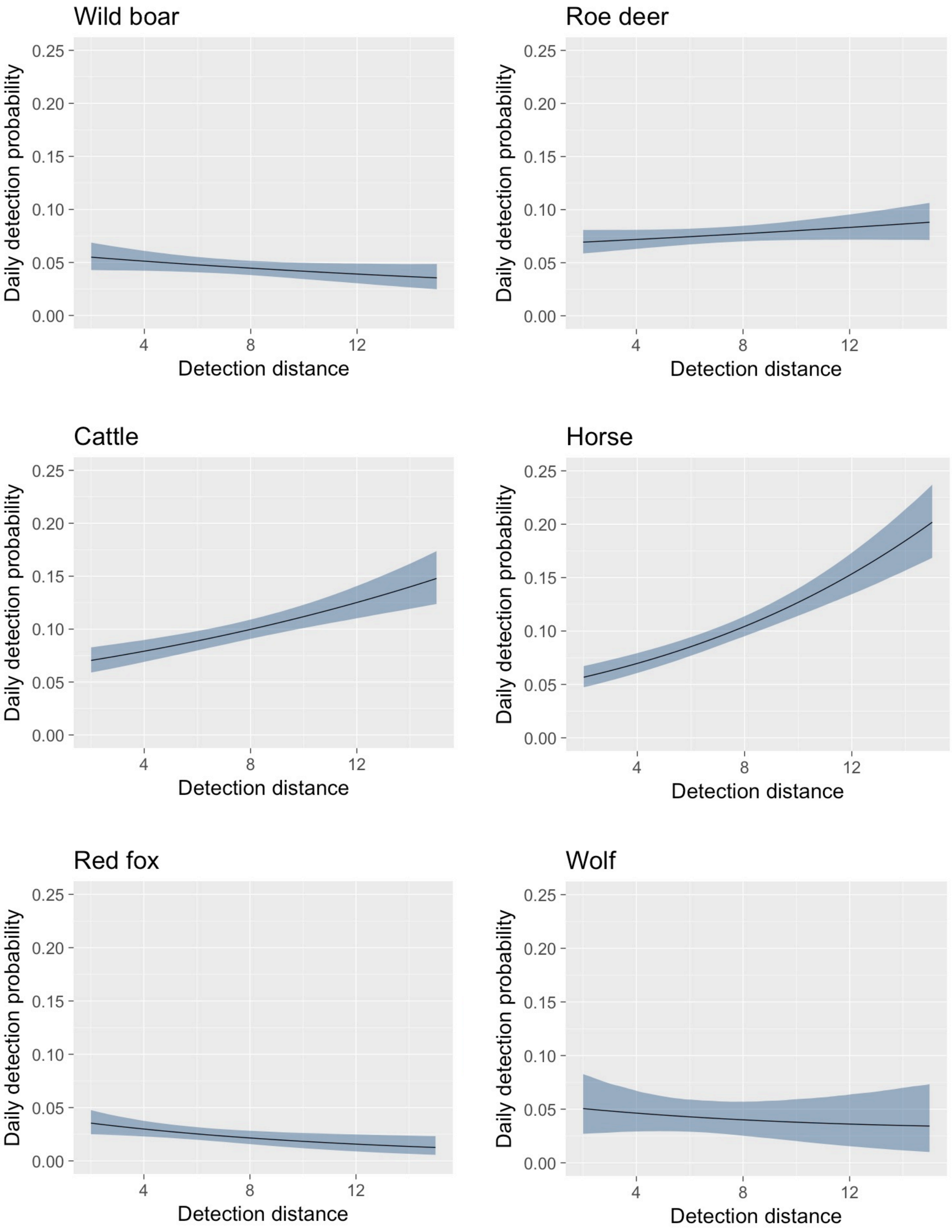

Figure 3.3: Detection probability for the target species across different maximum trigger distances. Lines represent mean posterior distributions and shaded areas envelop 95% credible intervals.

3.3.2 Marginal occupancy

Roe deer exhibited the highest mean marginal occupancy probability across all habitat types (Ψ_{mean}: 0.91-0.95) and wolves showed lowest mean marginal occupancy probability across all habitat types (Ψ_{mean}: 0.09-0.14). (See Supplementary information table SI 1 for all values).

Horses and roe deer did not show changes in marginal occupancy probability in response to changes in habitat variables. Marginal occupancy of wild boar increased with increases in oak forest cover. Cattle marginal occupancy increased with increasing distance to settlements (Figure 3.4, Table 3.3).

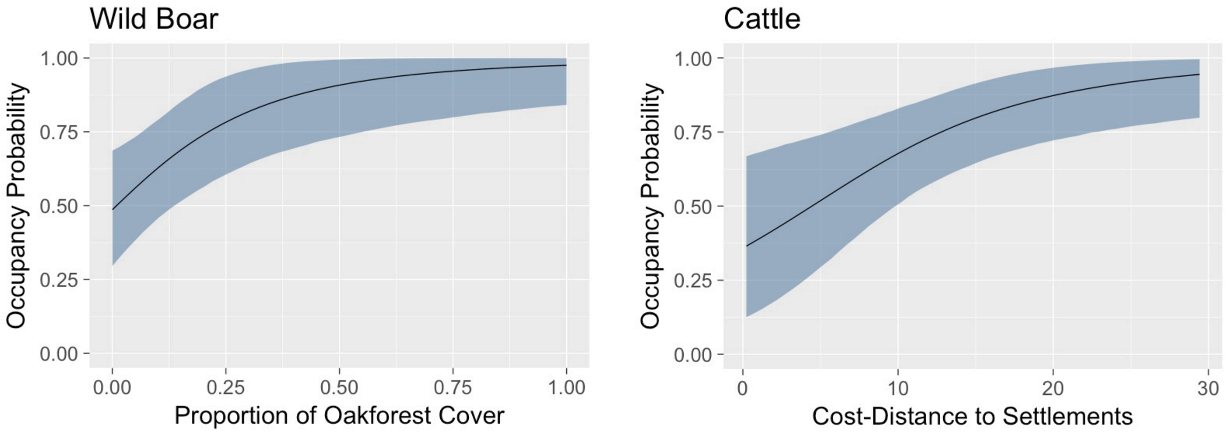

Figure 3.4: Proportion of oak forest cover predicted occupancy probability for wild boar. Cost-distance to settlements predicted occupancy probability of cattle. Lines represent mean posterior distributions of predicted relationships between probability of occurrence and changes in predictor variables. Blue shaded areas represent 95% credible intervals. Variables not included in the plot are assumed fixed at their observed mean.

Table 3.3: Slope coefficients indicating changes in marginal occupancy probabilities (on the logit scale) of ungulate species in response to a 1-unit change in respective predictor variables. 2.5% CI and 97.5% CI values indicate limits of the 95% credible intervals. Estimates where credible intervals did not overlap zero were defined as significant (bold values).

	Ψ	Intercept	Cost-Distance to Roads	% Oak	% Shrub	% Grass	Cost-Distance to Settlements
Horse							
	2.5% CI	-2.586	-0.563	-1.489	-1.346	-1.515	-0.441
	Mean	-0.931	0.131	-0.698	-0.554	-0.158	0.261
	97.5% CI	0.589	0.838	0.075	0.196	1.206	0.994
Cattle							
	2.5% CI	-2.520	-0.864	-0.240	-1.159	-1.602	**0.416**
	Mean	-0.787	-0.108	0.651	-0.384	-0.116	**1.269**
	97.5% CI	0.786	0.639	1.650	0.367	1.346	**2.243**
Roe deer							
	2.5% CI	-1.104	-1.234	-0.086	-0.573	-0.655	-0.922
	Mean	0.530	-0.223	1.421	0.389	0.675	0.136
	97.5% CI	2.299	0.789	3.461	1.423	2.024	1.363
Wild boar							
	2.5% CI	-3.370	-0.250	**0.218**	-1.252	-1.397	-1.722
	Mean	-1.315	0.484	**1.304**	-0.452	0.218	-0.791
	97.5% CI	0.511	1.277	**2.918**	0.311	1.843	0.039

3.3.3 Species interactions

We tested for pairwise interspecific interactions between all ungulate species and between ungulate species and the two main predators, wolf and fox. We did not find evidence for constant interspecific competition between any of the species pairs, i.e. in none of the species pairs was occupancy probability of one species significantly lower in the presence of a second species, regardless of changes in habitat (Intercept slopes positive, credible intervals did not overlap zero, Table 3.4).

On the contrary, we found positive interactions between the ungulate species. Independent of changes in habitat, roe deer conditional occupancy was higher in the presence of horses, wild boar and foxes, and vice versa. These constant pairwise interactions are represented by approximately parallel slopes. As an example, the pairwise interactions between roe deer, wild boar and red fox in response to increasing distance to roads is displayed in Figure 3.5.

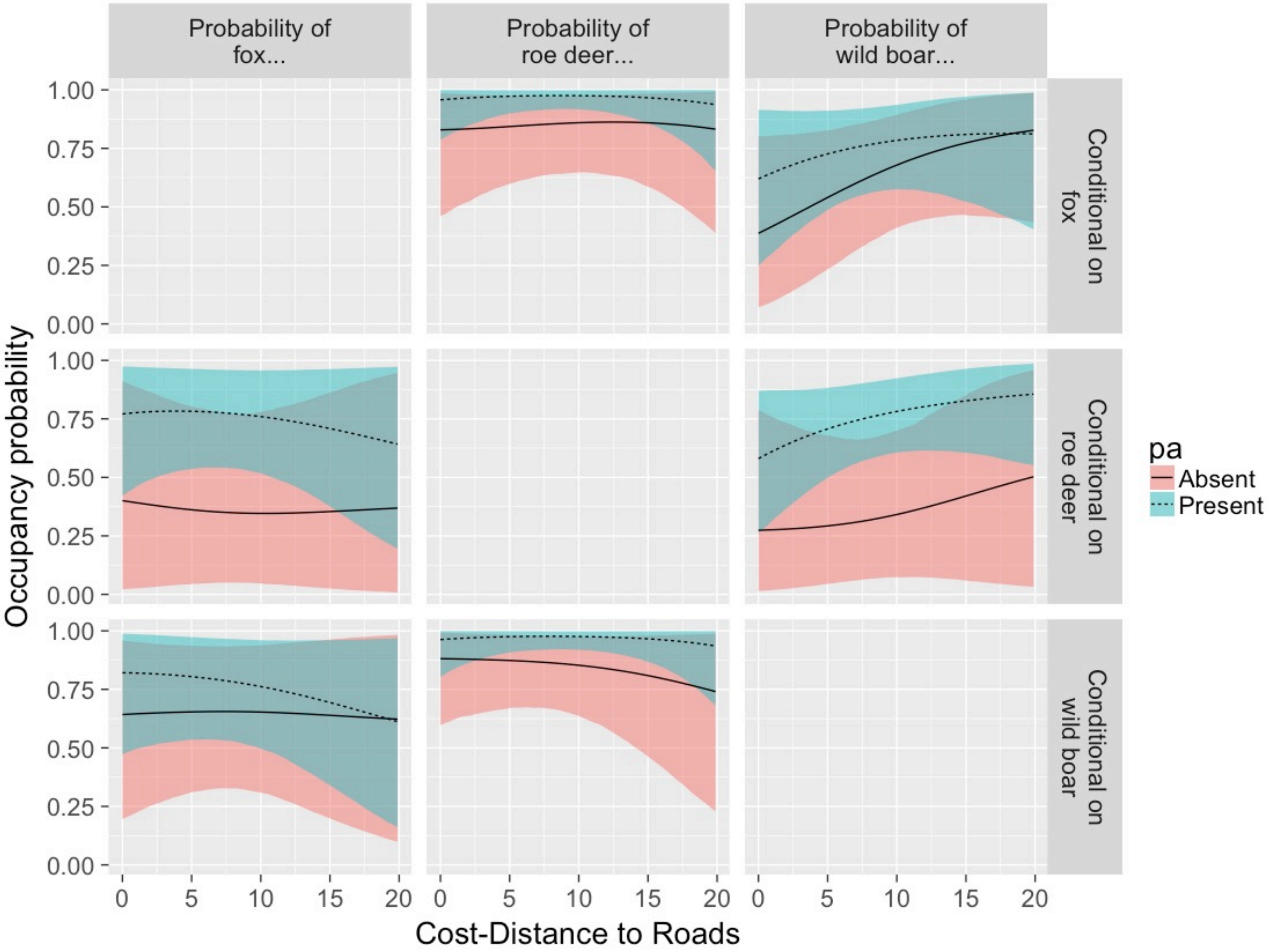

Figure 3.5: Occupancy probability of roe deer, wild boar and fox conditional on the presence or absence of another species. Independent of changes in habitat characteristics, occupancy probability of roe deer was higher in sites where red fox or wild boar were present and vice versa. Constant pairwise interactions are represented by approximately parallel slopes. Posterior distributions of predicted relationships between the probability of occurrence of one species conditional on the presence or absence of another species across increasing distance to roads.

Table 3.4: Slope coefficients indicating changes in conditional occupancy probabilities (on the logit scale) of pairs of ungulate and predator species in response to a 1-unit change in respective predictor variables. 2.5% CI and 97.5% CI values indicate limits of the 95% credible intervals. Estimates where credible intervals did not overlap zero were defined as significant (bold values).

	Ψ	Intercept	Cost-Distance to Roads	% Oak	% Shrub	% Grass	Cost-Distance to Settlements
Roe deer	2.5% CI	**0.057**	-1.655	-1.273	-1.977	-2.241	-1.871
–	Mean	**2.003**	0.028	0.953	-0.037	-0.442	0.022
Fox	97.5% CI	**4.443**	1.736	3.528	1.858	1.269	1.932
Roe deer	2.5% CI	-2.521	-2.779	-2.135	-1.471	-2.645	-3.432
–	Mean	-0.511	-0.790	0.131	0.339	-0.864	-1.346
Wolf	97.5% CI	1.566	1.074	2.417	2.166	0.873	0.560
Wild boar	2.5% CI	-1.144	-1.941	-1.787	-1.876	-0.149	-1.415
–	Mean	0.519	-0.451	0.338	-0.288	1.333	0.155
Fox	97.5% CI	2.185	0.977	2.599	1.243	2.921	1.801
Wild boar	2.5% CI	-2.094	-1.055	-1.774	-2.320	-1.659	-0.284
–	Mean	-0.237	0.615	0.154	-0.590	-0.092	1.362
Wolf	97.5% CI	1.580	2.401	2.205	1.080	1.453	3.211
Cattle	2.5% CI	-0.364	-1.463	-0.914	-1.897	-0.774	-1.614
–	Mean	1.103	-0.080	0.784	-0.420	0.581	-0.149
Fox	97.5% CI	2.659	1.269	2.551	1.037	1.953	1.354
Cattle	2.5% CI	-1.515	-2.233	-1.693	-2.361	-1.922	-2.161
–	Mean	0.198	-0.488	0.079	-0.555	-0.302	-0.401
Wolf	97.5% CI	2.081	1.198	1.996	1.117	1.289	1.349
Horse	2.5% CI	-2.305	-1.539	-1.241	-1.245	-0.975	-1.881
–	Mean	-0.781	-0.183	0.454	0.200	0.343	-0.397
Fox	97.5% CI	0.651	1.139	2.325	1.639	1.693	0.960
Horse	2.5% CI	-1.457	-1.210	-1.341	-2.638	-0.919	-1.357
–	Mean	0.253	0.357	0.149	-0.823	0.700	0.154
Wolf	97.5% CI	2.074	1.990	1.713	0.805	2.447	1.722

We found evidence for constant positive interspecific interaction between roe deer and wild boar (2.5 % confidence interval (CI)= 0.26, mean=1.97, 97.5% CI=3.93). Moreover, we found that the cost- distance to settlements influenced the probability of co-occurrence of roe deer and wild boar (2.5 % CI=0.24, mean=2.02, 97.5% CI=4.08). The effect of this interaction was more pronounced in wild boar which showed to be more likely to occupy sites in close vicinity to settlements if roe deer were also present. In greater distance to settlements wild boar occurred largely independently of roe deer (great overlap of credible intervals, Figure 3.6).

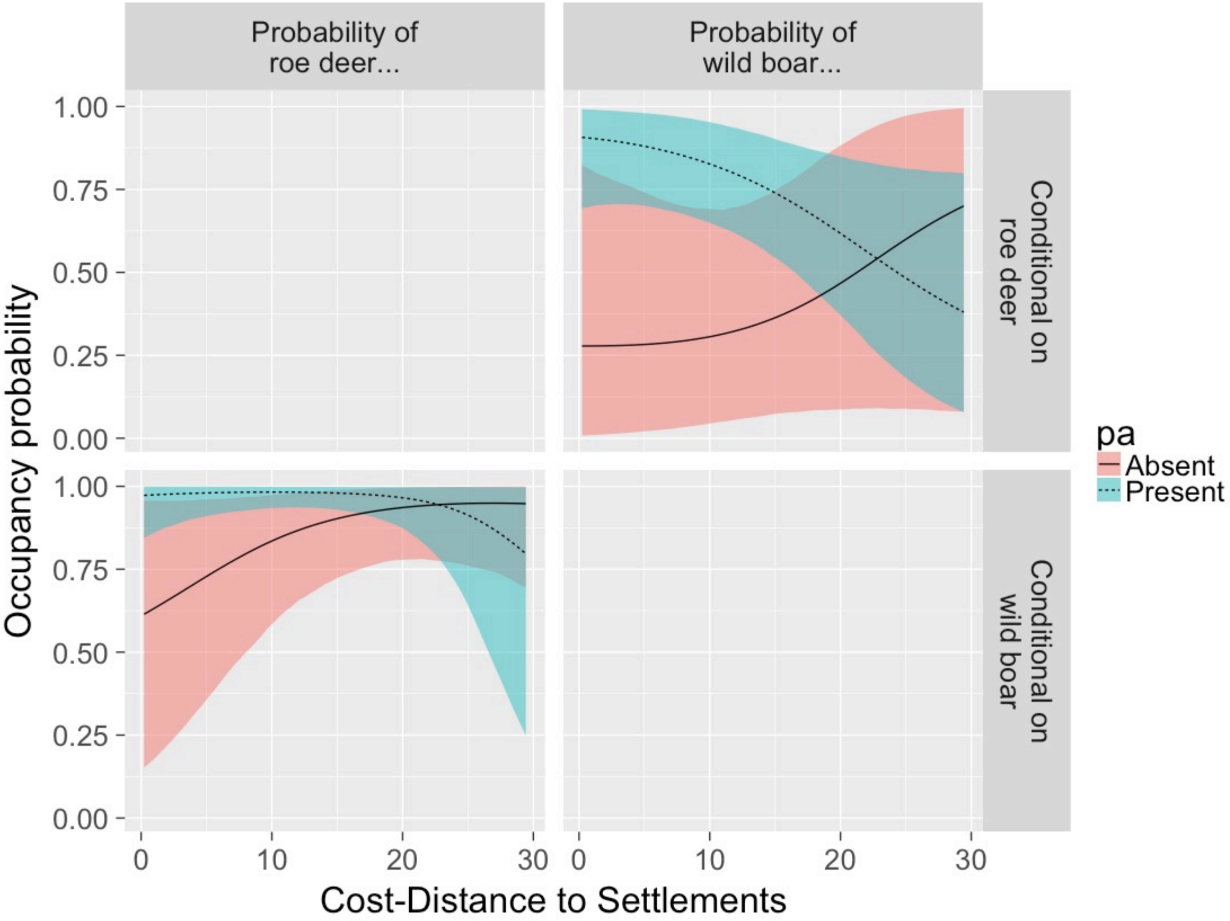

Figure 3.6: Occupancy of roe deer and wild boar decreased with increasing distance to settlements when the second species was present and increased when the second species was present. Posterior distributions of predicted relationships between the probability of occurrence of one species conditional on the presence or absence of another species across increasing distance to roads.

3.4 Discussion

We show that the occupancy probability of wild and domestic ungulate species was influenced by habitat characteristics and interspecific interactions. Our results suggest that the presence of domestic ungulates, wild predators or human infrastructure did not lead to competitive exclusion and displacement of wild ungulates.

Habitat choice of ungulates is determined by land cover and interspecific interaction, not by human disturbance or predators.

Oak forest cover proved to be an important habitat characteristic for wild boar. Although there was no strong evidence for this relationship, roe deer responded positively to increases in oak forest cover. A preference of roe deer for oak forest might have been masked by the overall very high occupancy of this species.

The preference for oak forest may be explained by several factors: First, areas with high tree cover provide shelter from unfavorable weather conditions and cover from predators. Second, oaks are among the most palatable deciduous tree species for browsers (Kramer, Groot Bruinderink, and Prins 2006) and their acorns provide an important energy source for wild boar (Massei, Genov, and Staines 1996). Finally, as the oak forests in the study area are relatively sparse and feature a rich understorey vegetation which may include plant species that are frequently consumed by browsers and grazers (e.g., Rita Tinoco Torres et al. 2012), they provide advantages in terms of both food availability and cover from predation, and adverse weather conditions (Rita Tinoco Torres et al. 2012).

We did not find evidence for wild ungulates avoiding human infrastructure. Particularly with regard to roe deer, these results are in contrast to findings of earlier work in the same region and elsewhere suggesting that roe deer perceive humans as predators and prefer areas far from roads and settlements (Tufto, Andersen, and Linnell 1996; Torres Tinoco, Virgós, Panzacchi, et al. 2012; Torres Tinoco et al. 2015). However, the species is protected in the Peneda-Gerês National Park and is banned from hunting, which may explain a lack of shyness of humans that was observed in other studies.

Although wild boar are hunted in the park, we also did not find evidence of wild boar avoiding human infrastructure. Hunting generally takes place in the form of battues rather than hide hunting and therefore does not introduce a stationary landscape of fear (Laundré, Hernández, and Ripple 2010). Moreover, it has been shown that wild boar respond to hunting pressure with shifts in circadian activity patterns rather than with spatial changes in habitat use (Keuling, Stier, and Roth 2008), which may explain why wild boar in our study region show no strong avoidance of settlements or roads.

The apparent preference of cattle for areas far from settlements may be attributed to the typical livestock management in the area in which cattle are led for grazing to high altitude pastures that are distant from the villages, between May and September (Moço et al. 2009).

In contrast to our expectations, we did not find signs of predator avoidance behavior in any of the ungulate species. In fact, we found that roe deer occupancy probability was higher in locations where foxes were also present, although foxes have been shown to be the main cause of neonatal mortality in roe deer in other European regions (Jarnemo et al. 2004). Female roe deer usually hide their newborn fawns under dense vegetation cover and only visit a few times a day (Jarnemo et al. 2004). It is possible that this behavior induced a detection bias and that we captured both foxes and roe deer predominantly in more open areas that are used for foraging or commuting and may be unsuitable both for hiding from predators and stalking prey.

Next to goats, horses have been reported as the dominant prey of the local wolf population, while wild boar, roe deer and cattle were not found in diet analyses of wolves in the study area (Vos 2000). In line with results on the latter three species, we found no evidence of spatial wolf avoidance behavior in any of the studied ungulate species. Further studies are needed to investigate whether predator avoidance is displayed in temporal habitat-use patterns of the prey species, and particularly horses.

Wild ungulates are not displaced by the presence of livestock.

Following the hypothesis that the presence of larger ungulate species leads to a displacement of smaller roe deer (Torres Tinoco, Virgós, Santos, et al. 2012; Chirichella, Apollonio, and Putman 2014) we expected to find signs of competitive exclusion between domestic and wild ungulates. However, we did not find evidence for displacement of any of the studied species due to interspecific competition, i.e. occupancy probabilities of each of the species were not negatively related to the presence of a second species. On the contrary, occupancy probabilities in roe deer correlated positively with those of horses, wild boar and foxes, suggesting no strong competitive exclusion effects between domestic and wild ungulates. At the same time, we found a preference for oak forest in wild boar, foxes and, to a lesser extent, roe deer, suggesting strong habitat overlap.

On the one hand, this lack of competitive exclusion may be explained by different feeding strategies: diet overlap between browsing roe deer and domestic grazers or omnivorous wild boar is low (Carvalho et al. 2018; Gill 2006). Although cattle and horses are both predominant grazers, morphological and physiological differences allow them to exploit different parts of the same resource, i.e. horses generally graze shorter swards that have higher nutritional value while cattle exploit taller swards and compensate for the lower nutritional value of these resources with their longer digestion and retention times (Apollonio, Andersen, and Putman 2010). On the other hand, ungulate species may even benefit from the presence of other ungulate guilds. For example, red deer occurrence was reported to be positively related to the presence of cattle and this association was explained with increased plant primary production in cattle grazing sites (Mattiello et al. 2002; Gordon 1988). Rooting (Sandom, Hughes, and Macdonald 2013), grazing, trampling and nutrient input can facilitate the establishment and survival of tree seedlings, by opening germination niches and reducing light competition from grasses which may enhance the quality of open areas as foraging habitat for browsers (reviewed in Gill 2006).

The observed lack of interspecific competition may also be a result of low herbivore densities in the park. Although roe deer densities in Peneda-Gerês National Park have increased considerably since the arrival of the species in the early 20th century, they are still below those found in central Europe (Torres Tinoco et al. 2015). We found that wild boar and roe deer were more likely to co-occur close to settlements and tended to avoid each other spatially in greater distance to settlements. Possibly, the higher probability of co-occurrence around settlements is caused by lower availability of suitable habitats, so that both species are forced to share the same areas while, with more suitable habitat available in greater distance to settlements they are able to avoid each other. Expected population increases in wild boar and roe deer (Acevedo et al. 2010) might therefore induce competitive exclusion in the future. Longer-term studies will be needed to investigate how habitat use patterns may change as a consequence of increasing densities and range expansions of wild ungulates and decreasing densities of free ranging livestock.

It is important to note that, based on our results, we cannot fully exclude the possibility of competition between domestic and wild ungulate species, or predator avoidance behavior of the ungulate species, as competition may also be displayed in behavioral differences such as different feeding strategies or temporal avoidance strategies (Amarasekare 2003), both of which cannot be captured with our study design. Despite this limitation, the multi-species occupancy approach we used here allows us to investigate patterns of co-occurrence in response to changes in environmental conditions. It enables us to distinguish between habitat preferences of single species and habitat use patterns resulting from interspecific interactions. Disentangling these processes provides a step towards answering the question whether competition does not occur because resources are not limited or because different characteristics of the habitat are used by different species, or if in turn common habitat use is caused by a shortage of suitable habitat, forcing the species to share their habitat (Apollonio, Andersen, and Putman 2010).

3.5 Conclusions

Land abandonment opens up opportunities for restoration of mammal communities through passive rewilding. To successfully assist recolonizations and restore ungulate communities and to mitigate human-wildlife conflicts, it is important to understand and anticipate potential competition or facilitation mechanisms between declining livestock and growing wild ungulate populations (Torres Tinoco et al. 2015).

Our results highlight the importance of oak forests for the integrity of large mammal communities in Northern Portugal, and suggest that hunting bans for roe deer, as implemented in Peneda-Gerês National Park, can be an important tool for aiding the population recovery of this ungulate in its southwestern European distributional edges.

Moreover, our study shows that recolonization of areas by wild herbivores can be possible in the presence of extensively managed, free-ranging livestock and that livestock can even improve habitat heterogeneity and forage quality, assisting the population recovery of a locally rare wild ungulate, the roe deer. Suggesting that rewilding and extensive agriculture are not mutually exclusive, our findings support novel narratives of passive rewilding that explicitly include and consider the human dimension of ecosystem restoration.

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Chapter 4

Interspecific interactions modulate response to wildfires in a community of free-ranging livestock and wild ungulates

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The work presented in this chapter is currently under preparation for submission to ***Restoration Ecology***.

Interspecific interactions modulate response to wildfires in a community of free-ranging livestock and wild ungulates

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Abstract

Rewilding is a promising approach to the restoration of large degraded landscapes. It aims at restoring self-sustaining ecosystems that can be maintained with minimal human management. Processes that are thought to be critical for the self-sustainability of ecosystems include trophic complexity, connectivity and natural disturbance events. Using camera trap data from three consecutive years, we studied the interaction between aspects of trophic complexity and natural disturbance events by comparing patterns of habitat choice and interspecific interaction between livestock and wild ungulates at burned and unburned sites in a marginal agricultural landscape in Northern Portugal. We found that wildfires positively influenced the occupancy probability of horses (*Equus caballus*) and cattle (*Bos taurus*), and that the presence of roe deer (*Capreolus capreolus*) and cattle influenced the response of horses to wildfires. Our results suggest, that interspecific interactions change the response to disturbance events.

4.1 Introduction

Almost half of the Earth’s ice-free terrestrial areas are currently under agricultural use (Foley *et al.* 2011) and the consequences of agricultural activities pose a major threat to natural ecosystems and biodiversity (Navarro and Pereira 2012). At the same time, large parts of the Northern Hemisphere are facing landscape abandonment, due to commercialization and industrialization of agriculture, slow population growth and ageing populations (MacDonald *et al.* 2000; Keenleyside and Tucker 2010), and low productivity of marginal agricultural land (MacDonald *et al.* 2000). This phenomenon is particularly common in the Mediterranean basin where limited soil productivity, topography, and accessibility limit the potential for agricultural intensification (Plieninger *et al.* 2014). With ongoing ecosystem degradation, the loss of important ecological processes (Cardinale *et al.* 2012; Pettorelli *et al.* 2017) can make ecosystems more vulnerable to environmental change and may hamper their ability to recover from perturbations (Holling 1973; Scheffer *et al.* 2001; Oliver *et al.* 2015).

At the same time the abandonment of vast areas of agricultural land opens up opportunities for large scale restoration through passive rewilding (Navarro and Pereira 2012; Queiroz *et al.* 2014). Rewilding aims at restoring resilient, self-sustaining ecosystems with minimal human management by promoting the interaction of important ecological processes, i.e. trophic integrity, natural disturbance regimes and dispersal potential (Chapter 2). It has been suggested, that the interaction of these processes contribute to the self-sustainability of ecosystems and that rewilding actions should therefore target multiple processes (Chapter 2) but there are few studies that focus on such interactions (e.g. Fuhlendorf et al. 2009).

Especially in ecosystems that have evolved under a regime of grazing, browsing and fires, the interactions between herbivores and fire is an important, yet largely ignored factor in the planning of rewilding or other restoration actions (Fuhlendorf *et al.* 2009). Acting as random disturbances in ecosystems, natural fire and grazing regimes alter vegetation patterns (Figure 4.1) and can increase habitat heterogeneity and species diversity (Fuhlendorf *et al.* 2009). Although herbivore communities, imposing grazing or browsing pressure, can be considered part of the natural disturbance regime of an ecosystem, they themselves respond to disturbance events, for example through behavioral changes (Figure 4.1). For example, fires often induce an increase in plant productivity and biomass that may benefit herbivorous species (Moe and Wegge 1997; Laterra *et al.* 2003; Maier *et al.* 2005). Herbivores, on the other hand, can influence the probability of ignitions by removing fuel load in grazed patches (Fuhlendorf and Engle 2001).

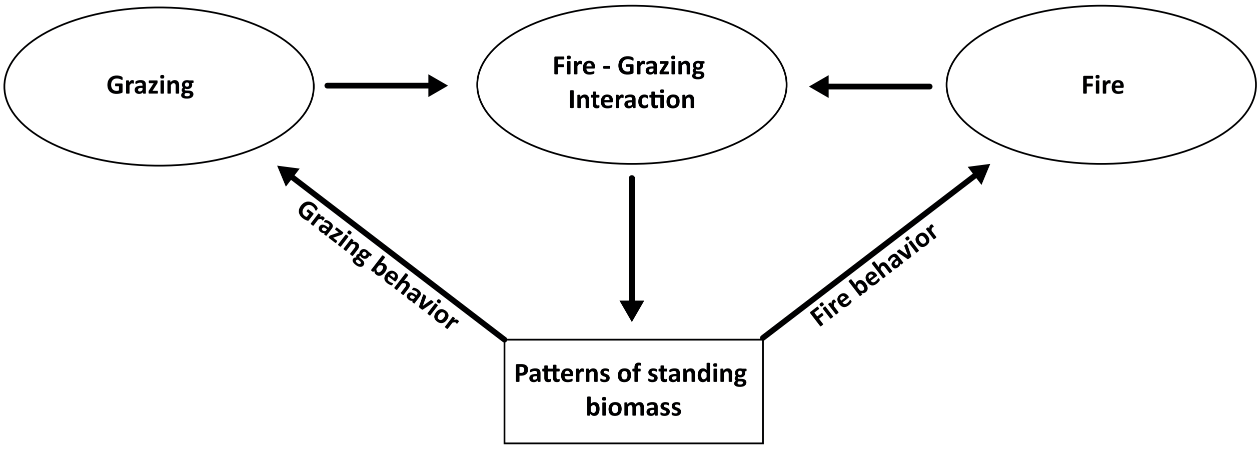


Figure 4.1: Natural fire and grazing/browsing regimes influence each other by changing fuel load and forage availability respectively. Coupled fire-grazing regimes influence and are influenced by habitat and vegetation structure (adapted from Fuhlendorf *et al*. 2009).

This study focused on the habitat use and possible interactions between semi-wild livestock (free-ranging horses and cattle) and the main wild ungulates roe deer and wild boar (*Sus scrofa*) in response to wildfires. Wild mammal species may respond to agricultural abandonment by increasing their population sizes and expanding their ranges, which may alter co-occurrence patterns with free-ranging livestock. Frequent wildfires introduce a regime of random disturbances that may alter patterns of habitat use and of interspecific interactions. These conditions are particularly likely to occur in marginal agricultural areas in the Mediterranean region where land abandonment is widespread and wildfires are frequent.

Here, we studied occupancy probability of domestic and feral ungulates in response to wildfires to investigate the relationship between habitat choice and interactions among different herbivore species, and natural disturbances. To test our hypothesis (H1) that fire events influence habitat use of both domestic and feral ungulates, we tested for differences in occupancy probabilities between unburned sites and sites that were affected by wildfires after the first sampling season. For the first sampling season, before the wildfires we expected to find no differences in occupancy levels between sites. For the second and third year of sampling we expected higher occupancy levels in recently burned patches than in unburned patches. We further hypothesized that (H2) species co-occurrence would be higher in burned patches as higher forage quality might attract multiple ungulate species to recently burned patches.

4.2 Material and methods

4.2.1 Study system

The study was conducted in the Peneda-Gêres National Park in North Western Portugal (42°N, 8°W). The National Park covers an area of approx. 703km^2 with elevations ranging from 50m to 1,548m above sea level. The region is influenced by Atlantic, Mediterranean and Continental climate with a mean temperature of 9.6°C and an annual precipitation of up to 2,800mm with a peak in December (433mm) and a drop to 36mm in August (Honrado 2003), and with frequent wildfires during summer. We sampled an area of approx. 16km^2 that is located in the Peneda mountain range which constitutes the northwestern part of the park and ranges in elevation between 300m and 1340m above sea level (Rodrigues 2010).

Since decades, the area is facing agricultural abandonment (van der Zanden *et al.* 2018). The parish of Castro Laboreiro has about 500 inhabitants (census 2011) and large parts of the villages in the area are abandoned (Rodrigues 2010). Today, the main agricultural activity is the extensive breeding of cattle, sheep (*Ovies gmelini aries*), domestic goats (*Capra aegagrus hircus*) and horses, and is still based on the traditional common use of lands (Sousa and Correira 2014).

The area is home to a largely intact mammal community with (large) predators such as Iberian wolf (*Canis lupus signatus*), red fox (*Vulpes vulpes*), and common genet (*Genetta genetta*), and large herbivores such as roe deer, red deer (*Cervus elaphus*), wild boar and Iberian ibex (*Capra pyrenaica)*. The Iberian ibex, the Iberian wolf and the locally rare roe deer are of high conservation concern to this region (Torres Tinoco *et al.* 2012).

The decrease in agricultural activity and the associated increase in habitat connectivity is likely to lead to increasing population densities and range expansions of wild ungulates (Acevedo *et al.* 2010). The abandonment of agricultural practices and the associated shrub encroachment can lead to larger and more frequent wildfires. The region therefore constitutes an interesting study case for the interaction among growing populations of herbivores and a natural disturbance regime.

4.2.2 Management of domestic ungulates

The local cattle breeds Cachena and Barrosã are used for meat production and are managed, i.e., they receive supplementary feeding and are kept in stables for some time of the year but graze unguarded on the common lands for most of the year. The Garrano horses are largely unmanaged and freely roam the area throughout the year. The Garrano and the cattle breeds are listed as endangered by the FAO (FAO 2016). Sheep and goats are usually guarded by a shepherd and guarding dogs. They are led to pastures for feeding and are kept in barns at night to prevent predation by wolves (own observation). As these species are prevented from exhibiting natural habitat choice, they were not included in the analysis.

4.2.3 Camera trapping

We used camera trap data from three consecutive years. Each spring, we deployed 64 cameras (Reconyx HC 600 Hyperfire HD) in a grid of approx. 16 km^2 with one camera per 0.25ha grid cell (approx. 500m spacing between each camera, Figure 4.2). We used a land cover map of the study area (Rodrigues 2010) to choose camera locations in advance and distributed them as uniformly as possible across the different habitat types. In most cases, the actual camera location deviated from the originally chosen one due to topographical barriers, but we aimed to not deviate from the original camera locations by more than 50m. In most cases the same camera locations and bearing angles were used for all three sampling seasons. If we had to change camera locations between sampling seasons (due to high risk of theft or excessive vegetation growth hindering animal detection), new locations were chosen in close vicinity to the original site.

Cameras were attached to trees or rocks at a height of approx. 80cm above the ground. Cameras were facing random directions to avoid detection biases (e.g. by directing cameras at animal trails). Cameras were triggered by movement. We set cameras to take pictures 24 hours a day and took a set of three pictures per trigger with no delay after trigger to increase the probability of obtaining identifiable images. The camera sensor was set to medium sensitivity and the flash was set to be balanced optimally between maximum flash range and shutter speed.

Cameras were operating between April 13th 2016 and August 22nd 2016, between 8th May 2017 and 3rd October 2017, and between 17th May and 15th October 2018. Due to theft or camera failure, the number of camera sites varied between years. We obtained data from a total of 60 cameras in 2016, 58 cameras in 2017, and 56 cameras in 2018. We processed all images manually and for each year built a matrix of presence/absence records, using one record per species, camera location and day.

Between the camera trapping periods 2016 and 2017 nine of the sites were affected by wildfires (in late summer 2016 and in April 2017 respectively, ICNF) (Figure 4.2).

For this study, we included presence/absence records of cattle, horses, roe deer and wild boar. Red deer (*Cervus elaphus*) and Iberian ibex (*Capra pyrenaica*) were recorded occasionally, but were not included in this analysis.

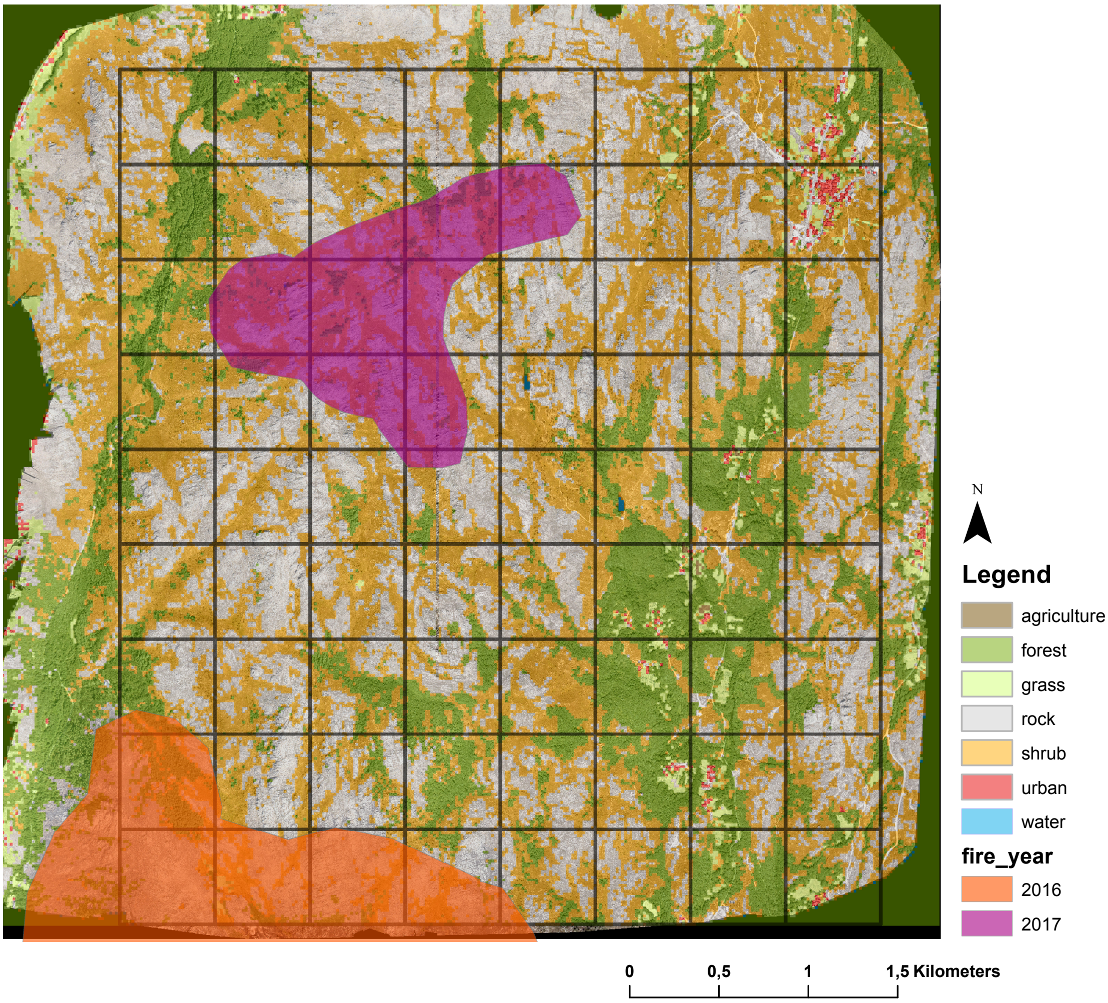


Figure 4.2: Map of the study area in Peneda-Gerês National Park in Northern Portugal (42°N, 8°W, Rodrigues 2010; ICNF). Cameras were distributed uniformly across different habitat types with one camera per grid cell. Between the study periods in 2016 and 2017 wildfires burned part of the study area.

4.2.4 Modelling framework

We adapted and used a multispecies occupancy model (Rota *et al.* 2016) that generalizes the single species-model developed by MacKenzie et al. (2002) to more than one species, using a multivariate Bernoulli distribution. Similar to the single-species model, a detection model is linked with a partially observed, latent process model.

In single-species occupancy models, the probability of presence of species *i* in site s, Ψ_{is} follows a univariate Bernoulli distribution $z \sim Bernoulli(\Psi)$, with the corresponding probability mass function

$$F(z|\Psi) = \Psi^{z}(1-\Psi)^{z-1} = \exp(z \log\left(\frac{\Psi}{1-\Psi)}\right) + \log(1-\Psi)). \quad (1)$$

From this probability mass function, we can derive the log odds a species occupies a site, the so-called natural parameter, that can be modelled as a function of covariates, assuming a logit link:

$$f = \log\left(\frac{\Psi}{1-\Psi}\right) = x'\beta\ . \quad (2)$$

Here, *x* is a vector of occupancy covariates and β is a vector of slope parameters, i.e. the log odds ratio of occupancy probability resulting from a 1-unit change in *x* (Rota *et al.* 2016).

Following Rota et al. (2016), we adapted the single-species model to accommodate four species. Expanding the univariate Bernoulli distribution to more than one dimensions, the multispecies occupancy model estimates the occupancy probability Ψ of species *i* conditional on the presence or absence of another species *j*, while accounting for non-detections (Rota *et al.* 2016). Note, that assuming higher order interactions are a function of marginal occupancy of one species and pairwise interactions of two species, we did not include higher order interactions (i.e. the probability that more than two species co-occur) into the model.

Including four species in the model results in 16 combinations of 1's (species present) and 0's (species absent) following a multivariate Bernoulli distribution where Z is a two-dimensional vector of 1's and 0's indicating a latent occupancy state for all four species, and Ψ is the probability of all possible sequences of 1's and 0's (Rota *et al.* 2016). For example, Ψ_{1111} represents the case where species all four species are present, and Ψ_{0000} represents the case where none of the species are present. The natural parameters for the co-occurrence of two species, e.g. species 1 and 2 are defined as:

$$f_{12} = \log\left(\frac{\Psi_{1100}\Psi_{0000}}{\Psi_{0100}\Psi_{1000}}\right) = x_{\gamma}'\gamma, \quad (3)$$

where *x* is a vector of occupancy covariates and α, β and γ are vectors of slope parameters.

γ can be interpreted as an interaction factor, that defines the difference in log odds ratios of occupancy probability of one species resulting from a 1-unit change in x when the other species is present or absent (Rota *et al.* 2016).

The full derivation of all natural parameters and the probability of co-occurrence of each species pair from the probability mass function for four species is given in Chapter 3 and the corresponding supplementary material.

4.2.5 Modelling marginal and conditional occupancy

We modelled *marginal occupancy* probabilities for each of the species, i.e. the probability of occurrence of species *i* dependent on a predictor variable given the occurrence of a second species *j* is not known.

Further, we explored evidence for species interactions while accounting for environmental variables by modelling *conditional occupancy.* This is possible because the multivariate Bernoulli distribution allows the influence of environmental variables on one species *i* to differ depending on the presence and absence of another species *j* (Rota *et al.* 2016).

4.2.6 Detection probability

Trigger reach of the cameras varied across sites due to differences in vegetation cover and topography. We modelled detection probability for species *i* at site *s* in survey *t* as a function of the maximum distance d_{ist} at which the camera still detects movement and trigger.

$p_{ist} = \text{logit}^{-1} (d'_{ist} \alpha_i)$, where α_s is a slope parameter that defines the change in detection probability with a 1-unit change in detection distance.

4.2.7 Occupancy covariates

We included burned/unburned as a categorical occupancy covariate in the model to compare occupancy probability in sites that were affected by the wildfires to those that were not affected. Fire data for the years 2016 and 2017 were obtained from the Portuguese Institute for Nature Conservation and Forests (ICNF). The data are provided by the EFFIS/WILDFIRE database run by the European Union and are obtained using MODIS daily images at 250m spatial resolution (European Union 2018).

For each study species and each study period, we calculated marginal occupancy probabilities in unburned sites and sites that were affected by wildfires after the first sampling season (“burned sites” hereafter). Note, that none of the sites were burned before or during the sampling season of 2016. To test for interspecific competition, we calculated conditional occupancy probabilities for each species pair and tested whether the presence or absence of a species influenced the occupancy probability of a second species in response to wildfires.

4.2.8 Model specifications and fit

We ran one model for each year. We used rStan version 2.18.2 (Stan Development Team 2018) to run all models. For each model, we ran two chains with 1,500 iterations each, after a burn-in phase of 500 iterations each. Convergence of chains was inspected visually using trace plots and adequate convergence was determined using the Brooks-Gelman-Rubin convergence diagnostic (Rhat<1.1, (Gelman *et al.* 2014)). All models achieved adequate convergence after 3,000 iterations. We chose a logistic prior distribution for all parameters as this results in a uniform distribution when assuming a logit link (Rota *et al.* 2016).

4.2.9 Differences between burned and unburned sites

To test for differences in occupancy probabilities between burned and unburned sites, we subtracted the mean values of the posterior distribution of occupancy probability in the unburned sites from those in the unburned sites (for each of the 3,000 iterations). For all estimates, we calculated 95% credible intervals. Estimates where the limits of the credible intervals overlapped zero were defined insignificant.

4.3 Results

In 2016, cameras were recording between 13th April and 22nd August, totaling to 6,409 operating days across 60 sites. In 2017, cameras were recording between 8th May and 3rd October, totaling to 7.828 operating days across 58 sites, and in 2018, cameras were recording between 17th May and 15th October, totaling to 8.379 operating days across 56 sites. Per site, camera operating days ranged from 21 to 152 days. 9 of the sampled sites were affected by wildfires during late August 2016 and during April 2017.

4.3.1 Differences in site use between years

Species differed in the way they used the sampled sites (Figure 4.3). Movement of cattle and wild boar was more restricted than that of horses and roe deer. Both, cattle and wild boar were never recorded in 15 of the sites. Roe deer was the most widespread species and there were only 5 sites in which the species was never recorded. All species exhibited high site fidelity and used more than half of the sites during at least 2 of the sampling years. Roe deer used more than two thirds (42 sites) for at least 2 of the sampling years.

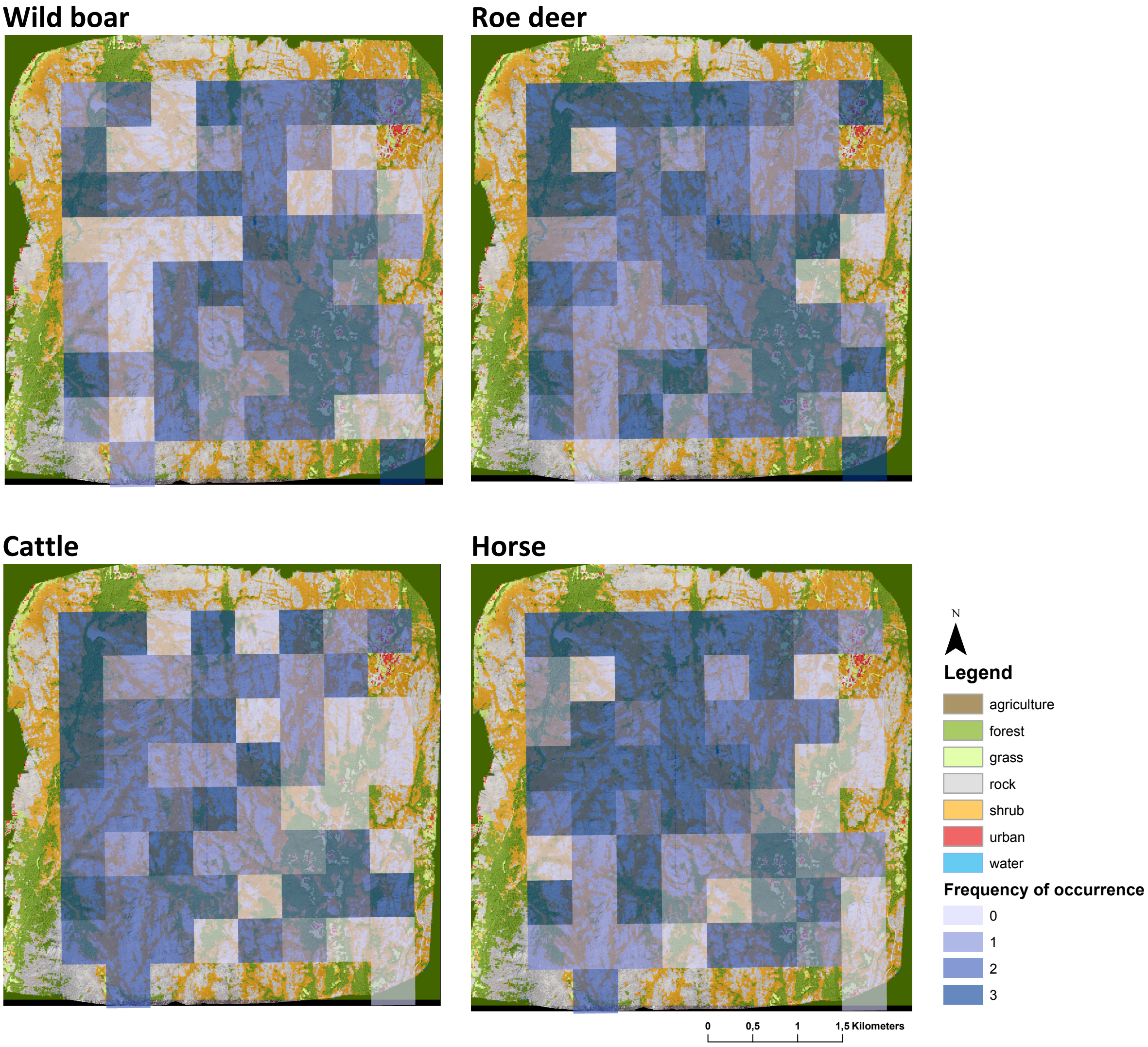

Wild boar
Roe deer
Cattle
Horse

Figure 4.3: Site fidelity across years. Colors represent numbers of years the sites were visited. No camera was placed in empty grid cells. Roe deer were the most widespread species and horses showed the highest site fidelity. Cattle showed a preference for the Western part of the study area while wild boar were more likely to be recorded in the Eastern part of the study area.

4.3.2 Detection probability

We modelled detection probability as a function of detection distance, i.e. the distance at which the camera would still detect movement and trigger. Detection probability was highest in 2016 and decreased in the following years (Figure 4.4, Tables SI 2 and SI 3). Detection probability for roe deer and wild boar was generally low. Detection distance had a significant effect on the detection probability of all species (Figure 4.4, Table SI 3). In most cases detection probability increased with increasing maximum trigger distance, except for the study period in 2018 where detection probability for wild boar and cattle decreased with increasing trigger distance (Figure 4.4, Table SI 3).

4.3.3 Marginal occupancy

Before the wildfires in 2016, marginal occupancy probability did not differ significantly between sites (Figure 4.5). In 2017, the first vegetation period after the wildfires, marginal occupancy probability of cattle and horses was significantly lower in the unburned sites than in the burned sites (Figure 4.5). This difference in marginal occupancy probability of horses was still evident in 2018. Although we did not observe significant differences in the marginal occupancy probabilities between burned and unburned sites in 2017 and 2018 for wild boar and roe deer, we did observe a similar trend with lower occupancy probabilities in unburned sites and stable occupancy probabilities in burned sites (Figure 4.5).

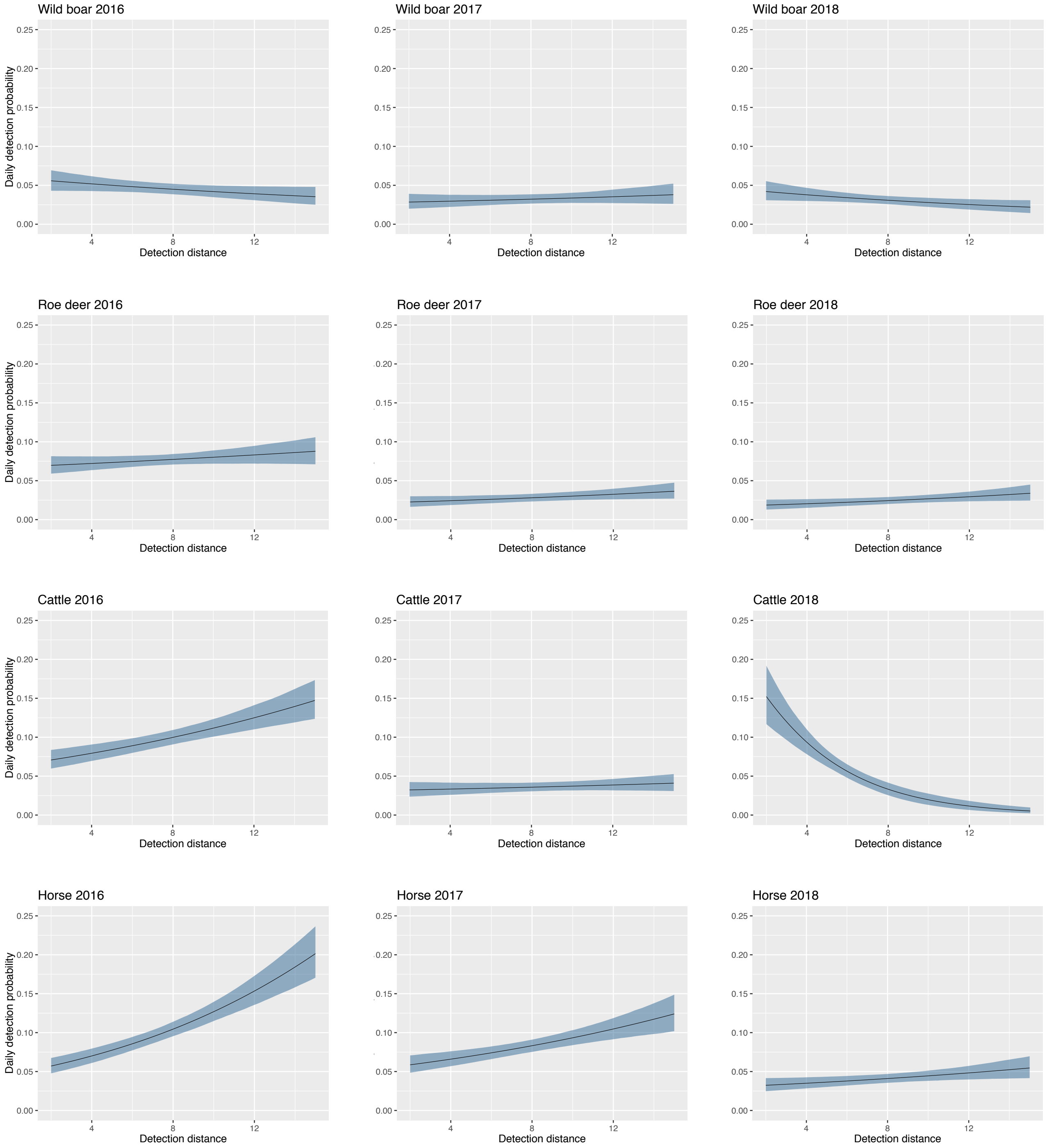


Figure 4.4: Detection probability for the target species across different maximum trigger distances. Lines represent mean posterior distributions and shaded areas envelop 95% credible intervals.

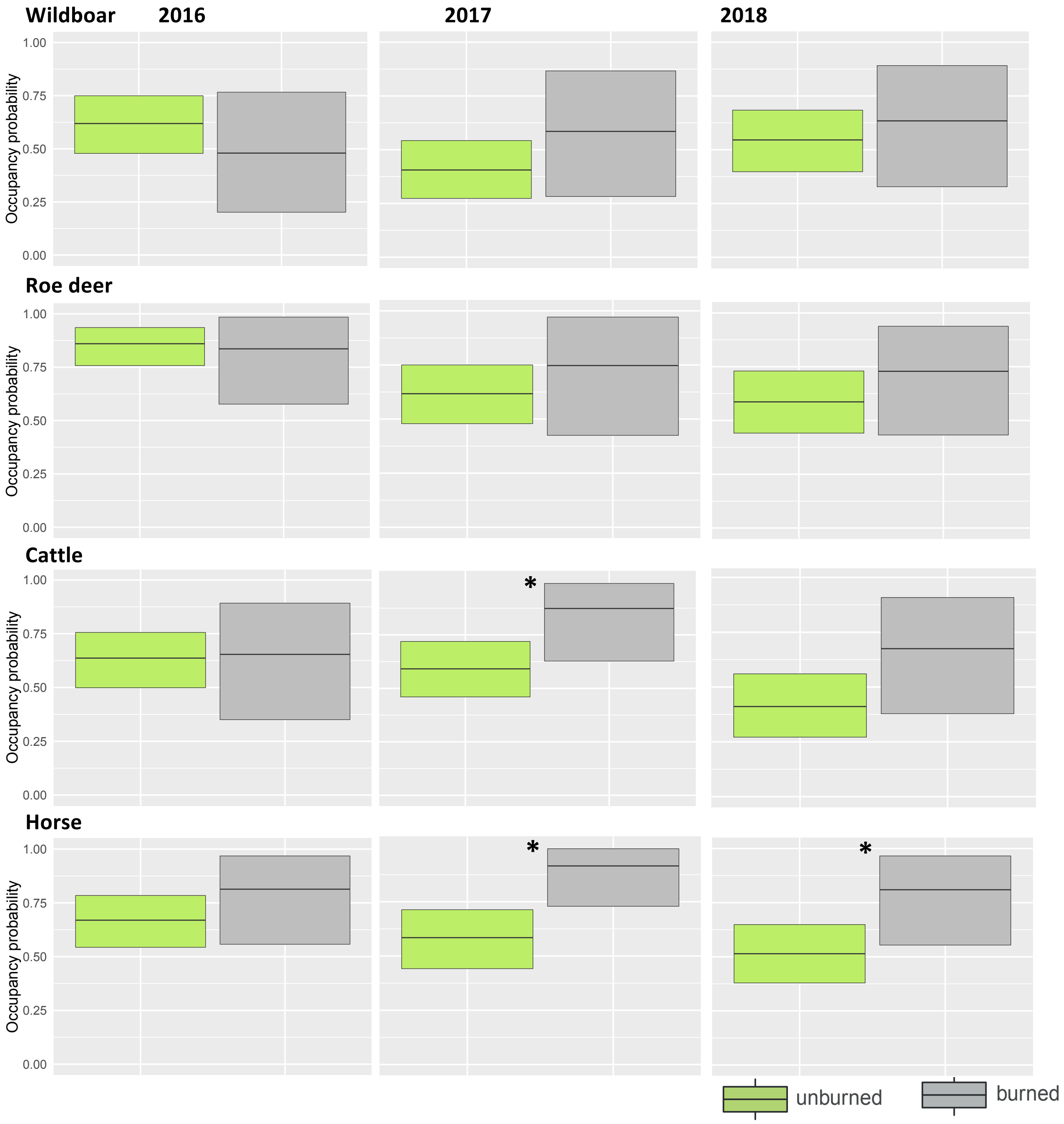


Figure 4.5: Differences in occupancy probability between unburned and burned sites. Occupancy probability of cattle and horses was significantly higher in burned sites during the first year after the fire. Occupancy probability of horses remained significantly higher in burned sites during the second year after the fire. Central marks represent the means, boxes envelope the 95% credible intervals. Significant differences are marked with asterisks. For exact values, see supplementary information, Table SI 4.

4.3.4 Conditional occupancy

The presence of cattle and roe deer influenced the response of horses to wildfires. Conditional occupancy of horses was significantly higher in burned sites in 2017 and in 2018 if cattle or roe deer were also present in a site, and did not differ significantly if cattle or roe deer were absent (Figures 4.6 (a-c)). See supplementary information Table SI 5 for all values.)

a) 2016

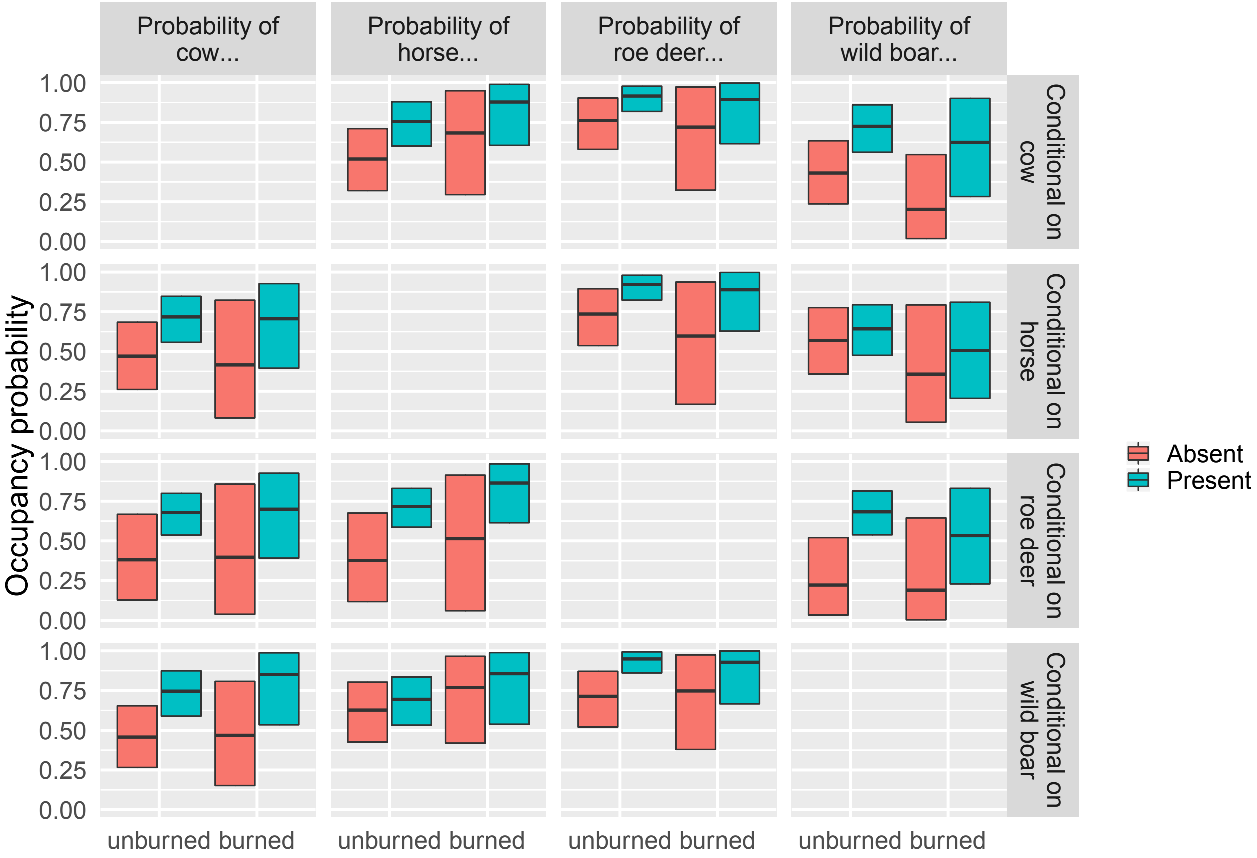
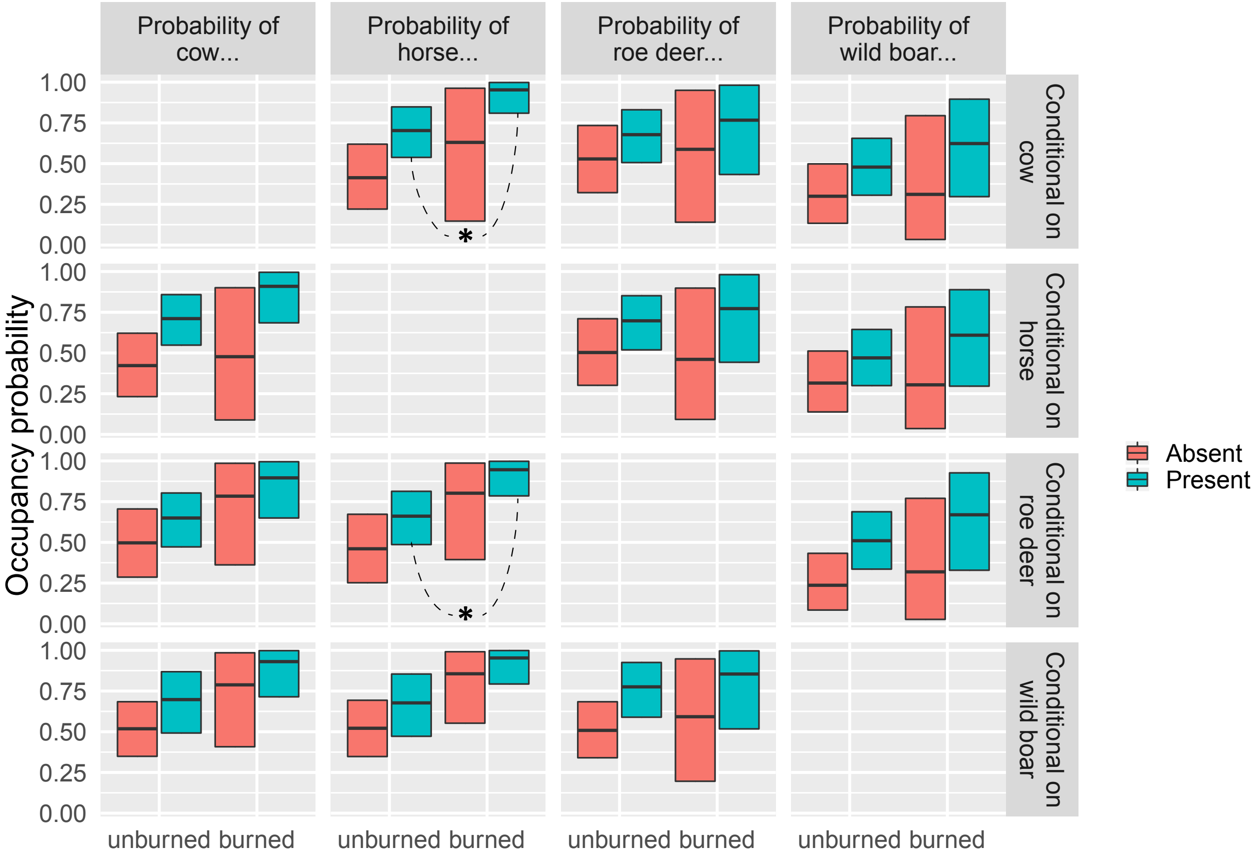


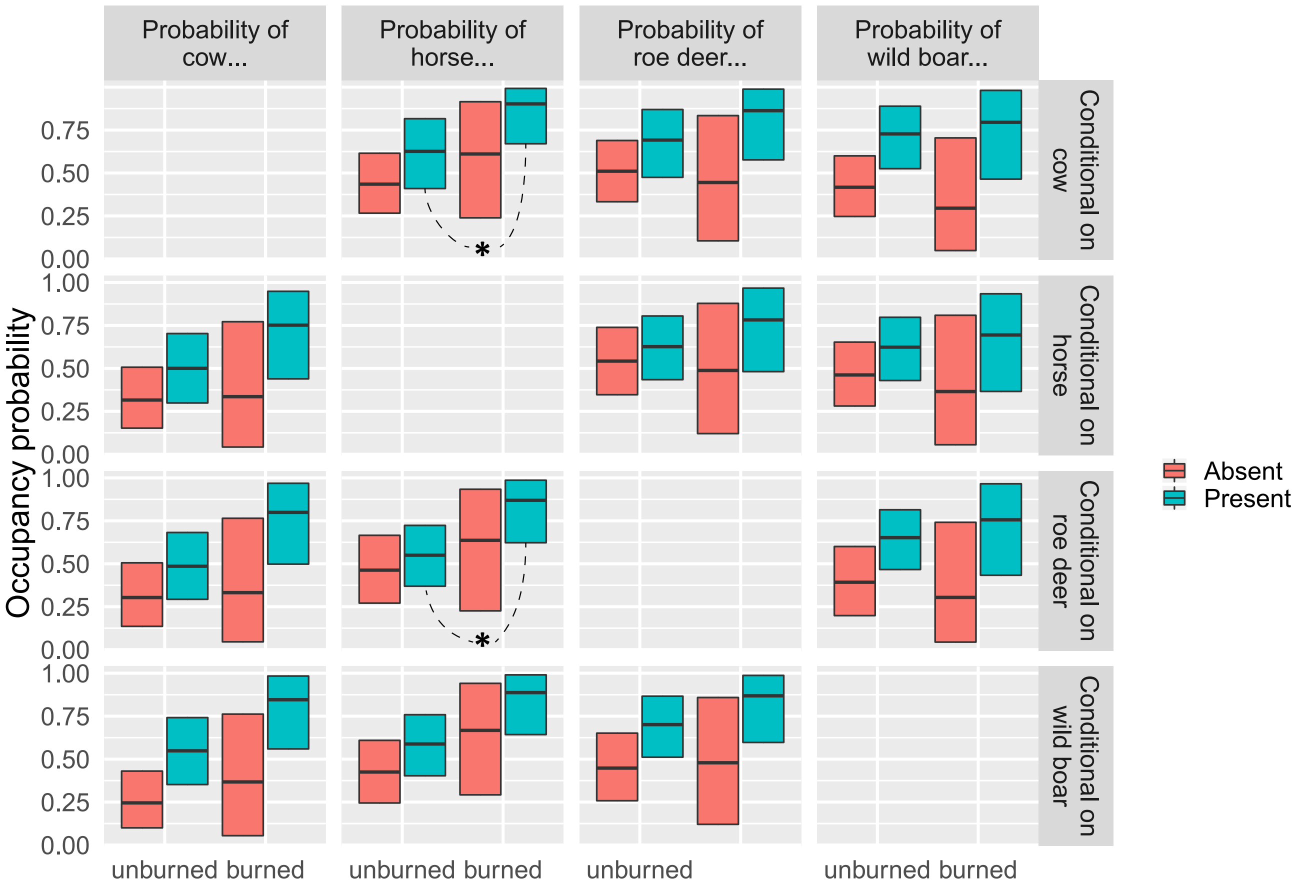
Figure 4.6 (a-c): Interspecific interaction modulates response of horses to fire.
a) Before the wildfires in 2016 occupancy probability was not significantly different between burned and unburned sites, regardless of the presence or absence of a second species. Central marks represent the means, boxes envelope the 95% credible intervals. Significant differences are marked with asterisks.

b) 2017



b) During the first year after the fire, occupancy probability of horses was significantly higher in burned sites if cattle or roe deer were present. If cattle or roe deer were absent, occupancy probability was not significantly higher in burned sites.

c) 2018



c) Also during the second year after the fire, occupancy probability of horses was significantly higher in burned sites if cattle or roe deer were present. If cattle or roe deer were absent, occupancy probability was not significantly higher in burned sites.

4.4 Discussion

There is a well-known relationship between fire and herbivory. The coupled impacts of both influence vegetation growth patterns, plant species communities, habitat heterogeneity and species diversity. Moreover, natural fires and natural herbivory influence each other in a bi-directional way. Grazers and browsers alter the spatial and temporal patterns of fire events by reducing fuel load (Fuhlendorf *et al.* 2009). At the same time, habitat use patterns are changed by fire because herbivores are attracted to freshly burned sites, as post-fire vegetation usually has higher nutrient content and is more palatable than unburned vegetation (Archibald *et al.* 2005; Allred *et al.* 2011).

Although it has been recognized that fire plays an important role in shaping mammal behavior and that grazing animals are attracted to recently burned areas, most studies on spatial behavior of mammals do not include fire as a direct effect (Allred *et al.* 2011). Moreover, most studies focusing on fires use an experimental setup with prescribed burning and a fixed number of ungulates, and do not take into account spatial interactions in complex landscapes (Fuhlendorf *et al.* 2009). Studies focusing on the interaction between fire and grazing, and the positive and negative feedbacks that may arise from it are still scarce (Fuhlendorf *et al.* 2009), and there is, to our knowledge, no study that investigated the effect of interspecific interactions on species' responses to fires. We addressed this gap by studying species' responses to a natural disturbance event while taking into account the effect of interspecific interactions.

Fires affect marginal occupancy probabilities of cattle and horses

We could show in a non-experimental, large-scale study that spatial behavior of herbivores is affected by wildfires. Our results suggest that domestic grazers prefer recently burned patches over unburned areas. These findings are in line with other studies (e.g. Hobbs et al. 1991; Raynor, Joern, and Briggs 2015; Cherry, Warren, and Conner 2017; Fuhlendorf et al. 2009; Archibald et al. 2005) and can be explained with post-fire increases in plant biomass and plant nutrient content.

In contrast to our expectations, we did not find a significant preference for burned areas in wild boar and roe deer in the years 2017 and 2018. As the model we used does not accommodate for multi-season approaches we had to run one model for each year. We could therefore not test directly whether differences in occupancy probabilities in unburned patches between years were significant. However, we did observe lower occupancy probabilities of both species in unburned patches for the years 2017 and 2018, whereas in burned patches, occupancy probability remained stable after 2016 (Figure 4.6). One reason why we did not find evidence for this trend may be that the areas that were affected by fire were mainly covered by shrubs and, to a lesser extent, by coniferous forest (Figure 4.2). Earlier research we conducted in the same area showed that wild boar are strongly associated with oak forests and also roe deer showed a weak positive relationship to areas with high proportions of oak forest cover (see Chapter 3), probably because oaks and acorns are important food sources for roe deer (Kramer *et al.* 2006) and wild boar (Massei *et al.* 1996). Horses and cattle are both predominant grazers and might benefit more strongly from increased biomass and nutrient levels in graminoid plants after a fire. This positive effect could be less pronounced for roe deer and wild boar. Another reason why we did not find a preference of burned areas could be predator avoidance behavior that may cause prey species to avoid freshly burned areas even though the abundance of tree seedlings and other high quality forage increases after wildfire because burned areas offer less shelter from predators (Cherry *et al.* 2017). However, since we did not find any predator avoidance behavior of roe deer and wild boar in an earlier study conducted in the same study area in 2016 (see Chapter 3), and earlier studies on the dietary composition of wolves in Portugal (Torres *et al.* 2015) and in the National Park (Vos 2000; Álvares 2011) revealed that wolves in this area prey mainly on domestic species this explanation seems less likely.

Finally, technical and methodological constraints may have confounded differences in the use of burned and unburned sites by wild boar and roe deer. From 2016 to 2017, we observed a decrease in detection probability (Figure 4.4), possibly caused by decreasing reliability of the cameras over time. Moreover, the modelling framework we used does not accommodate for multi-season occupancy analyses. Therefore, we could not directly compare occupancy probabilities between years to test the hypothesis that occupancy probability decreases in unburned sites, because ungulates favor burned sites.

Interspecific interactions alter horses’ response to wildfires

Most research on the effects of fire or grazing has concentrated on only one of the two processes (Fuhlendorf *et al.* 2009). However, it was pointed out that the two processes interact and influence each other. Investigating them separately may lead to a simplified understanding of coupled fire – grazing regimes where species-dependent effects of fire and grazing remain ignored (Fuhlendorf *et al.* 2009). Particularly the hypothesis that interspecific interaction dynamics in an ungulate community may also be altered by fire, or themselves determine the community’s response to fire remains largely ignored in the literature.

Our approach allowed us to investigate the role interspecific interactions play in shaping habitat choice patterns. By modelling conditional occupancy, we could test the effect of interspecific interactions on species' responses to fire. We found, that the preference of horses for recently burned areas was determined by the co-occurrence of roe deer and cattle. In sites where those species were absent, we did not find evident differences in the occupancy probability of horses between burned and unburned sites; if either roe deer or cattle were present, horses showed a preference for burned sites. These findings suggest that habitat choice of ungulates is not only determined by fire, but that interactions on the level of the ungulate community determine how strongly certain species respond to fire. Our results suggest, that the response of ungulates to fire may be more complex than previously assumed. Since there are several dynamics interacting, interspecific interactions coupled with a fire regime may increase habitat complexity and spatiotemporal heterogeneity in a landscape that is subject to a coupled grazing-fire regime. Alternatively, the observed increased probability of co-occurrence in burned sites could be a response to increased resource availability because of higher biomass production after fire. In this case, co-occurrence could be interpreted as the absence of competitive exclusion and as a result of similar habitat requirements of different ungulate species.

4.5 Outlook

A more specific understanding of the different mechanisms that act in coupled grazing-fire regimes can allow more accurate predictions of how ungulate communities and fire events interact and how these interactions impact vegetation regrowth and ultimately habitat heterogeneity. Here we compared occupancy probabilities before and shortly after a fire and could confirm an effect on occupancy probability on horses and cattle that persisted also during the second vegetation period after the burn. However, in landscapes under a coupled grazing fire-regime the time since burning usually varies among patches, creating a shifting mosaic that varies both spatially and temporally (Fuhlendorf *et al.* 2009). Including fire data from several years and accounting for the time since the last burning could help to improve the understanding of longer term developments of such landscapes. Such an analysis might reveal shifts in habitat use and interspecific interaction patterns over time that may promote spatiotemporal heterogeneity and biodiversity.

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Chapter 5

Synthesis and future research avenues

The first aim of this thesis was to develop a theory-driven, conceptual framework for rewilding that provides guidance for the question of what kind of empirical evidence is needed to test rewilding as a promising novel approach to restoration. The second aim of this thesis was to conduct empirical case studies that test components of the framework in an exemplary manner. Here, I synthesize the main findings of this dissertation, addressing the research gaps and questions identified in the introduction. I start by analyzing how rewilding relates to the umbrella concept of restoration and discuss how the conceptual framework presented in Chapter 2 contributes to successfully achieving restoration goals in a novel manner. Then, I revisit issues that hinder the application of rewilding and suggest ways to overcome these obstacles. Afterwards, I contextualize the empirical studies presented in Chapter 3 and 4 within the conceptual framework developed in Chapter 2. I discuss whether and how the results of my empirical work support the reasoning of the framework and how they contribute to a better understanding of the outcomes of rewilding, and more generally, of the interactions of ecosystem processes under changing environmental conditions. Finally, I discuss remaining questions and point out future avenues for rewilding research and application.

5.1 Rewilding with regard to restoration

Fifteen years ago, the Society of Ecological Restoration (SER) defined restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (The SER International Primer on Ecological Restoration 2004) and presented a list of nine attributes of restored ecosystems. These attributes refer to the *form* (i.e., "species composition, presence of native species"), *function* (i.e., "presence of functional groups, capacity of the physical environment to sustain populations, normal functioning and integration into the landscape"), and the *stability* of ecosystems (i.e., "elimination of threats, resilience and self-sustainability") (The SER International Primer on Ecological Restoration 2004).

Although the importance of this document is widely acknowledged ("ser.org"; Hallett *et al.* 2013; Shackelford *et al.* 2013), it has drawbacks that hamper its practical applicability: for instance, the SER acknowledges that resilience and self-sustainability have a dynamic component, yet the SER Primer offers little guidance on how these properties and the success of restoration measures can be assessed (Ruiz-Jaen and Mitchell Aide 2005; Hallett *et al.* 2013; Shackelford *et al.* 2013). Furthermore, restoration success is measured with regard to reference ecosystems or historical conditions (Shackelford *et al.* 2013), and reactions of ecosystems to current and future global change are not considered explicitly (Hallett *et al.* 2013; Shackelford *et al.* 2013).

There are now urgent calls for restoration approaches that focus more strongly on functional goals and dynamic systems rather than static or narrowly defined ecosystem properties (Shackelford *et al.* 2013; Higgs *et al.* 2018). Novel approaches to restoration should be open, flexible and accommodate for uncertainties associated with environmental change, thus allowing researchers and practitioners to address the challenges posed by global change (Higgs *et al.* 2018). While it is cautioned that narrow approaches to restoration may jeopardize our capacity to safeguard ecosystem integrity, a better understanding of the functioning, dynamics and development of ecosystems is urgently needed for such novel approaches to be successful (Higgs *et al.* 2018).

Rewilding can be a way to accommodate for these challenges, offering a new, forward-looking approach. Being a particular approach to restoration, many of its goals can be assigned to the attributes listed by the SER. While the original definition of rewilding and some of the contemporary approaches to it, namely trophic and Pleistocene rewilding, focus on certain species or species compositions (i.e., attributes of *"ecosystem form"*), the work presented in Chapter 2 frames rewilding around those attributes that are categorized as attributes of "*ecosystem stability"*, most notably resilience and self-sustainability. The restoration of trophic complexity, stochastic disturbances, and dispersal, and the interactions among them, can lead to increased self-sustainability of ecosystems and should be the guiding principle of all rewilding projects. The processes will themselves be promoted and supported by efforts to restore these attributes. Restoring trophic complexity, stochastic disturbances, and dispersal via rewilding does not require the invention of new restoration actions. Instead, we advocate using existing tools strategically to promote synergies among ecosystem processes (Chapter 2). The usefulness and success of these tools should be tracked through appropriate indicators. A recent paper by Torres *et al.* 2018 provides a list of indicators and suggests a method to assess progress in rewilding projects.

5.2 Projecting rewilding outcomes

Adopting a framework that focuses on trophic complexity, stochastic disturbances, and dispersal as three critical components of dynamics of natural ecosystems may facilitate better projections of restoration outcomes and allow researchers and managers to anticipate unexpected ecosystem trajectories (Chapter 2). This is partly reflected in the results of the empirical studies presented in Chapters 3 and 4. Those studies focus on some of the interactions among and within ecosystem processes, namely, trophic complexity and stochastic disturbances (Figure 1.1). The results of both studies suggest that interaction among processes can affect the response to other processes or environmental changes. They show that interspecific interaction affects habitat use patterns (interaction within the process of trophic complexity, Chapter 3), and that interspecific interaction among ungulates affects the response to wildfires (interaction between trophic complexity and natural disturbance, Chapter 4).

As current rapid environmental changes can make it difficult to find appropriate reference ecosystems or to restore previous conditions, better projections of how ecosystem processes react to changes are especially important (Hallett *et al.* 2013). Based on the results of Chapters 3 and 4, I argue that ignoring interspecific interactions leads to poorer predictions of how mammal communities react to changes in their environment and that in turn, studies accounting for such interactions are therefore particularly important.

5.3 Accounting for society

Several scientists have recently emphasized the importance of the societal dimension of restoration, i.e. the impact of people on ecosystems and the values they place in them (Hallett *et al.* 2013; Shackelford *et al.* 2013; Seddon *et al.* 2014). The rewilding framework presented in Chapter 2 accounts for the role of societies. It places special emphasis on the emotional and aesthetic value of wildness (see Chapman 2006, and Chapter 2 for a distinction between *wildness* and *wilderness*) that can be generated by the largely autonomous interaction of ecosystem processes, independent of whether they are experienced in an urban park or in a vast abandoned landscape (Chapter 2). The importance of societal acceptance and stakeholder engagement for the success of restoration (or rewilding) projects is widely acknowledged (e.g., Egan *et al.* 2011; Suding *et al.* 2015). Explicitly including it as an inherent and central part of the framework will promote rewilding initiatives and support the design of rewilding actions that generate mutual benefits for people and the ecosystem and will possibly even create economic revenues that may support the transition from farming to alternative livelihoods (as, for example, in the case of the Swiss National Park where tourism results in yearly economic revenues of approx. 20 million CHF (Backhaus *et al.* 2013)).

5.4 Overcoming the obstacles to rewilding

Lack of a consistent definition

Since the term rewilding has first been introduced in the late nineties (Soulé and Noss 1998), several attempts were made to re-define the concept and until today there is no agreed-upon definition of the concept (Seddon *et al.* 2014; Nogués-Bravo *et al.* 2016, Hayward 2019). Many of the suggested definitions were in fact tailored to certain approaches to rewilding, rather than the overall concept (Lorimer *et al.* 2015), and they were sometimes motivated by a political rather than a scientific agenda (Jørgensen 2015; Lorimer *et al.* 2015). I argue that the multiplicity of definitions has led to more confusion about the meaning and purpose of rewilding than contributing to scientific, evidence-based assessments of rewilding actions.

The framework presented in Chapter 2 is applicable to a wide variety of rewilding approaches. It accommodates for approaches ranging from passive rewilding that takes advantage and supports changes that are already happening, e.g., landscape abandonment or spontaneous comeback of species (Navarro and Pereira 2012; Fernández *et al.* 2017), to more active approaches like species reintroductions or even functional replacements (Donlan 2005; Svenning *et al.* 2016; Fernández *et al.* 2017). The framework is based on long-standing theory on ecosystem functioning, complexity and resilience. It identifies the central targets of rewilding actions (i.e., trophic complexity, dispersal and stochastic disturbances) while being flexible enough to accommodate for most approaches to rewilding and to be applied across spatial scales and to ecosystems ranging from urban parks to wilderness areas. It can therefore serve as a means to identify and compare existing rewilding projects and to design and monitor new ones (also see Torres *et al.* 2018).

Lack of evidence

Although rewilding has received considerable scientific interest since it was first introduced, studies assessing the outcomes of rewilding are still scarce (Svenning *et al.* 2016). Critics of rewilding have therefore pointed out that the concept is not sufficiently tested and its application may have unexpected, negative consequences for the state of ecosystems and biodiversity (Rubenstein and Rubenstein 2016; Nogués-Bravo *et al.* 2016).

With this dissertation, I aimed to address this criticism. The empirical research presented in Chapters 3 and 4 focuses on interactions among and within ecosystem processes. Chapter 3 focuses on the ecosystem process of trophic integrity, namely, on how species interactions influence habitat choice of ungulate species. In contrast to other studies, the results show that the locally rare roe deer is not displaced by the presence of domestic ungulates. On the opposite, roe deer were more likely to occur in sites that were also used by horses suggesting that roe deer could benefit from the presence of larger grazers maintaining open habitats (Gordon 1988). These results suggest that the interactions among domestic and wild herbivores contribute to ecosystem complexity and resilience. Further, a displacement of any of the ungulate species caused by the presence of large predators was not observed (see Figure 5.1 for an anecdotal record of predator prey interaction in Peneda-Gerês). The study highlights that it is important to acknowledge ecosystem dynamics and that ignoring them may lead to overly simplified assumptions of how an ecosystem may react to environmental changes. Moreover, the results of Chapter 3 can inform future management of this and similar systems facing abandonment and recovery of wild mammal populations. Showing that coexistence between feral and domestic mammals can be possible and even beneficial for the recovery of rare species, such findings may help to pave the way towards compromises between stakeholders with sometimes opposing views such as livestock breeders and conservationists.

The work presented in Chapter 4 constitutes a step further in testing the rewilding framework developed in Chapter 2. As in Chapter 3, I accounted for interspecific interactions among wild and domestic herbivores. Additionally, I included natural disturbance as a second ecosystem process and tested, whether interspecific interactions alter the response of ungulate species to wildfires. The results of this study show that natural disturbance events do not only influence habitat use patterns of ungulate species, but that the interaction between different ungulate species modulate their response to disturbance events. The dynamics within a process (here, the species community) and the interaction among different ecosystem processes identified in this chapter add a level of complexity that has not been shown before (but see Fuhlendorf *et al.* 2009).

Focusing on two of the processes identified as important in Chapter 2, namely trophic complexity and stochastic disturbances, the studies in Chapters 3 and 4 serve as examples of how the effects of interacting processes can be studied. The results of these works contribute to a detailed understanding of how environmental changes can impact ecosystem processes and their interaction. This knowledge can support the planning of rewilding projects and inform projections of rewilding trajectories. Situated in a mountainous region in southwestern Europe that is strongly influenced by marginal agricultural practices and has been facing land abandonment since decades, the results may be applicable to comparable regions in the Mediterranean basin that are experiencing similar changes.

Figure 5.1: A wolf attacks a group of Garrano horses and is driven off by the dominant mare. Peneda-Gerês National Park, 17th June 2016.

Conflict with people and insufficient knowledge of rewilding outcomes

Rewilding goals may sometimes contradict the needs and expectations of local communities, especially with regard to management of large mammals and natural disturbances. Moreover, the uncertainties associated with such an open-ended, dynamic approach to restoration are difficult to communicate to a wider public. This may lead to conflicts, and to the notion that rewilding activities are planned in a manner that excludes people from landscapes rather than designing rewilding projects with local support (Jørgensen 2015).

Participatory planning and identification and support of shared benefits of rewilding projects are therefore as important as efforts to increase the scientific evidence that contributes to a more robust understanding of the outcomes and potential risks and benefits of rewilding.

Both aims could be reached via a structured rewilding plan that should lead to resilient, self-sustaining and socially acceptable ecosystems. Based on the social-ecological particularities of the focus area, researchers, managers and stakeholders should establish flexible rewilding goals and identify appropriate rewilding actions aimed at restoring trophic complexity, stochastic disturbances and dispersal (Chapter 2). The involved actors should discuss desirable, ecological and socio-economic rewilding scenarios and agree on risk mitigation strategies and soft exit programs. The implementation of rewilding actions should be preceded by initial baseline monitoring to identify a range of potential rewilding actions and to allow an assessment of the progress of the rewilding project (Chapter 2). With the start of the implementation phase, continuous, standardized monitoring, careful comparison to reference systems and simulation modeling should accompany the rewilding actions and can help to project rewilding trajectories (Kulakowski *et al.* 2017). On the site level, regular evaluation of the monitoring results can help to identify cases in which active intervention is needed or where rewilding plans have to be adapted to avoid ecologically undesirable or socially unacceptable outcomes (Kulakowski *et al.* 2017).

The empirical studies presented in Chapters 3 and 4 provide important evidence on the outcomes of passive rewilding, in particular, on the interaction between domestic and wild ungulates. Such data should be provided to all stakeholders to inform decisions on the appropriate type and intensity of management actions (e.g., the extent to which extensive agricultural activities can co-exist with rewilding activities, Chapter 3, or if and how natural disturbance regimes should be managed, Chapter 4) and should be the basis for adaptations of the original plan. Depending on the diversity of stakeholders this may require preparing and disseminating information in different forms (Metzger *et al.* 2017), for example management recommendations for park managers or presentation of research results in layman's terms for local communities. In cases where human-wildlife conflicts arise, mediation may be required to reach satisfactory agreements for all stakeholders (Marshall *et al.* 2007).

Standardized monitoring protocols, that are employed across different rewilding areas, can generate evidence that help to improve the scientific understanding of the outcomes of rewilding in a wider context (Corlett 2016; Torres *et al.* 2018). The evaluation of monitoring results may also open up opportunities for unexpected compromises between apparently opposing goals of agricultural and restoration activities. For example, the study presented in Chapter 3 shows that recolonization of areas by wild herbivores can be possible in the presence of extensively managed, free-ranging livestock. Livestock grazing may improve habitat heterogeneity and forage quality for wild ungulates (Gordon 1988). Suggesting that rewilding and extensive agriculture are not mutually exclusive, our findings promote novel narratives of passive rewilding that explicitly include and consider the human dimension of ecosystem restoration.

It is key that the societal benefits of rewilding are accessible to the public (Chapter 2). Benefits should be offered via a broad array of opportunities for nature experiences (e.g., guided tours through the rewilding area, nature education tools, opportunities for leisure activities). Where possible, the development of sustainable business opportunities can be considered to increase the acceptance of rewilding among stakeholders and to generate funds for the implementation and the long-term monitoring of the rewilding area. Actively involving affected communities in decisions and outreach activities that inform the wider public about the outcomes of rewilding will likely increase the acceptance and success of rewilding projects (Zamboni *et al.* 2017).

5.5 Gaps in the framework

The field studies presented in Chapter 3 and 4 highlight some important aspects that are not fully addressed by the framework presented in Chapter 2. Although the importance of long-term planning is discussed in Chapter 2, the framework does not capture the temporal dimension of the dynamics among the three processes. For example, the camera trap data analyzed in Chapters 3 and 4 shows yearly fluctuations in occupancy probability for the observed species. In particular, the work of Chapter 4 indicates that spatial behavior may change in response to disturbance events.

Further, the framework does not capture the potential importance of land use history / land cover (LULC), and the affinity of species to certain habitats. The results of Chapter 3 show that spatial behavior is influenced by these factors. Although I did not find evidence for avoidance of human infrastructure in the study area, the presence of humans and/or of human infrastructure may potentially be an important factor influencing spatial behavior in areas more densely populated than the study region in Peneda-Gerês. While the applicability to a wide range of rewilding projects is one of the strengths of the framework, including LULC and temporal changes thereof might increase its usefulness. This could, for example be achieved by explicitly considering LULC in the assessment of the focus area in the first step of the structured plan proposed in Chapter 2 and by conducting longer term pilot studies that capture temporal variability of the processes.

5.6 Future avenues for rewilding research and application

This thesis can serve as a guideline for the planning and assessment of rewilding projects. The framework presented in Chapter 2 is based on long-standing ecological theory and provides a useful tool to frame, design, monitor and evaluate rewilding projects. It is complemented by the paper of Torres *et al.* 2018 in which we suggest a framework to measure the success of rewilding actions.

The field studies I conducted support some of the statements inferred from a synthesis of these theories. It provides examples of possible studies focusing on ecosystem processes, as well as evidence contributing to our understanding of how ecosystems develop and react to environmental fluctuations. The empirical studies in Chapters 3 and 4 provide important contributions to the much-needed evidence base on rewilding (Nogués-Bravo et al. 2016).

However, it is important to acknowledge that identifying resilience and resilience indicators in ecosystems remains challenging as this requires long-term, high-resolution data with low measurement error (van de Leemput *et al.* 2018). The most robust evidence for resilience theory has been gathered tested in narrow, experimental studies (van de Leemput *et al.* 2018) but such experiments are difficult to perform on the landscape-scale (van de Leemput *et al.* 2018). So far, the only real-world, whole-ecosystem experiment has been conducted in a freshwater lake and applied a treatment-control approach (Carpenter *et al.* 2011; van de Leemput *et al.* 2018). Further, it is to date not possible to measure, how close a particular ecosystem is to transition to an alternative stable state (Scheffer *et al.* 2012). These limitations make the assessment of success of rewilding projects and the projection of rewilding outcomes difficult.

Although the studies presented in Chapter 3 and 4 aimed at investigating ecosystem processes and the interaction among them, they were not designed to fully test the rewilding framework. The empirical study presented in Chapter 3 accounts only for spatial, but not for temporal dynamics, whereas the study presented in Chapter 4 aimed at clarifying feedback mechanisms among two of the processes that are identified as crucial in the framework but does not consider habitat connectivity and dispersal as the third essential ecosystem process identified in Chapter 2.

The results presented in this thesis should therefore be further complemented and generalized with broader empirical studies, particularly designed to test rewilding strategies as a long-term self-sustainable and dynamic approach to restoration. A study design that further tests the validity of the framework could, for example be set up similar to the study in Chapter 4, but test the interactions between habitat choice and disturbance events across a gradient of fragmentation to test for the influence of habitat connectivity. Such a study could include several response variables that serve as indicators of resilience, for example species diversity and functional redundancy, the presence of natural disturbance regimes, the permeability of terrestrial and aquatic landscapes, or the state and progress of natural succession. A list of indicators that could be used to measure the progress of rewilding is provided by Torres et al. (2018).

A remaining challenge is the long timescale on which ecosystem dynamics often take place. In consequence, it is possible that the time needed for ecosystem restoration via rewilding is incompatible with policy-relevant timeframes or with the needs and expectations of local communities (e.g., forest recovery after a wind-throw or a bark beetle pest may result in economic losses, or recolonization by large mammals may lag behind and opportunities for wildlife-based businesses will not open up before the establishment of viable populations).

Longer-term studies could increase our understanding of how ecosystems react to changes and could inform long-term planning of economic activities. Continuous monitoring and repeated analyses of multispecies occupancy probability similar to the study in Chapter 3 may yield interesting insights of how habitat choice and interaction patterns of domestic and wild ungulates, and large predators change over the course of longer time periods. Measurements of vegetation development and natural succession could complement a study on habitat choice and inform management decisions, for example regarding hunting legislation or forest management practices.

Likewise, the study design of Chapter 4 could be expanded to account for temporal changes, for example by including fire events (or other disturbance events) from several years. The results of such a study will likely lead to a more sophisticated understanding of ecosystem dynamics on different spatio-temporal scales and help to better anticipate rewilding trajectories (Kulakowski *et al.* 2017). Possibly, the challenge of studying long restoration timeframes could be overcome by taking advantage of longer-term datasets. Initiatives like eLTER ("eLTER H2020 project - Integrated European Long-Term Ecosystem & Socio-Ecological Research Infrastructure") may in the future become important providers of such data.

Already existing protected area networks offer opportunities for space-for-time replacements studies. Protected area networks like Natura 2000 or areas of the Green Infrastructure project (European Commission 2013) could be used to test the framework presented in Chapter 2 in different ecosystems. Moreover, the rewilding goal of restoring resilience and self-sustainability by promoting interacting ecosystem processes could complement already existing efforts to restore ecosystems and biodiversity.

5.7 Final remarks

Despite considerable efforts to halt biodiversity loss, human drivers such as climate change, resource consumption and overexploitation are imperiling the Earth's biodiversity (Butchart *et al.* 2010). In 2020, the signatory states to the Convention of Biological Diversity (CBD) will agree on actions towards the vision where "*By 2050 biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people*" (CBD 2010). Despite the fact that many of the goals for 2020 will likely not be reached (Tittensor *et al.* 2014), a new, optimistic narrative is emerging from conservation literature that advocates for novel, bold and inspiring approaches to halt the degradation of nature and biodiversity loss (Balmford and Knowlton 2017; Mace *et al.* 2018). The momentum of this narrative has been highlighted by the UN General Assembly who recently declared 2021 to 2030 the UN decade of ecosystem restoration (UN General Assembly 2019).

Rewilding aims at combining thorough, scientifically sound and empirically tested actions with an emotional narrative that can contribute to a positive, hopeful notion of conservation and can engage people to care and act for their environment.

For rewilding to be successful, it needs to fulfill certain standards, for example comparability, transparent goals and methods, measurements of progress, options to adapt original plans and generation of societal benefits. Given the dynamic nature of ecosystems, the rapid global change and the multiplicity of legislative frameworks across countries, this endeavor remains a challenge. This thesis contributes to fulfilling the standards mentioned, as it provides a flexible framework, offers guidance for the development and evaluation of management plans and offers two examples of studies that assess the effects of rewilding.

Of course, these are early steps towards successful rewilding and more empirical studies will be needed to investigate interactions of all three processes, test effects across different scales, in different biomes and different cultural/societal contexts. In that sense, the findings of this thesis can be a starting point to develop further research avenues to contribute to the scientific evidence about the outcomes and the potential of rewilding. Rewilding research that is designed following the framework and the examples presented in this thesis can shift the conservation focus towards ecological processes (Navarro and Pereira 2015) while taking into account uncertainty in societal and ecological outcomes. This thesis can therefore contribute to science-based policy changes that are urgently needed to tackle the challenges of biodiversity conservation in the 21st century.

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Appendix

A. Supplementary material for Chapter 3

Derivation of natural parameters from the probability mass function of a multivariate Bernoulli distribution for 4 species

In single-species occupancy models, presence and absence of the species follows a Bernoulli distribution $z \sim Bernoulli(\Psi)$, with the corresponding probability mass function

$$F(z|\Psi) = \Psi^{z}(1-\Psi)^{z-1} = \exp(z \log\left(\frac{\Psi}{1-\Psi)}\right) + \log(1-\Psi)). \quad (1)$$

From this probability mass function, we can derive the log odds a species occupies a site

$$f = \log(\frac{\Psi}{1-\Psi}). \quad (2)$$

Assuming a logit link this natural parameter can be modelled as a function of covariates:

$$f = \log\left(\frac{\Psi}{1-\Psi}\right) = x'\beta. \quad (3)$$

In a four-species occupancy model presence or absence of all combinations of species follows a Bernoulli distribution

$$Z \sim MVB(\Psi_{1111}, \Psi_{1110}, \Psi_{0111}, \Psi_{1011}, \Psi_{1101}, \Psi_{1100}, \Psi_{1010}, \Psi_{1001}, \Psi_{0110}, \Psi_{0011}, \Psi_{0101}, \Psi_{1000}, \Psi_{0100}, \Psi_{0010}, \Psi_{0001}, \Psi_{0000})$$

with the corresponding probability mass function

$$F(z|\Psi_{1111}, \Psi_{1110}, \Psi_{0111}, \Psi_{1011}, \Psi_{1101}, \Psi_{1100}, \Psi_{1010}, \Psi_{1001}, \Psi_{0110}, \Psi_{0011}, \Psi_{0101}, \Psi_{1000}, \Psi_{0100}, \Psi_{0010}, \Psi_{0001}, \Psi_{0000})$$

$= \Psi_{1111}^{z1z2z3z4} * \Psi_{1110}^{z1z2z3(1-z4)} * \Psi_{1101}^{z1z2(1-z3)z4} * \Psi_{1100}^{z1z2(1-z3)(1-z4)} * \Psi_{1011}^{z1(1-z2)z3z4} * \Psi_{1010}^{z1(1-z2)z3(1-}$

$^{z4)} * \Psi_{1001}^{z1(1-z2)(1-z3)z4} * \Psi_{1000}^{z1(1-z2)(1-z3)(1-z4)} * \Psi_{0111}^{(1-z1)z2z3z4} * \Psi_{0110}^{(1-z1)z2z3(1-z4)} * \Psi_{0101}^{(1-z1)z2(1-z3)z4} * \Psi_{0100}^{(1-}$

$$ {}^{z1)z2(1-z3)(1-z4)} * \Psi_{0011}^{(1-z1)(1-z2)z3z4} * \Psi_{0010}^{(1-z1)(1-z2)z3(1-z4)} * \Psi_{0001}^{(1-z1)(1-z2)(1-z3)z4} * \Psi_{0000}^{(1-z1)(1-z2)(1-z3)(1-z4)}. \quad (4) $$

Expanding the equation, we derive

$$ F(z|\Psi_{1111}, \Psi_{1110}, \Psi_{0111}, \Psi_{1011}, \Psi_{1101}, \Psi_{1100}, \Psi_{1010}, \Psi_{1001}, \Psi_{0110}, \Psi_{0011}, \Psi_{0101}, \Psi_{1000}, \Psi_{0100}, \Psi_{0010}, \Psi_{0001}, \Psi_{0000}) $$

$$ = \Psi_{1111}^{z1z2z3z4} * \Psi_{1110}^{z1z2z3-z1z2z3z4} * \Psi_{1101}^{z1z2z4-z1z2z3z4} * \Psi_{1100}^{z1z2 - z1z2z3- z1z2z4+z1z2z3z4} * \Psi_{1011}^{z1 z3z4 - z1z2z3z4} * \Psi_{1010}^{z1z3-z1z2z3-z1z2z4+z1z2z3z4)} * \Psi_{1001}^{z1z4-z1z2z4-z1z3z4+z1z2z3z4)} * \Psi_{1000}^{z1-z1z3-z1z4+z1z3z4-z1z2+z1z2z3+z1z2z4-z1z2z3z4} * \Psi_{0111}^{z2z3z4-z1z2z3z4} * \Psi_{0110}^{z2z3-z2z3z4-z1z2z3+z1z2z3z4} * \Psi_{0101}^{z2z4-z1z2z4-z2z3z4+z1z2z3z4} * \Psi_{0100}^{z2-z2z4-z2z3+z2z3z4-z1z2+z1z2z4+z1z2z3-z1z2z3z4} * \Psi_{0011}^{z3z4-z1z3z4-z2z3z4+z1z2z3z4} * \Psi_{0010}^{z3-z3z4-z2z3-z1z3+z1z3z4+z1z2z3+z2z3z4-z1z2z3z4} * \Psi_{0001}^{z4-z1z4-z2z4-z3z4+z1z2z4+z1z3z4-z1z2z3z4} * \Psi_{0000}^{1-z1-z2-z3-z4+z3z4+z2z4+z2z3-z2z3z4+z1z4+z1z3-z1z3z4+z1z2-z1z2z4-z1z2z3+z1z2z3z4}. \quad (5) $$

Finding the logarithm of the equation, we derive

$$ F(z|\Psi_{1111}, \Psi_{1110}, \Psi_{0111}, \Psi_{1011}, \Psi_{1101}, \Psi_{1100}, \Psi_{1010}, \Psi_{1001}, \Psi_{0110}, \Psi_{0011}, \Psi_{0101}, \Psi_{1000}, \Psi_{0100}, \Psi_{0010}, \Psi_{0001}, \Psi_{0000}) $$

$$ = \exp\Big(z1 * \log\left(\frac{\Psi_{1000}}{\Psi_{0000}}\right) + z2 * \log\left(\frac{\Psi_{0100}}{\Psi_{0000}}\right) + z3 * \log\left(\frac{\Psi_{0010}}{\Psi_{0000}}\right) + z4 * \log\left(\frac{\Psi_{0001}}{\Psi_{0000}}\right) + z1z2 * \log\left(\frac{\Psi_{1100} * \Psi_{0000}}{\Psi_{1000} * \Psi_{0100}}\right) + z1z3 * \log\left(\frac{\Psi_{1010} * \Psi_{0000}}{\Psi_{1000} * \Psi_{0010}}\right) + z1z4 * \log\left(\frac{\Psi_{1001} * \Psi_{0010}}{\Psi_{1000} * \Psi_{0001}}\right) + z2z3 * \log\left(\frac{\Psi_{0110} * \Psi_{0000}}{\Psi_{0100} * \Psi_{0010}}\right) + z2z4 * \log\left(\frac{\Psi_{0101} * \Psi_{0000}}{\Psi_{0100} * \Psi_{0001}}\right) + z3z4 * \log\left(\frac{\Psi_{0011} * \Psi_{0000}}{\Psi_{0010} * \Psi_{0001}}\right) + z1z2z3 * \log\left(\frac{\Psi_{1110} * \Psi_{1000} * \Psi_{0100} * \Psi_{0010}}{\Psi_{1100} * \Psi_{1010} * \Psi_{0110} * \Psi_{0000}}\right) + z1z2z4 * \log\left(\frac{\Psi_{1101} * \Psi_{1000} * \Psi_{0100} * \Psi_{0001}}{\Psi_{1100} * \Psi_{1001} * \Psi_{0101} * \Psi_{0000}}\right) + z1z3z4 * \log\left(\frac{\Psi_{1011} * \Psi_{1000} * \Psi_{0010} * \Psi_{0001}}{\Psi_{1010} * \Psi_{1001} * \Psi_{0011} * \Psi_{0000}}\right) + z2z3z4 * \log\left(\frac{\Psi_{0111} * \Psi_{0100} * \Psi_{0010} * \Psi_{1000}}{\Psi_{0110} * \Psi_{0101} * \Psi_{0011} * \Psi_{0000}}\right) + z1z2z3z4 * \log\left(\frac{\Psi_{1111} * \Psi_{1100} * \Psi_{1010} * \Psi_{1001} * \Psi_{0110} * \Psi_{0101} * \Psi_{0011} * \Psi_{0000}}{\Psi_{1110} * \Psi_{1101} * \Psi_{1011} * \Psi_{1000} * \Psi_{0111} * \Psi_{0100} * \Psi_{0010} * \Psi_{0010} * \Psi_{0001}}\right) + \log(\Psi_{0000})\Big). \quad (6) $$

Corresponding to the single species occupancy model, we can derive the log odds ratio $f = \log\left(\frac{\Psi}{1-\Psi}\right)$ that each combination of species is present in a site, from equation (6):

$$f1 = \log\left(\frac{\Psi_{1000}}{\Psi_{0000}}\right)$$

$$f2 = \log\left(\frac{\Psi_{0100}}{\Psi_{0000}}\right)$$

$$f3 = \log\left(\frac{\Psi_{0010}}{\Psi_{0000}}\right)$$

$$f4 = \log\left(\frac{\Psi_{0001}}{\Psi_{0000}}\right)$$

$$f12 = \log\left(\frac{\Psi_{1100} * \Psi_{0000}}{\Psi_{1000}\Psi_{0100}}\right)$$

$$f13 = \log\left(\frac{\Psi_{1010} * \Psi_{0000}}{\Psi_{1000}\Psi_{0010}}\right)$$

$$f14 = \log\left(\frac{\Psi_{1001} * \Psi_{0000}}{\Psi_{1000}\Psi_{0001}}\right)$$

$$f23 = \log\left(\frac{\Psi_{0110} * \Psi_{0000}}{\Psi_{0100}\Psi_{0010}}\right)$$

$$f34 = \log\left(\frac{\Psi_{0011} * \Psi_{0000}}{\Psi_{0010}\Psi_{0001}}\right)$$

$$f24 = \log\left(\frac{\Psi_{0101} * \Psi_{0000}}{\Psi_{0100} * \Psi_{0001}}\right)$$

$$f123 = \log\left(\frac{\Psi_{1110} * \Psi_{1000} * \Psi_{0100} * \Psi_{0010}}{\Psi_{1100} * \Psi_{1010} * \Psi_{0110} * \Psi_{0000}}\right)$$

$$f124 = \log\left(\frac{\Psi_{1101} * \Psi_{1000} * \Psi_{0100} * \Psi_{0001}}{\Psi_{1100} * \Psi_{1001} * \Psi_{0101} * \Psi_{0000}}\right)$$

$$f134 = \log\left(\frac{\Psi_{1011} * \Psi_{1000} * \Psi_{0010} * \Psi_{0001}}{\Psi_{1010} * \Psi_{1001} * \Psi_{0011} * \Psi_{0000}}\right)$$

$$f234 = \log\left(\frac{\Psi_{0111} * \Psi_{0100} * \Psi_{0010} * \Psi_{1001}}{\Psi_{0110} * \Psi_{0101} * \Psi_{0011} * \Psi_{0000}}\right)$$

$$f1234 = \log\left(\frac{\Psi_{1111} * \Psi_{1100} * \Psi_{1010} * \Psi_{1001} * \Psi_{0110} * \Psi_{0101} * \Psi_{0011} * \Psi_{0000}}{\Psi_{1110} * \Psi_{1101} * \Psi_{1011} * \Psi_{1000} * \Psi_{0111} * \Psi_{0100} * \Psi_{0010} * \Psi_{0001}}\right)$$

(7)

The probability of co-occurrence of each species pair can then be expressed via the multinomial logit link, e.g.

$$\Psi 0100 = \frac{\exp(f2)}{\left(\begin{array}{c} 1+\exp(f1)+\exp(f2)+\exp(f3)+\exp(f4) \\ +\exp(f1+f2+f12)+\exp(f1+f3+f13)+\exp(f1+f4+f14) \\ +\exp(f2+f3+f23)+\exp(f2+f4+f24)+\exp(f3+f4+f34) \\ +\exp(f1+f2+f3+f12+f13+f23) \\ +\exp(f1+f2+f4+f12+f14+f24) \\ +\exp(f1+f3+f4+f13+f14+f34) \\ +\exp(f2+f3+f4+f23+f24+f34) \\ +\exp(f1+f2+f3+f4+f12+f13+f14+f23+f24+f34) \end{array}\right)} \tag{8}$$

$$\Psi 1100 = \frac{\exp(f1)+\exp(f2)+\exp\,(f12)}{\left(\begin{array}{c} 1+\exp(f1)+\exp(f2)+\exp(f3)+\exp(f4) \\ +\exp(f1+f2+f12)+\exp(f1+f3+f13)+\exp(f1+f4+f14) \\ +\exp(f2+f3+f23)+\exp(f2+f4+f24)+\exp(f3+f4+f34) \\ +\exp(f1+f2+f3+f12+f13+f23) \\ +\exp(f1+f2+f4+f12+f14+f24) \\ +\exp(f1+f3+f4+f13+f14+f34) \\ +\exp(f2+f3+f4+f23+f24+f34) \\ +\exp(f1+f2+f3+f4+f12+f13+f14+f23+f24+f34) \end{array}\right)} \tag{9}$$

$$\Psi 0000 = \frac{1}{\left(\begin{array}{c} 1+\exp(f1)+\exp(f2)+\exp(f3)+\exp(f4) \\ +\exp(f1+f2+f12)+\exp(f1+f3+f13)+\exp(f1+f4+f14) \\ +\exp(f2+f3+f23)+\exp(f2+f4+f24)+\exp(f3+f4+f34) \\ +\exp(f1+f2+f3+f12+f13+f23) \\ +\exp(f1+f2+f4+f12+f14+f24) \\ +\exp(f1+f3+f4+f13+f14+f34) \\ +\exp(f2+f3+f4+f23+f24+f34) \\ +\exp(f1+f2+f3+f4+f12+f13+f14+f23+f24+f34) \end{array}\right)} \tag{10}$$

Supplementary tables

Table SI 1a: Marginal occupancy probabilities across distance to road

	Min.	25% Quantile	Median	Mean	75% Quantile	Max.
Horse	0.7066	0.7385	0.7598	0.7517	0.7684	0.7697
Cattle	0.7326	0.7514	0.7597	0.7571	0.765	0.7669
Roe deer	0.9191	0.9304	0.9357	0.9341	0.939	0.9401
Wild boar	0.619	0.714	0.7866	0.7699	0.8338	0.8616
Wolf	0.0525	0.06077	0.07733	0.08701	0.10778	0.15878
Fox	0.5385	0.5875	0.6362	0.631	0.6767	0.7056

Table SI1 b: Marginal occupancy probabilities across percentage cover of oak forest

	Min.	25% Quantile	Median	Mean	75% Quantile	Max.
Horse	0.4011	0.4693	0.5835	0.5945	0.73	0.7791
Cattle	0.6726	0.7424	0.7588	0.7553	0.775	0.7833
Roe deer	0.8341	0.9512	0.961	0.9477	0.963	0.9638
Wild boar	0.6195	0.797	0.8278	0.8007	0.8327	0.8347
Wolf	0.0749	0.07576	0.07816	0.07935	0.08177	0.08948
Fox	0.3626	0.7219	0.8999	0.8185	0.9603	0.9817

Table SI 1c: Marginal occupancy probabilities across percentage cover of shrub

	Min.	25% Quantile	Median	Mean	75% Quantile	Max.
Horse	0.552	0.6813	0.783	0.759	0.8474	0.8842
Cattle	0.595	0.705	0.7893	0.7682	0.841	0.8693
Roe deer	0.9177	0.9283	0.9352	0.9334	0.9395	0.941
Wild boar	0.6008	0.7101	0.7938	0.7733	0.8459	0.8745
Wolf	0.02748	0.05112	0.10453	0.14411	0.21878	0.39642
Fox	0.5917	0.6263	0.6547	0.6476	0.672	0.6796

Tabelle SI 1d: Marginal occupancy probabilities across percentage cover of grassland

	Min.	25% Quantile	Median	Mean	75% Quantile	Max.
Horse	0.6207	0.6704	0.7632	0.7385	0.806	0.8084
Cattle	0.5083	0.6284	0.7771	0.7289	0.8339	0.8381
Roe deer	0.8459	0.8931	0.9347	0.9198	0.9486	0.9535
Wild boar	0.4566	0.6029	0.7837	0.7277	0.8571	0.8707
Wolf	0.0829	0.08442	0.08933	0.09353	0.09832	0.13186
Fox	0.5021	0.5625	0.6557	0.6553	0.7472	0.8109

Tabelle SI 1e: Marginal occupancy probabilities across distances to settlements

	Min.	25% Quantile	Median	Mean	75% Quantile	Max.
Horse	0.6013	0.6999	0.7733	0.7516	0.8125	0.8306
Cattle	0.3759	0.6213	0.8117	0.7536	0.9072	0.9516
Roe deer	0.9038	0.9273	0.9354	0.9322	0.9406	0.9426
Wild boar	0.483	0.6319	0.748	0.7157	0.8114	0.8476
Wolf	0.06209	0.07197	0.08889	0.09516	0.11472	0.1527
Fox	0.4467	0.5631	0.677	0.6538	0.7516	0.7925

B. Supplementary material for Chapter 4

Supplementary tables

Table SI 2: Summary detection probabilities.

	Wild boar			Roe deer			Cattle			Horse		
	2016	**2017**	**2018**	**2016**	**2017**	**2018**	**2016**	**2017**	**2018**	**2016**	**2017**	**2018**
Mean detection probability	0.04	0.03	0.03	0.08	0.03	0.03	0.1	0.04	0.05	0.12	0.09	0.04
Standard deviation	0.006	0.003	0.006	0.005	0.004	0.004	0.022	0.003	0.041	0.042	0.019	0.006

Table SI 3: Change in detection probability p per 1-unit change in detection distance. 2.5% CI and 97.5% CI values indicate thresholds of 95% credible intervals. Estimates where credible intervals overlapped zero were defined as insignificant. Asterisks indicate the species whose detection probability was significantly influenced by changes in detection distance.

	Wild boar			Roe deer			Cattle			Horse		
	2016	**2017**	**2018***	**2016**	**2017***	**2018***	**2016***	**2017**	**2018***	**2016***	**2017***	**2018***
2.5% CI	-0.077	-0.023	**-0.101**	-0.008	**0.002**	**0.004**	**0.037**	-0.02	**-0.352**	**0.084**	**0.034**	**0.007**
Mean	-0.037	0.023	**-0.052**	0.019	**0.038**	**0.047**	**0.063**	0.019	**-0.276**	**0.110**	**0.063**	**0.042**
97.5% CI	0.002	0.067	**-0.005**	0.045	**0.075**	**0.089**	**0.087**	0.056	**-0.206**	**0.136**	**0.09**	**0.076**

Table SI 4: Differences in marginal occupancy probabilities between burned and unburned sites. Negative values indicate lower occupancy probability in unburned sites. 2.5% and 97.5% CIs envelope 95% credible interval. 95% CIs not overlapping zero are considered significant and are shown in bold.

	Wild boar			Roe deer			Cattle			Horse		
	2016	**2017**	**2018**	**2016**	**2017**	**2018**	**2016**	**2017***	**2018**	**2016**	**2017***	**2018***
2.5% CI	-0.175	-0.496	-0.37	-0.128	-0.396	-0.38	-0.305	**-0.495**	-0.55	-0.372	**-0.531**	**-0.51**
Mean	0.151	-0.188	0.09	0.054	-0.123	-0.15	-0.036	**-0.322**	-0.27	-0.185	**-0.377**	**-0.31**
97.5% CI	0.459	0.168	0.22	0.358	0.241	0.16	0.297	**-0.036**	0.05	0.098	**-0.166**	**-0.03**

Table SI 5: Differences in conditional occupancy probabilities between burned and unburned sites. Negative values indicate lower occupancy probability in unburned sites. 2.5% and 97.5% CIs envelope 95% credible interval. 95% CIs not overlapping zero are considered significant and shown in bold.

	2016	**2017**	**2018**
Wild boar – Cattle absent			
2.5% CI	-0.090	-0.513	-0.268
Mean	0.240	-0.096	0.145
97.5% CI	0.471	0.218	0.396
Wild boar – Cattle present			
2.5% CI	-0.195	-0.431	-0.322
Mean	0.090	-0.100	-0.083
97.5% CI	0.437	0.252	0.261
Cattle – Wild boar absent			
2.5% CI	-0.360	-0.456	-0.515
Mean	-0.007	-0.181	-0.101
97.5% CI	0.312	0.191	0.173
Cattle – Wild boar present			
2.5% CI	-0.300	-0.345	-0.539
Mean	-0.120	-0.119	-0.303
97.5% CI	0.202	0.242	0.003
Wild boar – Horse absent			
2.5% CI	-0.168	-0.366	-0.294
Mean	0.228	0.057	0.113
97.5% CI	0.532	0.288	0.407
Wild boar – Horse present			
2.5% CI	-0.178	-0.415	-0.352
Mean	0.138	-0.093	-0.081
97.5% CI	0.453	0.252	0.272
Horse – Wild boar absent			
2.5% CI	-0.209	-0.365	-0.355
Mean	0.217	0.126	0.109
97.5% CI	0.590	0.506	0.436
Horse – Wild boar present			
2.5% CI	-0.297	-0.401	-0.455
Mean	-0.022	-0.130	-0.176
97.5% CI	0.327	0.229	0.191
Wild boar – Roe deer absent			
2.5% CI	-0.319	-0.378	-0.291
Mean	0.051	0.055	0.111
97.5% CI	0.271	0.258	0.372
Wild boar – Roe deer present			
2.5% CI	-0.156	-0.423	-0.366
Mean	0.150	-0.101	-0.115
97.5% CI	0.472	0.246	0.217
Roe deer – Wild boar absent			

2.5% CI	-0.294	-0.505	-0.382
Mean	-0.050	-0.219	-0.026
97.5% CI	0.317	0.212	0.301
Roe deer – Wild boar present			
2.5% CI	-0.075	-0.361	-0.385
Mean	-0.004	-0.162	-0.176
97.5% CI	0.256	0.045	0.106
Cattle – Horse absent			
2.5% CI	-0.324	-0.348	-0.413
Mean	0.068	0.060	0.004
97.5% CI	0.390	0.363	0.271
Cattle – Horse present			
2.5% CI	-0.241	-0.314	-0.537
Mean	0.000	-0.102	-0.259
97.5% CI	0.329	0.226	0.070
Horse – Cattle absent			
2.5% CI	-0.462	-0.617	-0.488
Mean	-0.175	-0.338	-0.188
97.5% CI	0.200	0.070	0.169
Horse – Cattle present			
2.5% CI	-0.306	**-0.413**	**-0.498**
Mean	-0.136	**-0.247**	**-0.281**
97.5% CI	0.141	**-0.075**	**-0.031**
Cattle – Roe deer absent			
2.5% CI	-0.375	-0.448	-0.432
Mean	0.006	-0.142	-0.003
97.5% CI	0.286	0.283	0.271
Cattle – Roe deer present			
2.5% CI	-0.271	-0.361	-0.571
Mean	-0.032	-0.133	-0.322
97.5% CI	0.290	0.224	0.003
Roe deer – Cattle absent			
2.5% CI	-0.232	-0.515	-0.296
Mean	0.020	-0.243	0.075
97.5% CI	0.402	0.165	0.393
Roe deer – Cattle present			
2.5% CI	-0.105	-0.388	-0.416
Mean	-0.003	-0.189	-0.178
97.5% CI	0.275	0.141	0.113
Roe deer – Horse absent			
2.5% CI	-0.189	-0.426	-0.309
Mean	0.127	-0.033	0.059
97.5% CI	0.520	0.337	0.401
Roe deer – Horse present			
2.5% CI	-0.091	-0.376	-0.399

Mean	0.009	-0.174	-0.166
97.5% CI	0.273	0.132	0.153
Horse – Roe deer absent			
2.5% CI	-0.497	-0.548	-0.491
Mean	-0.137	-0.264	-0.187
97.5% CI	0.201	0.175	0.187
Horse – Roe deer present			
2.5% CI	-0.325	**-0.445**	**-0.535**
Mean	-0.159	**-0.264**	**-0.328**
97.5% CI	0.103	**-0.078**	**-0.052**

C. Curriculum vitae

Dipl. – Biol. Andrea Perino

PERSONAL INFORMATION

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EDUCATION/ACADEMIC EMPLOYMENT

Current position

2019-present	***Science-Policy coordinator*** German Centre for Integrative Biodiversity Research (iDiv), Halle – Jena - Leipzig

Previous positions

2014-2019	***Doctoral student (under the supervision of Henrique M. Pereira)*** German Centre for Integrative Biodiversity Research (iDiv) Martin Luther University Halle-Wittenberg (MLU), Germany
2013-2014	***Environmental consultant*** Büro für ökologische Fachplanungen, Andrea Hager, Heuchelheim, Germany
2006-2013	***Studies in Biology (Diplom) and New German History of Literature*** Albert-Ludwigs-Universität Freiburg im Breisgau, Germany

Other employment

2010-2012	**Freelance Journalist** Laborjournal, Freiburg i. Brsg. and Badische Zeitung, Freiburg i. Brsg.

ACADEMIC ACTIVITIES

Reviewing

2018	Journal of Applied Ecology

Teaching

2015/2016	Teaching Assistant, Nature Conservation course for the master program, taught by Dr. Henrique Pereira at Martin Luther University of Halle-Wittenberg.

Supervision

2016	Maria Pleger (6 weeks internship)
2017	David Matuschek (6 weeks internship)
2017	Janna Mrozek (6 weeks internship)
2016/2017	Elisabeth Sellenriek (Co-supervision of M.Sc. thesis)

Involvement in multi-party projects

2017-ongoing	Promoting and shaping the EU Restoration Agenda through mobilisation of Rewilding principles

Other activities

2018	Co-organizer and co-chair of session „Rewilding prospects for reconciling biodiversity restoration and human well-being”. 5th European Congress of Conservation Biology (ECCB), Jyväskylä, Finland.
2017	Member of the organizing committee of a workshop on the social-economic opportunities for rewilding & experts meeting on promoting and shaping the EU restoration agenda through mobilization of rewilding principles.
2016	Scientific advisor for the research- and development project (F + E-Vorhaben): "Anforderungen an den dauerhaften Schutz und das Management von Wildnisgebieten‟ (BfN, BMU), led by EUROPARC Deutschland e.V. and DUH Umweltschutzservice GmbH
2016	Member of the organizing committee of a workshop on the ecological and societal impacts of rewilding
2014-2019	Member of the graduate school of the German Centre for Integrative Biodiversity Research (yDiv).

Leipzig, den 25.03.2019

Andrea Perino

D. List of publications and conference contributions

Publications of the dissertation

Perino, A., Pereira, H. M., Navarro, L.M., Fernández, N., Bullock, J.M., Ceaușu, S., Cortés-Avizanda, A., van Klink, R., Kuemmerle, T., Lomba, A., Pe'er, G., Plieninger, T., Rey Benayas, J.M., Sandom, C., Svenning, J.-C., Wheeler, H. (2019): Rewilding complex ecosystems (**accepted for publication**, *Science*)

Peer reviewed publications

Torres, A., Fernández, N., zu Ermgassen, S., Helmer, W., Revilla, E., Saavedra, D., **Perino, A.**, Mimet, A., Rey-Benayas, J.M., Schepers, F., Selva, N., Svenning, J.-C., Pereira, H. M. (2018): Measuring rewilding progress, Philosophical Transactions of the Royal Society B: Biological Sciences, 2018, Vol 373, Issue 1761

Käding C., Freytag A., Rodner E., **Perino A**., Denzler J. (2016) Large-Scale Active Learning with Approximations of Expected Model Output Changes. In: Rosenhahn B., Andres B. (eds) Pattern Recognition. GCPR 2016. Lecture Notes in Computer Science, vol 9796. Springer, Cham

Invited talks and posters (selection)

Perino, A. Pereira, H.M., et al. Rewilding complex ecosystems. **5th European Congress for Conservation Biology (ECCB)**. Jyväskylä, Finland. 2018 (talk)

Perino, A. Pereira, H.M., et al. Rewilding complex ecosystems. Restore function not state. BES, GFÖ, NECOV and EEF Joint Annual Meeting. Ghent, Belgium. 2017 (talk)

Perino, A., Brust, C.-A., Käding, C., Jäger, J., Reus, G., Krause, C., Denzler, J., Pereira, H.M. CARPE DIEM. A tool to automatically detect and identify animal species from camera traps. **International Congress of Conservation Biology (ICCB).** Cartagena, Columbia. 2017 (talk)

Perino, A. Navarro, L.M., Pereira, H.M. Modeling the impact of mammal populations on natural succession in abandoned landscapes. iDiv Annual Conference. Leipzig, Germany. 2015 (talk)

Perino, A., Navarro, L.M., Pereira, H.M. Seeds vs. Herbivores. Methods to investigate the role of herbivory and seed limitation in determining successions in European abandoned landscapes. **27th International Congress for Conservation Biology and the 4th European Congress for Conservation Biology (ICCB-ECCB).** Montpellier, France. 2015 (poster)

E. Authors’ contributions

Chapter 2
Perino, A., Pereira, H. M., Navarro, L.M., Fernández, N., Bullock, J.M., Ceaușu, S., Cortés-Avizanda, A., van Klink, R., Kuemmerle, T., Lomba, A., Pe'er, G., Plieninger, T., Rey Benayas, J.M., Sandom, C., Svenning, J.-C., Wheeler, H. (2019): Rewilding complex ecosystems (**accepted for publication**, *Science*)

All authors developed the ideas for this paper during a workshop in 2016 and contributed with comments and revisions to the submitted version of the manuscript.
Writing: Perino, A. (70%), Pereira, H.M. (30%).
Figure design: Perino, A. (50%), Navarro, L.M. (30%), Pereira, H.M. (10%), Fernández, N. (10%)

Chapter 3
Perino, A., Pereira, H.M.: Habitat choice and coexistence of free ranging livestock and wild ungulates in an area facing rapid land abandonment.
Design/Analysis: Perino, A. (90/%), Pereira, H.M. (10%)
Writing: Perino, A. (90/%), Pereira, H.M. (10%)
Field work/Data collection: Perino, A. (60%), Wolf, F. (40%)

Chapter 4
Perino, A., Pereira, H.M.: Interspecific interactions modulate response to wildfires in a community of free ranging livestock and wild ungulates.
Design/Analysis: Perino, A. (90/%), Pereira, H.M. (10%)
Writing: Perino, A. (90/%), Pereira, H.M. (10%)
Field work/Data collection: Perino, A. (60%), Wolf, F. (40%)

Leipzig, den 25.03.2019

Andrea Perino

F. Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Rewilding complex ecosystems – a theoretical framework and empirical contributions“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.
Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.
Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Leipzig, den 25.03.2019

Andrea Perino