Impacts of invasive Opuntia cacti on wild mammals in Kenya

PETER SAMUEL STEWART

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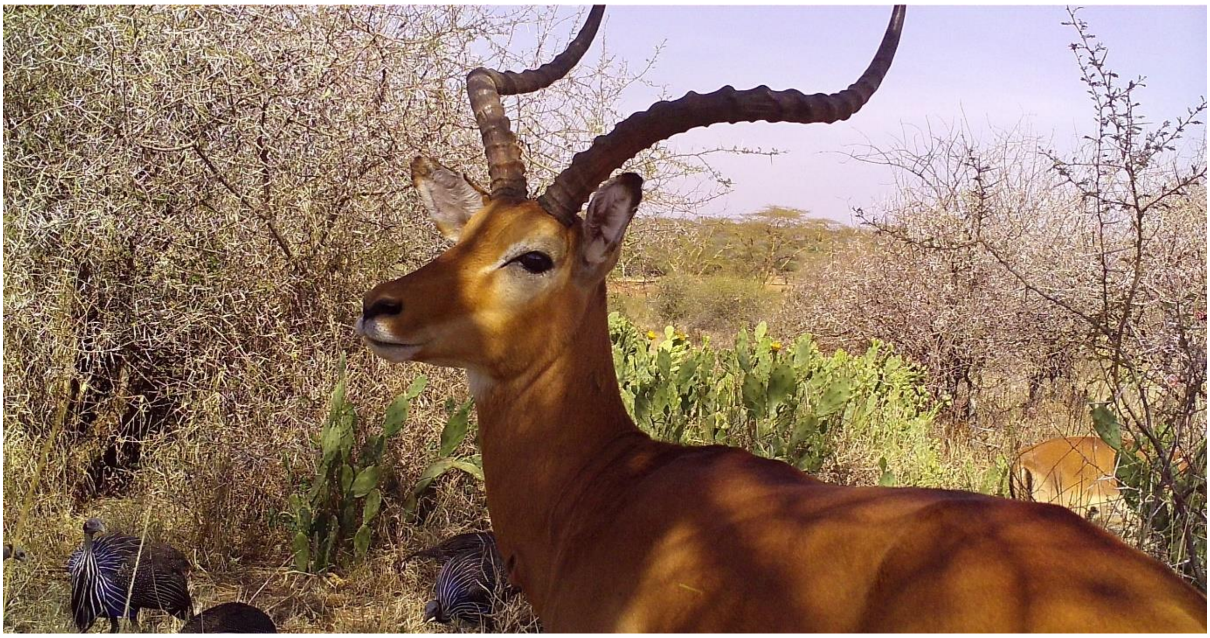

Peter S. Stewart

Department of Biosciences

Durham University

2023

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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis was conducted by the author unless indicated otherwise.

Peter S. Stewart

2023

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Chapter 1

Introduction

Introduction

Writing in 1958, Charles Elton – a founding figure of the field that is now invasion ecology – declared: "We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora" (Elton 1958, p. 22). Elton's words hold just as true today; the intervening period has seen a marked increase in the rate of new species introductions, and this trend shows no sign of abating (Seebens *et al.* 2017). Consequently, biological invasions are now regarded as one of the foremost threats to ecosystems worldwide (Pyšek *et al.* 2020).

In this introductory chapter I briefly overview the biological invasion process, outlining key factors which come into play from the point of initial transport and introduction, through the subsequent establishment phase, and then to the spread of the invader across the landscape. I also briefly review the impacts of invasive species. I then explore the invasion of Laikipia County, Kenya, by *Opuntia* cacti, which is the main subject of my thesis. Throughout these sections, I identify key knowledge gaps in our understanding of biological invasions in general, and the Laikipia *Opuntia* invasion in particular. I conclude with an overview of the four main chapters of my thesis, with a focus on how each chapter will address these gaps.

Biological invasions: an overview

Invasive species (Box 1) are currently regarded as one of the most serious threats to ecosystems and human well-being (Pyšek *et al.* 2020). This threat continues to grow; the rate at which species have been introduced into new regions has increased markedly since 1800, and for most taxa this trend shows no sign of slowing (Seebens *et al.* 2017). Non-native species are now found on every continent, with some hotspot regions containing hundreds of these species (Dawson *et al.* 2017). The distributions of established non-native taxa are correlated with human population density and economic activity (GDP), as well as climatic factors including temperature and precipitation (Dawson *et al.* 2017). Non-native species occurrence and abundance are also associated with the type and intensity of land use, with the strength of these relationships varying among invasive taxa (Liu *et al.* 2023). In general, larger areas also tend to be more heavily invaded: after accounting for size, islands and coastal areas stand out as particularly high in non-native species richness (Dawson *et al.* 2017). Furthermore, the distributions of some non-native taxa still bear the imprint of European colonialism; the composition of non-native plant communities is more similar among regions which were previously occupied by the same empire than among randomly selected regions (Lenzner *et al.* 2022). The challenge posed by invasive species is only likely to increase in the future as new species continue to be introduced (Seebens *et al.* 2021). Moreover, we have probably already accrued a substantial 'invasion debt', as many future invasive species will have been introduced already (Pyšek *et al.* 2020). Climate change is also expected to play an exacerbating role, particularly for temperature-sensitive taxa such as terrestrial arthropods (Hulme 2017).

Biological invasions begin when species are introduced across biogeographic barriers. This introduction stage occurs through a number of human-mediated pathways. Some species, particularly vertebrates, are deliberately transported by humans and released into the wild (Hulme *et al.* 2008). A classic example is the European rabbit (*Oryctolagus cuniculus*), which was introduced to Australia for sport hunting (Alves *et al.* 2022). Other species, especially vascular plants, are deliberately transported and released into captivity (*e.g.*, zoos, gardens, aquaculture), but later escape into the wild (Hulme *et al.* 2008). For instance, escape from botanical gardens is an important introduction pathway for non-native plant species (Dawson *et al.* 2008). In addition to these intentional pathways, several unintentional pathways play a critical role, particularly for invertebrates, fungi, and other microorganisms (Hulme *et al.* 2008). First, a species may be inadvertently transported as a contaminant on a traded

Box 1: What is an invasive species?

For the purpose of this thesis, invasive species are defined as those which have been introduced across biogeographic boundaries (*i.e.*, they are non-native) by the action (either deliberate or accidental) of humans, and which have subsequently formed established populations that are growing in abundance and/or expanding in range. It is worth noting that invasion ecology has a history of imprecise terminology usage (Lockwood *et al.* 2013, p. 25) which most invasion ecologists regard as a problem (Shackleton *et al.* 2022). Furthermore, there is significant polarisation within the invasion ecology community about whether certain characteristics, such as the potential for impact, should be used to define "invasive species" (Shackleton *et al.* 2022). I suggest that these definitional issues are particularly acute in invasion ecology because the definition of "invasive species" is often tightly linked to policy and management (Beck *et al.* 2008). Consequently, I argue that it is important to be aware of the different ways in which "invasive species" can be defined, and to be clear about how we are defining them in a given situation.

Definitions of "invasive species" can be mapped onto three main axes (Fig. 1). First, biogeographic definitions define invasive species as being non-native (allochthonous) to a region. Some definitions refine the biogeographic axis by requiring that the species is introduced due to human agency. Second, population-dynamic definitions emphasise rapid increases in abundance and local range size as defining features of invasive species. In the extreme, invasive species are entirely defined by explosive population dynamics, meaning that "invasive species can also be native" (Valéry *et al.* 2009). Finally, impact definitions characterise invasive species by their impacts on the environment and people; at the extreme end of this axis, "invasive" is essentially a synonym for "pest".

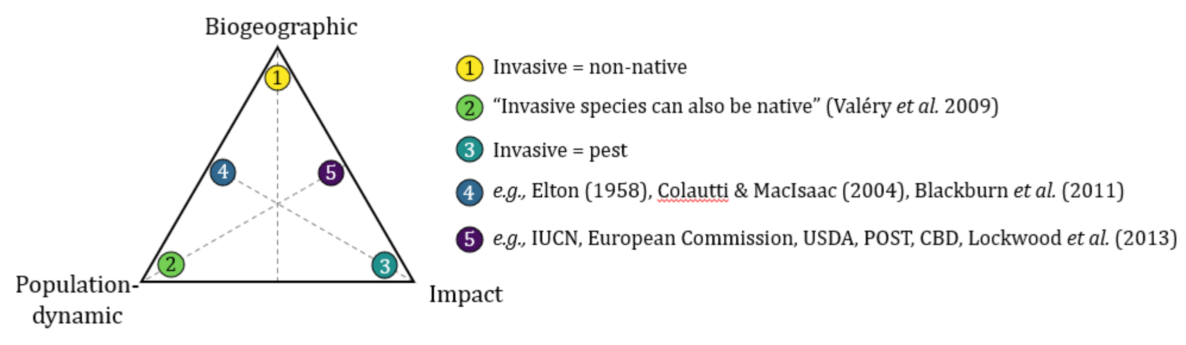

Figure 1. Some definitions of "invasive species" organised by whether they include a biogeographic, population-dynamic, or impact component. Dashed lines represent the three main axes; axis labels are shown at the maximum value of each axis (*i.e.*, the top of the triangle represents purely biogeographic definitions of "invasive species").

Most influential definitions of invasive species do not map onto the extremes of any one axis, but instead occupy the intermediate space where at least two axes are diagnostic. For example, Elton (1958, p. 7, 10) argued that biological invasions are a kind of "ecological explosion" which occur when "a foreign species successfully invades another country”. Similar population-dynamic-biogeographic definitions have been used in several influential papers, including the “unified framework for biological invasions” proposed by Blackburn *et al.* (2011); in this framework, invasive species are those which have undergone introduction, establishment, and spread in a new region. A similar definition is implied by the earlier stage-based framework of Colautti and MacIsaac (2004).

A contrasting set of definitions, which are often employed by governments and non-governmental organisations (NGOs), are situated on the biogeographic and impact axes (Fig. 1). For example, the International Union for Conservation of Nature (IUCN 2023) define invasive species as: “introduced by humans, either intentionally or accidentally, into places outside of their natural range, negatively impacting native biodiversity, ecosystem services or human economy and well-being.” Similar definitions are used by the European Commission (European Commission 2023), the United States Department of Agriculture (USDA; Executive Order 13112, 1999), and the United Kingdom’s Parliamentary Office of Science and Technology (POST; 2022), and in the Convention on Biological Diversity (CBD; 2021), all include a biogeographic and impact component. Biogeographic-impact definitions are also used within the scientific community, including the highly cited textbook by Lockwood *et al*. (2013).

commodity, which may be another species (*e.g.,* crop plants or seeds) or a derived commodity (*e.g.,* timber; Hulme *et al.* 2008). For instance, the plant pathogen *Phytophthora ramorum* was introduced to several regions in Europe and North America through the trade of infected nursery plants (Grünwald *et al.* 2012). Second, species can be transported as stowaways within or attached to a transport vector, such as a ship (Hulme *et al.* 2008); the release of contaminated ballast water is a key pathway for the zebra mussel (*Dreissena polymorpha*; Strayer 2009), one of the world’s most damaging invasive species (Lowe *et al.*, 2000). Third, species can be introduced when humans connect areas by creating novel dispersal corridors such as canals or bridges (Hulme *et al.* 2008). For example, the construction of the Suez Canal caused the introduction of several hundred non-native species to the Mediterranean Sea (Galil *et al.* 2015). Finally, species can disperse unaided from areas which have already been invaded (Hulme *et al.* 2008).

Once introduced into a new region, a number of factors potentially determine whether a species is able to establish and form a self-sustaining population. The simplest models of population growth tell us that this will occur when the rate of births (plus immigration) outweighs the rate of deaths (plus emigration; Coulson & Godfray 2007), highlighting the fundamental importance of factors governing reproduction and survival. These factors include properties of the introduced species, such as life history traits like lifetime reproductive output, growth rate, and lifespan (Capellini *et al.* 2015; Allen *et al.* 2017). The abiotic and biotic characteristics of the environment are also important, as is their interplay with the characteristics of the introduced species. For instance, the degree of overlap between the climate of the recipient environment and the climatic niche of the introduced species can influence the probability of a successful establishment event (Alaniz *et al.* 2021). Biotic interactions between the native community and the introduced species also play a key role in the establishment phase (Mitchell *et al.* 2006); classic hypotheses such as the biotic resistance hypothesis (Elton 1958), enemy release hypothesis (Keane & Crawley 2002) and Darwin's naturalisation hypothesis (Darwin 1859, p. 88) emphasise the importance of competitors and natural enemies of the introduced species. However, it is becoming increasingly clear that native mutualists can also be vital in determining whether a population becomes established (Traveset & Richardson 2014). Real biological invasions also include complexities that are not represented in the simpler models of population growth. For instance, demographic and environmental stochasticity can determine the fate of an introduction, particularly when the founder population is small (Lande 1988, 1993). Small founder populations can also exhibit genetic bottlenecks (*e.g.,* Puillandre *et al.* 2008) that can influence establishment success. The importance of these effects can be diminished by the introduced species' propagule pressure, which is a function of the size, number, and spatiotemporal patterning of propagules which arrive in the system (Simberloff 2009).

Following establishment, a subset of non-native species goes on to spread: under definitions which include a population-dynamic element (Box 1), these species are now defined as invasive. For a species to spread, it must overcome dispersal barriers which would otherwise prevent it from reaching new locations, and then overcome environmental barriers imposed by differences between these new locations and the site of the original establishment (Blackburn *et al.* 2011). As with the establishment phase, the characteristics of the introduced species (*e.g.,* dispersal-related traits such as seed size), the abiotic environment (*e.g.,* the spatial arrangement and connectivity of suitable habitat patches), and the native community (*e.g.,* the presence of native competitors) can influence the prospective invader's ability to overcome these barriers (Theoharides & Dukes 2007). For many prospective invaders, biotic interactions are vital for overcoming dispersal barriers (Mitchell *et al.* 2006). For example, seed dispersal by native frugivores is a key contributor to the spread of many invasive plant species (Bartuszevige & Endress 2008; Padrón *et al.* 2011).

As spread operates over longer timescales than the initial establishment phase, evolutionary changes in the introduced species and the native community can play an increased role; several hypotheses focus on the role of post-establishment evolution in biological invasions (Atwood & Meyerson 2011), including the well-known evolution of increased competitive ability hypothesis (Blossey & Notzold 1995). Evolutionary changes have also been invoked as an explanation for a common observation about the spread phase: spread often follows establishment after a considerable time lag, which may last several decades (Crooks 2005). Numerous other non-mutually exclusive explanations for this phenomenon have also been proposed, including Allee effects (*e.g.,* Drake & Lodge 2006), feedback loops between multiple invasive species ("invasional meltdown"; Simberloff 2009), post-establishment changes in environmental characteristics such as land use (*e.g.,* Strum *et al.* 2015), and the introduction of new genotypes due to continuing propagule pressure (Simberloff 2009).

Invasive species can have profound impacts on ecosystems and humans. While some frameworks conceptualise impact as a separate stage which follows establishment and spread (*e.g.,* Levine *et al.* 2003), impacts can occur at any time from the point of initial introduction (Ricciardi *et al.* 2013). The ecological impacts of invasive species range widely in scale. At the levels of individual native organisms and populations of native species, invaders can affect variables including fitness, growth, behaviour, and abundance (Vilà *et al.* 2011; Anton *et al.* 2019). The impacts of biological invasions on native species echo through evolutionary time, as invasive species divert the evolutionary trajectory of native species through hybridisation, niche displacement, and a host of other mechanisms (Mooney & Cleland 2001). Ultimately, invasive species can drive native species to local or global extinction; invasive species contributed to a third of the animal extinctions and a quarter of the plant extinctions recorded in the 2017 IUCN red list (Blackburn *et al.* 2019). At broader scales, invasive species can impact biodiversity, disrupt interactions between native species (*e.g.,* mutualisms) and alter the structure of interaction networks (*e.g.,* pollination networks, frugivory networks), alter nutrient cycling and its constituent processes (*e.g.,* nitrification), and drive regime shifts (Traveset & Richardson 2006; Vilà *et al.* 2011; Kotta *et al.* 2018; Anton *et al.* 2019). These broad-scale impacts may be driven by fine-scale impacts (*e.g.,* changes in biodiversity as a consequence of local extinctions) and vice versa (*e.g.,* disruption of interaction networks affecting the abundance of native species), illustrating the interconnectedness of impacts at different scales.

Invasive species can also negatively affect people, either directly or as a result of ecological impacts. The human impacts of invasive species include negative effects on human health, either because the invasive organism itself is dangerous (*e.g.,* giant hogweed (*Heracleum mantegazzianum*) sap causes burns; Baker *et al.* 2017) or because the invader facilitates other dangerous organisms such as pathogens or parasites (Hulme 2014). Furthermore, invasive species can disrupt ecosystem services (*e.g.,* food and water provision, wildfire regulation) upon which people depend, with consequences for well-being (Pejchar & Mooney 2009). In some cases, disruption can be so severe that people are displaced from an area, as in the case of people from the Lake Baringo area in Kenya who were displaced from their homes by the invasive tree *Prosopis juliflora* (Mwangi & Swallow 2005; Witt 2010). Another perspective on invasive species' human impacts can be adopted by estimating the costs of biological invasions in financial terms. These estimates have included the total global cost of invasive species (*e.g.,* USD ≥ 1.288 trillion; Zenni *et al.* 2021) as well as estimates restricted to specific geographic regions (*e.g.,* USD 9.8 billion for Germany; Haubrock *et al.* 2021), taxa (*e.g.,* USD 63.7 billion for freshwater macrofouling bivalves; Haubrock *et al.* 2022), or management interventions (*e.g.,* USD 1.3 to 11 per square metre to remove invasive *Miscanthus* species; Lowry *et al.* 2022). Furthermore, invasive species can disrupt cultural traditions. For example, First Nations Australians from the Borroloola region have been negatively affected by the loss of culturally important animal species caused by cane toads (*Rhinella marina;* van Dam *et al.* 2002). Invasive species can also affect people in less tangible ways, such as by changing how people perceive the aesthetic value of a landscape (Kueffer & Kull 2017).

Predicting, detecting, and intervening to mitigate the impacts of invasive species are key goals in invasion ecology (Ricciardi *et al.* 2013; Simberloff *et al.* 2013). Ideally, any impacts which are not entirely avoided by preventing the initial introduction are dealt with through early detection and decisive intervention (Simberloff *et al.* 2013). This ideal is facilitated by having a mechanistic understanding of impact. Knowledge of the mechanisms by which impacts occur can allow for better predictions of future impacts, detection of impacts which are already occurring, and the design and implementation of management interventions which are effective and avoid unintended consequences (van Riel *et al.* 2000; Levine *et al.* 2003; Ricciardi *et al.* 2013; Crystal-Ornelas & Lockwood 2020).

While recent decades have seen a substantial level of research into the impacts of invasive species and advances in our understanding of the mechanisms involved (Levine *et al.* 2003; Ricciardi *et al.* 2013; Crystal-Ornelas & Lockwood 2020), there remain major obstacles to reaching a strong mechanistic understanding of impact. One of these obstacles is the limited scope in which invasive species' impacts are studied; not only are studies of impact restricted to relatively short temporal scales, but also to certain spatial scales (Crystal-Ornelas & Lockwood 2020). To date, the majority of studies have focused on impacts at the levels of populations (*e.g.,* abundance, average fitness) and communities (*e.g.,* biodiversity), while studies of individual-level (*e.g.,* growth, behaviour) or genetic impacts are relatively rare (Crystal-Ornelas & Lockwood 2020). This restricted understanding is problematic not only because it inhibits our understanding of fine-scale impacts, but also because the interconnected nature of impacts at different scales implies that a lack of understanding at one scale affects our understanding at other scales. Consequently, improving our knowledge of the finer-scale impacts of invasive species is a vital research problem. Given the central importance of behaviour in many biotic interactions, and the fundamental importance of biotic interactions in invasion ecology (Mitchell *et al.* 2006), the impacts of invasive species on animal behaviour represent a particularly important topic for investigation. To address this outstanding research gap, I will be exploring the behavioural impacts of invasive *Opuntia* cacti in Laikipia County, Kenya.

Opuntia invasions in Laikipia County, Kenya

Opuntia is a genus of the cactus family (Cactaceae), commonly referred to as prickly pear cacti (Majure *et al.* 2012). Native to the Americas, *Opuntia* species are found in arid habitats throughout Central America, the south-western United States, the Caribbean, and the Galápagos Islands (Hamann 2001; Rebman & Pinkava 2001; Reyes-Aguero *et al.* 2006; Majure *et al.* 2014). This widespread distribution, coupled with their high level of diversity – modern estimates place the number of extant species at around 180 to 200, making *Opuntia* one of the most speciose genera of cacti (Nyffeler & Eggli 2010; Novoa *et al.* 2015; Martínez-González & Morales-Sandoval 2021) – has garnered *Opuntia* a reputation as one of the most successful groups of cacti (Rebman & Pinkava 2001). Unfortunately, the success of *Opuntia* has not been confined to its native range; *Opuntia* species have also been introduced to every continent except Antarctica and are invasive in regions including East and Southern Africa, Australia, the Mediterranean, and parts of South-East Asia (Pasiecznik 2007, Pasiecznik & Rojas-Sandoval 2007, Pasiecznik 2015). In fact, *Opuntia* may be regarded as the archetypal invasive plant – prickly pears are the first invasive plant named in Elton's (1958) foundational book on invasion ecology. The impacts of *Opuntia* invasions have been severe, and one species –

Opuntia stricta – is considered to be one of the world's most damaging invasive species (Lowe *et al.*, 2000).

Several species of *Opuntia* are invasive in Laikipia County, Kenya. In total, six *Opuntia* species (*O. stricta*, *O. engelmannii*, *O. ficus-indica*, *O. monacantha*, *O. microdasys*, and *O. elatior*) were introduced to Laikipia in the 20th century, with three of these (*O. stricta*, *O. engelmannii*, and *O. ficus-indica*) becoming invasive (Witt 2017). In common with most invasive vascular plants worldwide (Hulme *et al.* 2008), *Opuntia* species were deliberately introduced to Laikipia County (Strum *et al.* 2015; Githae 2019). *O. stricta* (Fig. 1A) and *O. ficus-indica* were introduced to the town of Doldol in the 1950s by the British colonial administration for ornamental purposes and to act as live fences (Strum *et al.* 2015; Githae 2019). Both species are now widespread in Laikipia; *O. stricta* is particularly abundant in the north-eastern areas close to Doldol, while *O. ficus-indica* is present at higher densities in the south of the county (Witt 2017; Witt *et al.* 2020a). *O. engelmannii* (Fig. 1B) was introduced to the area that is now Loisaba Conservancy in the 1970s, also to serve as an ornamental plant and live fence (Loisaba Conservancy 2019a); the source of the invasion is thought to be a quarry where unwanted plants were discarded (Witt *et al.* 2020a). At the time of introduction, land managers were apparently unaware of the potential for *Opuntia* to become invasive (Loisaba Conservancy 2019a), perhaps because *O. stricta* experienced a lag phase of several decades before undergoing rapid expansion (Strum *et al.* 2015). Although *O. engelmannii* is far less widespread than the other invasive *Opuntia* species – the invasion is currently confined to Loisaba Conservancy and some adjacent areas, including the northern region of Mpala Research Centre (Witt 2017) – the density of *O. engelmannii* in invaded areas is very high.

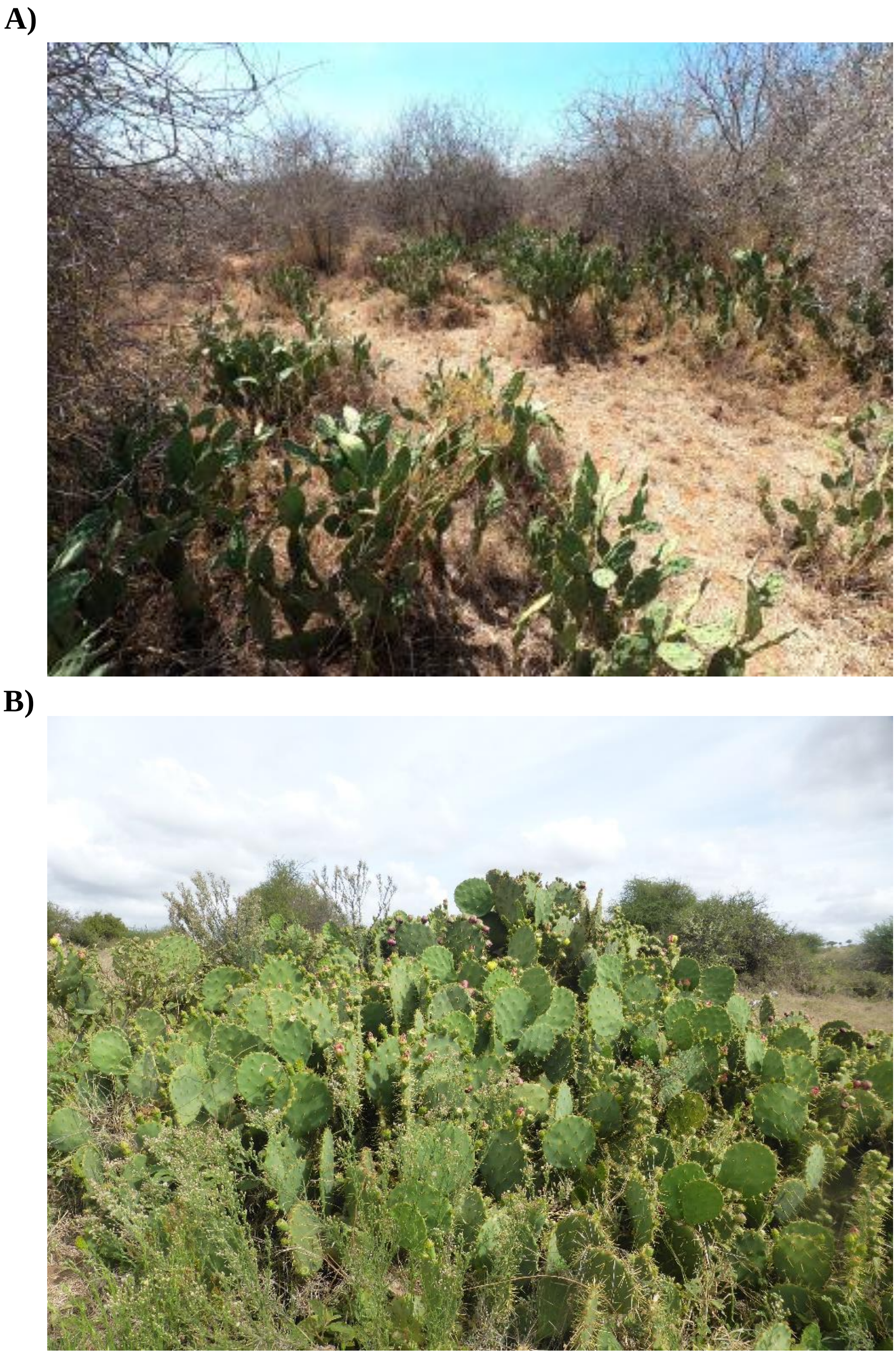

Figure 1. **A)** *Opuntia stricta* and **B)** *Opuntia engelmannii*.

The factors underlying *Opuntia*'s establishment and spread in Laikipia are not fully understood, but two key aspects of *Opuntia*'s biology are likely to be important contributors to its success. The first is related to *Opuntia*'s climatic niche. The climate of Laikipia – which is mainly semi-arid, with a highly variable pattern of rainfall – closely matches the estimated climatic niche of *Opuntia* (Witt *et al.* 2020a). The second is related to *Opuntia*'s reproductive biology. Many *Opuntia* species, including the three which are invasive in Laikipia, can reproduce vegetatively (Reyes-Aguero *et al.* 2006). This form of reproduction occurs when cladodes (*i.e.,* pads) are detached from the parent plant and fall on the ground, where they subsequently take root and grow to form new stands (Reyes-Aguero *et al.* 2006). This mode of dispersal can be facilitated by animals, especially large herbivores like elephants (*Loxodonta africana*; (Foxcroft & Rejmánek 2007), that detach and scatter the cladodes. While the majority of vegetative dispersal is expected to occur in the immediate vicinity of the parent stand, cladodes can sometimes be transported in rivers (Dance *et al.* 2003) resulting in longer-range dispersal. However, most *Opuntia* species are not restricted to vegetative dispersal – they also produce large numbers of fleshy fruits which are consumed by a diverse array of animals (Mellink 2002; Reyes-Aguero *et al.* 2006). The dispersal of seeds resulting from the consumption of *Opuntia* fruits is thought to have been instrumental in the success of *Opuntia* invasions in other regions (*e.g.,* Foxcroft *et al.* 2004; Padrón *et al.* 2011), and is also likely to have played a critical role in the invasion of Laikipia (Strum *et al.* 2015). However, investigations into the role of animals in dispersing *Opuntia* in Laikipia have mostly focused on elephants and olive baboons (*Papio anubis*) – whether other animals play a role is unclear, because frugivory has not been systematically studied.

In addition to *Opuntia*'s climatic niche and reproductive biology, environmental factors may also influence the spread of *Opuntia* in Laikipia County. For example, soil characteristics are likely to be important. Laikipia County includes both red soils (Ferric and Chromic Luvisols) and black cotton soil (Pellic vertisol), as well as transitional soils which separate the two main types (Augustine *et al.* 2011; Mutuku & Kenfack 2019; Kimuyu *et al.* 2021). However, *Opuntia* appears to be confined to red soil areas; in the field, I never observed any *Opuntia* growing on black cotton soil or on transitional areas such as the Mpala plateau. This pattern is unlikely to be driven by dispersal limitation as, in some areas, invaded red soils and uninvaded black cotton soils are separated by only a few hundred metres, and potential dispersers are likely to move between the areas (*e.g.,* elephants from the same family group have been observed on both transitional plateau soils and low-lying red soil areas; Oduor *et al.* 2020). A more plausible explanation is that the black cotton and transitional soils are somehow unsuitable for *Opuntia* growth, perhaps because they are prone to waterlogging.

Biotic resistance conferred by native herbivores may also act to slow the spread of *Opuntia* in Laikipia County (Wells *et al.* 2023). The evidence for this point comes from long-term herbivore exclusion experiments at Mpala Research Centre; unfenced (*i.e.,* herbivore-accessible) plots have significantly fewer *Opuntia* plants than plots which exclude herbivores (Wells *et al.* 2023). However, it is currently unclear whether these results are due to herbivores consuming *Opuntia*, or indirectly result from herbivores' effects on the native plant community. Furthermore, other effects of the herbivore exclusion plots – such as reduced frugivore access, leading to less fruit removal and hence increased fruit deposition inside the exclusion plots – may explain the observed results. Our ability to assess these competing explanations is hampered by the lack of published natural history information concerning interactions between *Opuntia* and native animals.

Changes in human land use may influence the *Opuntia* invasion. In particular, Strum *et al.* (2015) argued that the rapid expansion of *O. stricta*, which occurred more than 50 years after the initial introduction, was driven by the sedentarisation of pastoralist communities and consequent increase in livestock grazing pressure. The subsequent invasion areas including Mpala Research Centre, where livestock grazing pressure is relatively low, may be ascribed to propagule pressure from adjacent grazing areas. However, it seems unlikely that changes to grazing practices explain the invasion of *O. engelmannii*, which originated within the area that is now Loisaba Conservancy. One possibility is that another type of disturbance – such as wildfire – facilitated the invasion. Another possible explanation is that differences in the *Opuntia* species' biology may explain why *O. engelmannii* was able to invade without facilitation from grazing – for example, *O. engelmannii* may be more resistant to herbivory than *O. stricta*, and hence better able to invade conservancy areas where wild herbivores are abundant.

Finally, the spread of *Opuntia* is influenced by land managers' efforts to contain and reverse the invasion through the use of biological and mechanical control. Cochineal (*Dactylopius opuntiae*), a sap-sucking insect, is currently the main biological control agent in use in Laikipia County; preliminary analyses indicate that cochineal is effective against *O. stricta*, destroying the cactus' cladodes and reducing flowering and fruiting (Witt *et al.* 2020). Following the success of a pilot study conducted in 2014, cochineal has been introduced to several areas of

Laikipia, and continues to form a key part of the management of *O. stricta* (Shackleton *et al.* 2017). However, the effectiveness of cochineal against other *Opuntia* species – particularly *O. engelmannii* – appears to be limited. Consequently, work is ongoing to find and introduce new *D. opuntiae* biotypes which may be more effective against *O. engelmannii*. In the absence of an effective biocontrol option, most management of *O. engelmannii* is achieved via mechanical control (Loisaba Conservancy 2019b).

The rapid spread of *Opuntia* has been linked to a variety of impacts on people living in Laikipia County. Heavily invaded areas are unsuitable for livestock and crops; consequently, the invasion has resulted in loss of livelihoods, food insecurity, and the displacement of local people (Shackleton *et al.* 2017; Witt 2017). In areas where people live alongside *Opuntia*, the sharp spines result in injuries and often blind livestock (Shackleton *et al.* 2017). Furthermore, ingestion of *Opuntia* fruit also poses a threat to livestock; the fruit is coated in small spines which cause infection in the mouth and intestines, reducing livestock value (particularly as tripe is a valued delicacy) and increasing mortality (Ueckert *et al.* 1990; Hanselka & Paschal 1991; Shackleton *et al.* 2017). These impacts result in substantial economic losses: *O. stricta* alone resulted in annual losses averaging $500-1000 USD per household for many residents of the Doldol area (Shackleton *et al.* 2017).

While the socio-economic impacts of *Opuntia* are well-established, the ecological impacts are not as well understood. Although the *Opuntia* invasion is often assumed to negatively affect biodiversity and the abundance of native species in Laikipia (Githae 2019), and such effects have been demonstrated in other systems (*e.g.*, Tesfay & Kreyling (2021) for *O. ficus-indica* in Eritrea), empirical data on *Opuntia*'s ecological effects in Laikipia are lacking. This lack of information is particularly problematic because Laikipia County is a key stronghold for biodiversity, with the region supporting key populations of endangered species including Grevy's zebra (*Equus grevyi*; Rubenstein *et al.* 2016), reticulated giraffe (*Giraffa reticulata*; Muneza *et al.* 2018) and African wild dog (*Lycaon pictus*; O'Neill *et al.* 2022). Consequently, investigating the ecological impacts of *Opuntia* is an urgent priority for research.

Thesis overview

In this thesis, I examine the behavioural impacts of invasive plants, with particular reference to the invasion of Laikipia County, Kenya, by *Opuntia* cacti. As discussed above, impacts which are mediated through changes to native animal behaviour represent a neglected, yet tremendously important, aspect of invasive species' impacts. In the second chapter, I address this topic by reviewing the impacts of invasive plants on animal behaviour. To promote a mechanistic understanding of these impacts, I synthesise the disparate literature within a novel mechanistic framework. In so doing, I aim to facilitate the prediction, detection, and design of effective interventions to mitigate invasive plants' behavioural impacts.

The impacts of biological invasions on animal behaviour can manifest as changes in the patterns of animal species' occurrence. However, the patterns and drivers of occurrence are intrinsically difficult to study; ecologists are often constrained to the use of observational data, due to the logistical and ethical challenges associated with manipulating ecological systems at scale. A common approach to overcoming this hurdle is to use models, such as occupancy models, which relate variation in species occurrence to one or more environmental covariates. This presents a new challenge: how do we choose between competing models, each with a different set of environmental covariates? In the third chapter of my thesis, I use simulations to explore model selection in occupancy models. The results from these simulations subsequently guide my analytical approach in Chapter 4.

In the fourth and fifth chapters of my thesis, I turn to the case of the ongoing *Opuntia* invasion in Laikipia County. In these chapters, I use a dataset which I collected at Mpala Research Centre and Loisaba Conservancy in 2021. The dataset contains over one million camera trap images from 101 sites, in addition to measurements of *Opuntia* cover and volume at multiple spatial scales, morphological measurements of several hundred *Opuntia* stands, and data on other habitat characteristics (*e.g.*, native vegetation). These data are supplemented by additional data provided by Mpala Research Centre, including GIS layers and weather data. To process the camera trap images, I created Prickly Pear Project Kenya (https://www.zooniverse.org/projects/peter-dot-stewart/prickly-pear-project-kenya) on the Zooniverse platform, where members of the public were able to view and classify the camera trap images. Ultimately, the project engaged over 8000 volunteers; the volunteers' classifications for the camera trap images also form part of the data generated as part of my thesis.

The ecological impacts of *Opuntia* are not well understood. However, it is likely that behavioural impacts comprise a key part of *Opuntia*'s ecological impacts, because *Opuntia* profoundly alters the physical structure of the habitat and provides resources via its abundant fruit. In the fourth chapter of my thesis, I explore *Opuntia*'s behavioural impacts by quantifying the effects of *Opuntia* on the occupancy and activity of eight key mammal species. My approach in this chapter is directly informed by the mechanistic framework from Chapter 2 and the results from Chapter 3. The appendices of Chapter 4 contain supplementary analyses including prior predictive simulations, simulation-based model validation, analysis of the volunteers' classification accuracy for the camera trap images, and results obtained under alternative modelling assumptions to those used in the main text.

Biotic interactions, particularly seed dispersal by native frugivores, are thought to be instrumental in the success of *Opuntia*'s invasion in Laikipia. However, our understanding of these interactions is limited by a lack of fundamental biological information. To address this problem, I use my dataset to address two key knowledge gaps. First, I quantify the relationship between height and fruiting in *O. stricta* and *O. engelmannii*, and how both height and fruiting are related to local habitat characteristics. Second, I document the interactions between animals and *Opuntia* using my camera trap images. The appendices of Chapter 5 contain supplementary analyses including prior predictive simulations, and analyses to explore the robustness of my results to unobserved site-level confounds.

Chapter 2

Impacts of Invasive Plants on Animal Behaviour

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Abstract

The spread of invasive species is a threat to ecosystems worldwide. However, we know relatively little about how invasive species affect the behaviour of native animals, even though behaviour plays a vital role in the biotic interactions which are key to understanding the causes and impacts of biological invasions. Here, I explore how invasive plants – one of the most pervasive invasive taxa – impact the behaviour of native animals. To promote a mechanistic understanding of these behavioural impacts, I begin by introducing a mechanistic framework which explicitly considers the drivers and ecological consequences of behavioural change, as well as the moderating role of environmental context. I then synthesise the existing literature within this framework. I find that while some behavioural impacts of invasive plants are relatively well-covered in the literature, others are supported by only a handful of studies and should be explored further in the future. I conclude by identifying priority topics for future research, which will benefit from an interdisciplinary approach uniting invasion ecology with the study of animal behaviour and cognition.

Introduction

Every continent harbours invasive species (Dawson *et al.* 2017), and their global accumulation shows little sign of slowing (Seebens *et al.* 2017). The ecological impacts of invasive species range from the level of individual native organisms to wide-scale ecosystem patterns and processes (Vilà *et al.* 2011), yet ecologists have largely focused on impacts at population and community levels, such as on biodiversity and abundance; the fine-scale impact of invasive species on native animal behaviour is less-studied, but of particular concern (Crystal-Ornelas & Lockwood 2020).

Animal behaviour is central to many biotic interactions, and biotic interactions are key to understanding the causes and impacts of biological invasions (Mitchell *et al.* 2006). While the importance of animal behaviour has long been recognised in explaining the causes of invasions (Holway & Suarez 1999), we have only recently begun to consider the impacts of invasive species on native animals' behaviour, and the resulting ecological consequences (Sih *et al.* 2010; Wong & Candolin 2015; Langkilde *et al.* 2017; Wilson *et al.* 2020). Previous syntheses covering the behavioural impacts of invasive species have largely focused on invasive animals, which affect native animals' behaviour by acting as novel predators, competitors, and prey (Sih *et al.* 2010; Langkilde *et al.* 2017). However, relatively little progress has been made towards a general understanding of how invasive plants affect native animal behaviour, despite recent research and conceptual advances in the field. Given the urgent conservation challenge posed by plant invasions, and the fact that this challenge is only likely to increase in the foreseeable future (Vilà *et al.* 2011; Dawson *et al.* 2017; Seebens *et al.* 2017), this lack of coherent understanding requires attention.

Plant invasions can impact animal behaviour in many ways, with myriad ecological consequences. Here, I synthesise existing research on these impacts within a mechanistic framework that outlines the factors which generate and moderate them (Fig. 1), and offer directions for future research (Table 1). My aims are twofold. First, I aim to promote mechanistic thinking about invasive plants' behavioural impacts. Not only would a mechanistic understanding enable informed, effective action to mitigate impacts while avoiding unintended harm (van Riel *et al.* 2000), but it may also facilitate both the detection and prediction of impacts, enabling proactive management which accurately prioritises key invaders and targets them before they become unmanageable. To this end, I have organised my review around the mechanistic framework (Fig. 1). Second, the study of animal behaviour offers insights and powerful tools for tackling the conservation challenges presented by invasive plants (Sutherland 1998; Buchholz 2007; Greggor *et al.* 2019a; Greggor *et al.* 2020), and I aim to stimulate both behavioural and conservation biologists to work towards a better understanding of the multiple impacts of invasive plants. I propose key questions for future research (Table 1) with this interdisciplinarity in mind.

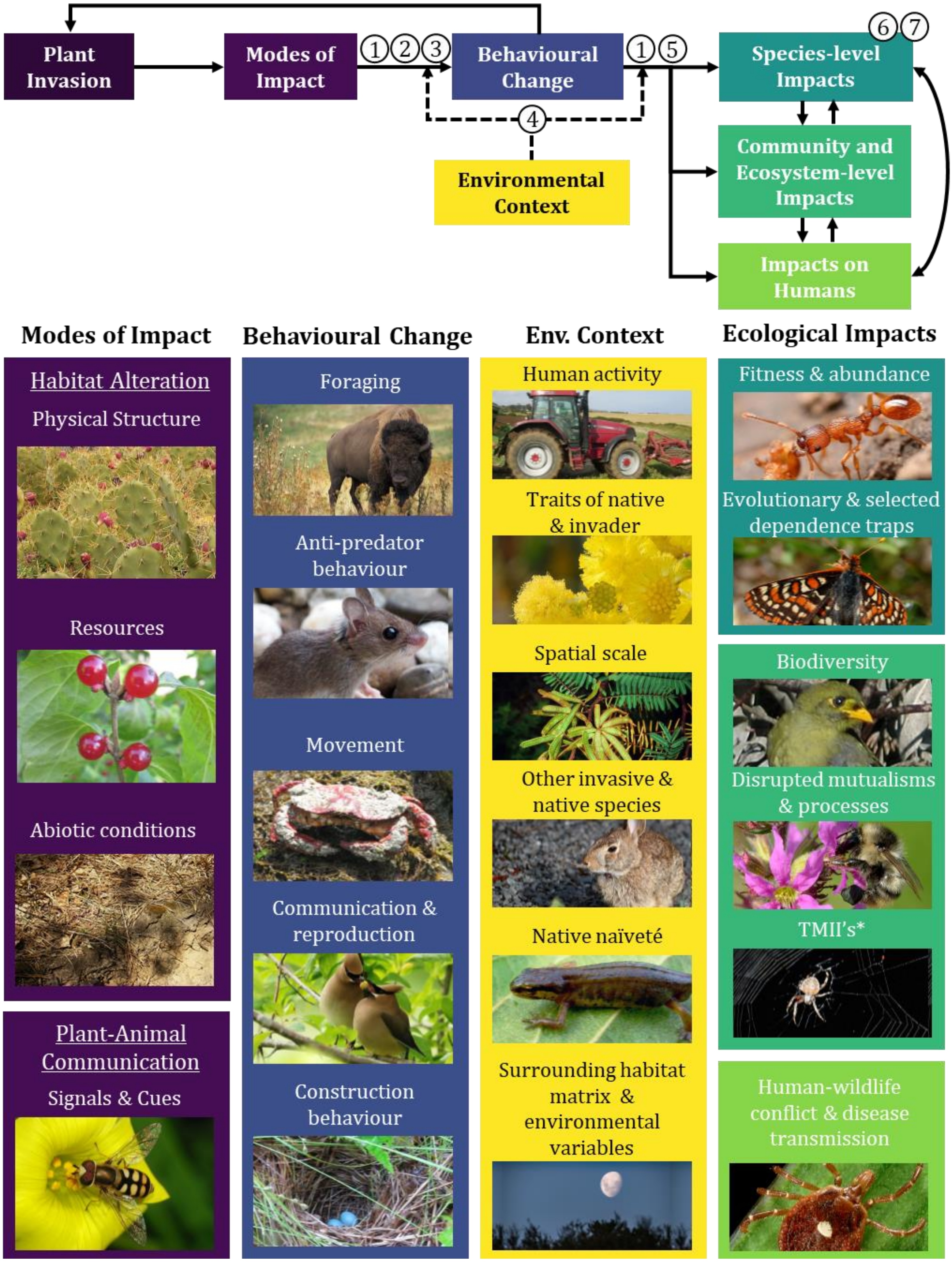

Figure 1. Mechanistic framework (top panel) outlining the impacts of invasive plants on animal behaviour, with examples presented in bottom panels. Plant invasion generates a suite of changes within a habitat or ecosystem (modes of impact), driving behavioural changes in native species. These

behavioural changes impact the native species, the wider community and ecosystem, and human beings, and generate feedback loops which influence the future spread of invasive plants. How modes of impact translate to behavioural change, and the wider impacts of behavioural change, is influenced by environmental context. Solid lines represent causal links, dashed lines represent moderating factors. Numbers in top panel refer to key questions for future research discussed in Table 1. *TMII's = trait-mediated indirect interactions. Image credits and descriptions are given in Appendix A, Table S1.

Table 1. Priority questions for future research, with explanation of the rationale and the implications of understanding each question for predicting and managing the behavioural impacts of invasive plants. The place of each question within my mechanistic framework is shown by the circled numbers in the top panel of Fig. 1.

Question	Rationale	Implications
1. How do behavioural impacts and their ecological consequences scale with invader abundance, extent, and density?	The shape of the relationship between abundance/extent/density and impact influences how impacts will change in magnitude as the invasion progresses, and determines the proportion of the invasive population that must be removed to mitigate these impacts.	Improved prediction of future impacts under different scenarios of invasion. Management can be optimised so that enough of the invader is removed to mitigate behavioural impacts, while minimising financial and opportunity costs associated with unnecessary additional removal efforts.
2. Are certain modes of impact or types of invasive plant more likely to induce certain types of behavioural change?	Predicting behavioural impacts is important for proactive management, but it has not yet been possible to identify commonalities or general patterns in how modes of impact translate to behavioural change. As the literature continues to grow, it may be possible to address this question by meta-analysis or other approaches.	Potential future impacts of recently introduced species can be estimated, and management can be targeted at the most probable and problematic modes of impact.
3. What is the role of native animals' behavioural constraints in the behavioural impacts of invasive plants?	Constraints shape the behavioural response of native animals, and also partly determine which underlying mechanism dominates this response. There may be general rules underlying the role of constraints (*e.g.*, behavioural plasticity may dominate in sink populations because selection is constrained by the immigration of animals from non-invaded habitats), but these are yet to be tested. Alternatively, the role of constraints may turn out to be highly taxon- or guild-specific.	Behavioural impacts and their ecological consequences can be better predicted. Management can be targeted at the specific underlying mechanism.
4. How can we account for environmental context when predicting the behavioural impacts of invasive plants?	The behavioural impacts of invasive plants are highly context-dependent, so, where possible, this context must be accounted for in modelling and other approaches designed to predict these impacts.	Predictions of impacts from newly introduced or emerging invasive species can be tailored to the specific species and habitat involved.
5. What mitigation strategies are effective at reducing the behavioural impacts of invasive plants?	The behavioural impacts of invasive plants can have profound ecological effects. Effective strategies for mitigating these impacts will likely depend on the modes of impact and mechanisms behind the behavioural	Testing and documenting the results of management strategies is vital for informing and improving evidence-based conservation (Sutherland *et al.* 2004).

	change, as well as in different environmental contexts.	
6. How do we identify selected-dependence traps?	Selected-dependence traps can be triggered by well-meaning management efforts, threatening the survival of the species they are intended to protect. A method for identifying these traps before they are triggered would help to prevent this from occurring.	Once identified, traps could be targeted by management efforts aiming to ‘defuse’ them.
7. How can we ‘disarm’ selected-dependence traps?	Freeing the native animal from its dependence on the invasive plant would permit control of the invader without harming the native. Devising and testing methods to achieve this goal is a key topic for future research.	Management practices would be more effective and avoid unintended harm.

Modes of impact – how invasive plants drive behavioural change

When a plant invader becomes established in a habitat, it generates an array of effects that can alter animal behaviour, which I call modes of impact. These can be grouped into two general categories: habitat alteration, and plant-animal communication.

A plant invasion will usually generate multiple modes of impact simultaneously. For example, the dense vegetation of invasive *Rhododendron ponticum* affords wood mice *(Apodemus sylvaticus)* protection against their key predator, the tawny owl *(Strix aluco)*, but also decreases local food availability by preventing the growth of native food plants (Malo *et al.* 2013). Therefore, how *Rhododendron* affects mouse behaviour depends on the interplay between these modes of impact. While animals should behave to maximise their fitness based on the information available to them, this behavioural response is likely to be imperfect – and may even be maladaptive – because animals do not possess perfect knowledge about the environment. This issue is exacerbated by native animal naïveté (Carthey & Banks 2014).

(a) Habitat alteration

Invasive plants can drastically alter the physical structure of environments they invade (Crooks 2002; Asner *et al.* 2008), introducing novel structural elements (Crooks 2002), or altering pre-existing structures by outcompeting or facilitating (Vitousek *et al.* 1987; Oduor *et al.* 2018) native plants and influencing the dynamics of succession (Vitousek *et al.* 1987). Furthermore, effects on fire regimes (Brooks *et al.* 2004) and nutrient cycles (Vilà *et al.* 2011) both drive and are driven by further habitat shifts. Temporal changes in structure also occur. For instance, the invasive shrub *Rhamnus cathartica* has an extended phenology relative to native plants in the community, extending vegetation cover into the Autumn (Bartowitz & Orrock 2016). Synergistic effects between multiple invasive plant species can also cause structural changes that are not observed where either species invades alone (Asner *et al.* 2008).

Plant invasions can also alter the distribution, availability, and quality of resources – typically food, but sometimes water (Le Maitre 2004) or construction material (Heckscher *et al.* 2014). Invasive plants may increase local food availability, usually by providing fruit (Gleditsch & Carlo 2011; Padrón *et al.* 2011; Mokotjomela *et al.* 2013) or nectar (Ghazoul 2004), or else decrease food availability by outcompeting or physically restricting access (Oduor *et al.* 2018) to native food plants. Temporal changes to food availability may occur due to phenological differences between invasive and native plants (Carson *et al.* 2016). Where invasive plants do provide resources, these may not be accessible to all native animals. For example, nectar viscosity can restrict consumption to appropriately adapted species (Willmer 2011). Novel foods may also differ from native foods in their energetic or nutritional content (Mokotjomela *et al.* 2013). Thus, even food-providing invaders can decrease overall food availability, if they replace more accessible or nutritious native food plants. Furthermore, where these foods contain novel compounds, they may alter behaviour directly (Tiedeken *et al.* 2016), or indirectly by affecting physiology or morphology (Witmer 1996; Jones *et al.* 2010; Hudon *et al.* 2013).

Finally, invasive plants affect a variety of other abiotic characteristics which can influence behaviour. These include effects on temperature (Stellatelli *et al.* 2013; Carter *et al.* 2015) and light availability (Crooks 2002; Asner *et al.* 2008) due to shading, alteration of the habitat's chemical properties by leachates (Watling *et al.* 2011; Hickman & Watling 2014; Iglesias-Carrasco *et al.* 2017) or leaf litter (Tuttle *et al.* 2009), changes to soil properties (Kourtev *et al.* 1998; Crooks 2002), and effects on hydrology and oxygen availability in aquatic systems (Crooks 2002). Furthermore, signals and cues emitted by invasive plants, often as volatile chemicals, change the informational background against which native species communicate (Harvey & Fortuna 2012). These signals and cues can, however, affect native animals more directly: through the mode of plant-animal communication.

(b) Plant-animal communication

Information is transmitted from plants to animals both as signals selected to benefit the plant, and as incidental cues which animals detect (Schaefer & Ruxton 2011). Such plant-animal communication is central to key plant-animal interactions, including pollination, frugivory, and herbivory (Schaefer & Ruxton 2011), and is an important path through which invasive plants can affect native animal behaviour (Harvey & Fortuna 2012). These signals and cues can be visual, chemical, structural, and occasionally acoustic (Schaefer & Ruxton 2011; Schöner *et al.* 2016).

As invasive species often share no recent evolutionary history with the native species they encounter, we might expect native species to be naïve towards the signals and cues emitted by the invader (Carthey & Banks 2014). This naïveté is not always absolute, as native animals may have experience with native plants which are functionally similar to the invader, or with previous invaders. Rather, naïveté is likely a continuum of experience ranging from complete unfamiliarity to a degree of familiarity which may allow for a behavioural response similar to that observed with native plants (Banks & Dickman 2007; Carthey & Banks 2014).

Behavioural changes in native animals

(a) Mechanisms and constraints

The modes of impact generated by plant invasion drive animals to alter their behaviour. Animals change their behaviour through three distinct but non-mutually exclusive types of mechanism, which interact with environmental context to determine the behavioural consequences of plant invasion (Fig. 2). First, behaviour changes within an individual's lifetime through behavioural plasticity. Learning processes, including associative, recognition, and social learning (Shettleworth 2010) play a fundamental role in this plasticity. Second, several non-genetic mechanisms operate between generations, including epigenetic effects (Langkilde *et al.* 2017), parental effects (Reddon 2012; Donelan *et al.* 2020), and cultural transmission through inter-generational social learning (Barrett *et al.* 2019; Whiten 2019). These mechanisms are less studied in the context of behavioural impacts of invasive species, although epigenetics in particular has received attention recently (Langkilde *et al.* 2017). Finally, behaviour evolves through natural selection. The selection pressure can be the invader itself (*e.g.,* a poisonous invader selecting for avoidance), or other native or invasive species (*e.g.,* predators selecting for native prey sheltering in invasive plants).

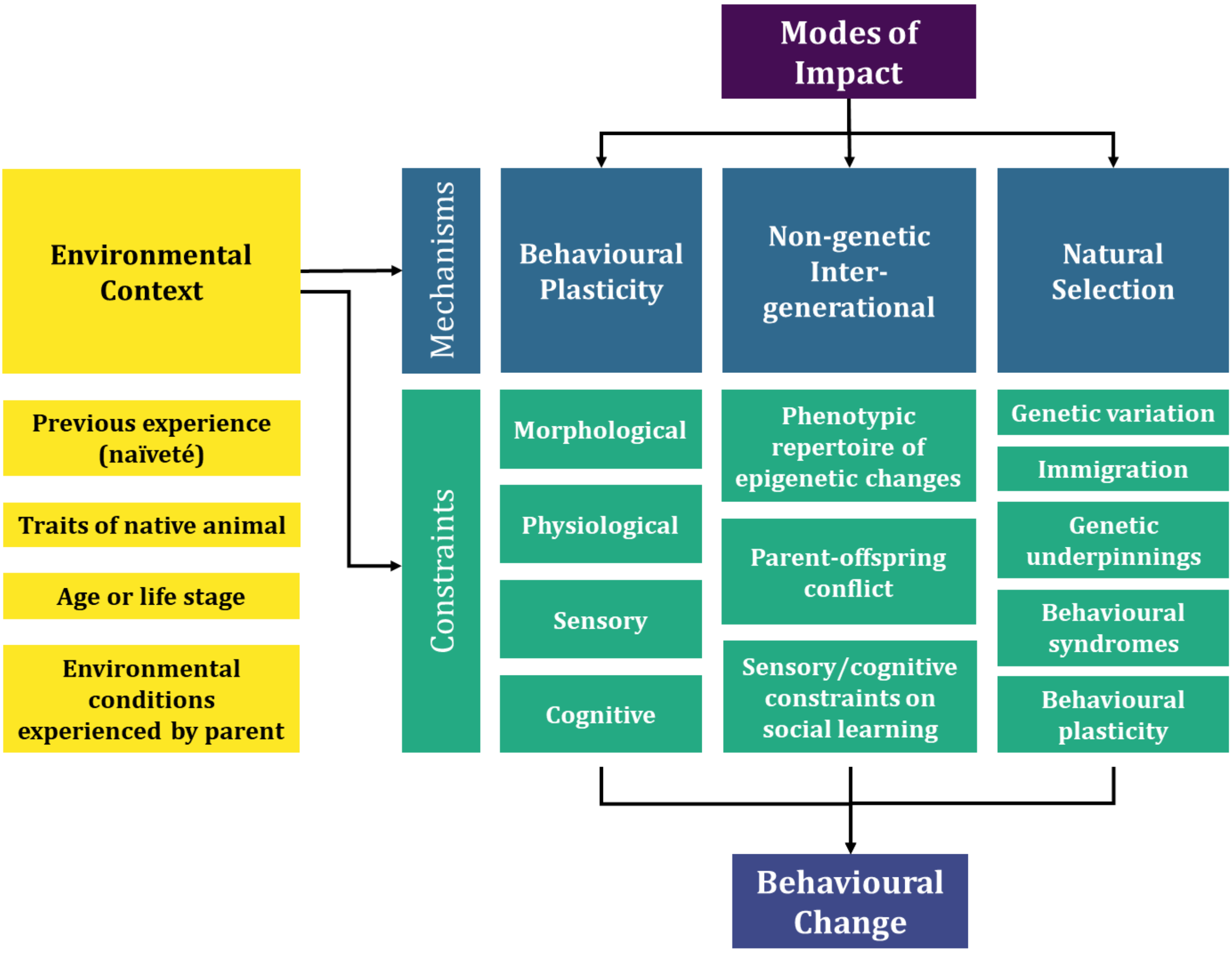

Figure 2. Mechanisms underlying native animals' behavioural responses to plant invasion. Animals respond to the invader's modes of impact by three non-mutually exclusive types of mechanism (upper panels), each of which is subject to a variety of constraints (lower panels). The relative importance of different mechanisms and constraints is influenced by environmental context (examples in left-side panels).

Explicitly considering these mechanisms can inform effective management practices. For instance, where behavioural change occurs through plasticity, the field of animal cognition offers techniques that conservationists can use to reduce maladaptive or ecologically harmful behaviours (Greggor *et al.* 2020), such as habituating native animals to the novel cues of an invader (Greggor *et al.* 2014). However, where behavioural change has arisen through selection these methods will be ineffective, and different management techniques will be required.

Considering mechanisms is also important to avoid management causing unintended harm. For instance, animals which develop preferences for resources provided by an invasive plant may revert to pre-invasion behaviour after removal of the invader if these preferences are learned, but reversion may not be possible if the preferences arose due to natural selection (Singer & Parmesan 2018), causing harm if the invader is removed.

Animal behaviour is not infinitely flexible; multiple constraints influence how modes of impact translate to behavioural change (Fig. 2). Accounting for these constraints could enable improved predictions of the behavioural changes caused by plant invasions (Table 1). The behavioural response of an individual animal is constrained by its physiology, morphology, sensory and cognitive traits. For example, animals may be unable to detect novel cues emitted by an invader, or may misidentify novel cues if their sensory systems are not sufficiently attuned to distinguish them from other cues. These sensory constraints could be accounted for in predictions using approaches such as state-dependent detection theory (Trimmer *et al.* 2017; Ehlman *et al.* 2019). Importantly, constraints can vary throughout an animal's life, so that invasive plants affect behaviour differently at different ages (Langkilde *et al.* 2017). Likewise, inter-generational non-genetic mechanisms are subject to constraints (Fig. 2). Epigenetic change typically involves switches between a limited repertoire of phenotypes (Rando & Verstrepen 2007) which will limit adaptation. Parental effects can be limited by the offspring's learning ability and further restricted by parent-offspring evolutionary conflict, so are generally subtle (Uller *et al.* 2013). Finally, cultural transmission is likely subject to sensory and cognitive constraints which limit how animals obtain and process information from conspecifics.

The effects of selection on behaviour are also constrained (Fig. 2), by factors including generation time, available genetic variation in the population (Futuyma 2010), immigration of animals from non-invaded habitats (Bourne *et al.* 2014) and the genetic underpinnings of adaptive behavioural phenotypes which influence how easily they are selected for (Futuyma

2010). Additionally, genetic correlations between behavioural traits – behavioural syndromes – can further constrain the evolution of behaviour (Sih *et al.* 2004). Finally, behavioural plasticity can itself constrain evolution, because in some circumstances plasticity can shield the genotype from selection (Ghalambor *et al.* 2007).

Accounting for constraints is also useful for determining the underlying mechanisms involved. For instance, in species with a long generation time, populations with low genetic variation, sink populations, or when genes underlying a behaviour are shielded from selection, behavioural plasticity – rather than selection – is expected to dominate behavioural change. Mathematical models could be used to further explore these predictions and generate others, as has been done for other aspects of environmental change (*e.g.,* Botero *et al.* 2015; McNamara *et al.* 2016); modelling and testing these predictions to uncover whether general rules govern how constraints influence the mechanisms of invader-induced behavioural change is an important topic for future research (Table 1).

Finally, a focus on constraints can provide insight into the ecological consequences of behavioural change (Greggor *et al.* 2019b). For example, constraints imposed by behavioural plasticity on the evolution of host preferences may explain why native *Pieris macdunnoughii* butterflies continue to oviposit on invasive *Thlaspi arvense*, even though no larvae laid on *T. arvense* survive to adulthood (Steward & Boggs 2020).

(b) Foraging behaviour

Much of the research into invasive plants' effects on foraging behaviour has focused on animals which are involved in pollination and dispersal mutualisms with plants. From the perspective of these pollinators and frugivores, invasive plants can be viewed as a novel food resource, with the plant providing fruit, nectar, or pollen, advertised by the signals associated with fruit or flowers (Traveset & Richardson 2006; Bartomeus *et al.* 2016; Russo *et al.* 2019). For native animals to access these resources, they must recognise and respond to the plant's signals, and be morphologically and physiologically equipped to handle the resource (Bartomeus *et al.* 2016). Social learning, which is present in key animal mutualist taxa such as social bees (Jones & Agrawal 2017), can facilitate recognition and handling of these novel resources: individuals may learn where to direct existing foraging behaviours by observing conspecifics (Galef 1981) or conspecific cues (Laland & Plotkin 1991) around the novel resource, refine handling behaviours by stealing and consuming partially handled foods (Terkel 1995), or learn entirely new handling behaviours from experienced conspecifics (Palameta & Lefebvre 1985). Additionally, social learning can sometimes occur from observing heterospecific individuals, not just conspecifics (Dawson & Chittka, 2012).

Most effects of invasive plants on the behaviour of frugivores and pollinators occur via resource provision and signals, although some other modes of impact may be involved. First, invasive plants can affect frugivore behaviour by outcompeting native fruiting plants (Oguchi *et al.* 2017). Second, toxic secondary metabolites present in nectar may drive behavioural change. For instance, grayanotoxins in *Rhododendron ponticum* nectar cause solitary bees *(Andrena carantonica)* to exhibit malaise behaviours including excessive grooming and paralysis (Tiedeken *et al.* 2016). However, whether metabolites drive changes in foraging behaviour has not yet been investigated.

Behavioural impacts of invasive plants on pollinators and frugivores are usually examined as changes in visitation behaviour. Native pollinators and frugivores may visit invasive plants more than native plants either because the animals prefer the novel food resource (Sallabanks 1993; Chittka & Schürkens 2001; Mokotjomela *et al.* 2013) or simply because the invader is more abundant (Williams *et al.* 2011). These changes in visitation behaviour vary among native animals and are likely influenced by the degree of native naïveté (King & Sargent 2012). However, predicting effects of invasion on visitation has been challenging. For example, Gibson *et al.* (2012) were unable to predict visitation changes from invasive/native floral trait dissimilarity, perhaps because the traits measured were only related to overall floral display size (Gibson *et al.* 2012). Consideration of other traits, and the dietary breadth and flexibility of native pollinators, may yield better predictions.

Invasive plants can also affect the foraging behaviour of native herbivores. Invasive plants are often well-defended against herbivory, which can deter herbivores from foraging in an area. In North American grasslands, areas invaded by *Euphorbia esula*, which exudes a toxic latex, are avoided by bison *(Bos bison)* and deer *(Odocoileus sp.)* (Trammell & Butler 1995). In *Euphorbia*-invaded pasture, cattle similarly avoid the area (Lym & Kirby 1987). This effect was driven by associative learning (Kronberg *et al.* 1993), which might also underlie the avoidance displayed by bison and deer. Invasive plants can also cause avoidance by affecting access to native food plants, such as by physically restricting access through physical defences or by outcompeting the native plants (Valtonen *et al.* 2006).

Native predators' foraging behaviour can also be affected. Changes in habitat structure can reduce predators' ability to catch prey, causing predators to avoid invaded areas (Carniatto *et al.* 2013; Hardesty-Moore *et al.* 2020), alter their microhabitat use (Valley & Bremigan, 2002), or roam further (Julian *et al.* 2012) and forage faster (Theel & Dibble, 2008) to obtain resources. Conversely, invasive plants can cause a local increase in predators, even when they protect prey from predation (Dutra *et al.* 2011; Wolf *et al.* 2018), perhaps because the reduced chance of a predator catching an individual is outweighed by the increased abundance of prey. More complex interactions involving native predators and prey can also arise. For instance, a native herbivore foraging on an invasive plant can stimulate the plant to release volatiles which attract the herbivore's predators (Harvey & Fortuna 2012).

Invader-induced changes in habitat structure could also drive shifts in the foraging strategy of predators. For instance, seahorses *(Hippocampus erectus)* shift from active to sit-and-wait predation when structural complexity is experimentally increased by adding artificial seagrass (James & Heck 1994). That similar effects driven by invasive plants have not yet been documented (Appendix A, Table S2) might reflect an apparent tendency in studies of invasive plant impacts on foraging behaviour – to focus on space use (*e.g.,* visitation, habitat use) instead of finer-scale behaviours (*e.g.,* handling behaviours, foraging strategies).

(c) Anti-predator behaviour

Most animals are prey for other animals, and invasive plants can affect these species' anti-predator behaviour. First, by changing habitat structure invasive plants can affect the spatial distribution of predation risk, as well as how prey perceive the distribution of this risk – the so-called "landscape of fear" (Laundre *et al.* 2010) – which are key determinants of prey space use (Fortin *et al.* 2005; Laundre *et al.* 2010). Numerous studies demonstrate that where invasions form dense, structurally complex stands, small mammals aggregate in abundance (Braithwaite *et al.* 1989; Edalgo *et al.* 2009; Mattos & Orrock 2010; Dutra *et al.* 2011; Malo *et al.* 2013; Johnson & de León 2015; Sommers & Chesson 2016; Wolf *et al.* 2018; Utz *et al.* 2020; Wei *et al.* 2020), and these effects are at least partly driven by changes in native species' perception of predation risk (Johnson & de León 2015; Utz *et al.* 2020). These refuge effects have also been documented in other taxa, such as fish (Figueiredo *et al.* 2015) and zooplankton (Montiel-Martínez *et al.* 2015). Although less-often documented, the converse has also been observed, where native species perceive patches of invasive vegetation as risky and hence avoid them (Ceradini & Chalfoun 2017b).

By altering habitat structure invasive plants can also influence how predation risk varies over time, and so affect prey activity. Effects can be on a diurnal scale, for instance when invasive plants provide cover for prey during the day (Bogacka-Kapusta & Kapusta 2013) or on moonlit nights (Guiden & Orrock 2019), or they can occur over longer timescales, such as when invasive plants senesce later than native plants and so extend the seasonal pattern of prey activity (Bartowitz & Orrock 2016). So far, these effects and their ecological implications have received relatively little attention.

As with foraging behaviour, the effects of invasive plants on anti-predator behaviours other than space use remain under-explored. Studies on invasive animals have shown that prey can modify their behaviour where formerly effective anti-predator strategies are ineffective against an invasive predator (Langkilde *et al.* 2017); conceivably, invasive plants could induce similar effects. For example, anthropogenic changes in habitat structure can alter vigilance behaviour (Tellería *et al.* 2001), and similar changes could arise from plant invasion.

Sometimes, invasive plants can interfere more directly with native animals’ anti-predator behaviour. *Lonicera maackii* leachates cause tadpoles *(Anaxyrus americanus* and *Lithobates blairi)* to swim to the surface – a behaviour which exposes them to predation risk – likely by interfering with their respiratory physiology (Watling *et al.* 2011). Leachates can also cause *A. americanus* tadpoles to surface even in the presence of predator cues, and slow movement responses to those cues, further increasing predation risk (Hickman & Watling 2014).

(d) Movement

As well as structuring space use through affecting animals’ foraging and anti-predator behaviour, invasive plants can affect movement more directly. Typically, this happens when invader-generated structural changes either facilitate (Cronin & Haynes 2004) or hinder animal movement (Habel *et al.* 2016). Structural changes can also make an area dangerous for an animal to move through, causing animals to avoid invaded areas – the Dungeness crab *(Cancer magister)* avoids patches of invasive cordgrass *(Spartina alterniflora)* because the grass’s rigid structure increases stranding risk (Holsman *et al.* 2010). Furthermore, invasive plants can structure movement patterns by affecting abiotic conditions, such as ground-level temperature (Stellatelli *et al.* 2013; Carter *et al.* 2015) or water clarity (Sammons *et al.* 2003).

(e) Communication and reproductive behaviour

Habitat properties influence the ability of animals to communicate with one another, affecting how signals and cues travel through the environment (Randlkofer *et al.* 2010) and changing the informational background against which these signals and cues are presented (Harvey & Fortuna 2012). Therefore, by altering the habitat or emitting their own signals and cues, invasive plants can interfere with animal communication. However, only one study (Appendix A, Table S2) appears to have demonstrated an invasive plant disrupting communication like this – leachates released by *Eucalyptus globulus* interfere with mate detection in palmate newts *(Lissotriton helveticus*; Iglesias-Carrasco *et al.* 2017).

Invasive plants can also interfere with communication and mating by affecting species' traits. Alteration of avian plumage caused by ingestion of invasive honeysuckle *(Lonicera spp.)* fruits, which contain high levels of carotenoids (Witmer 1996; Jones *et al.* 2010; Hudon *et al.* 2013), can decouple individual quality from colouration and potentially interfere with assortative mating (Jones *et al.* 2010; Rodewald *et al.* 2011).

Invasive plants also affect other aspects of reproductive behaviour. Oviposition is a critical part of the life cycle of many insects, which can be affected through several mechanisms. Invasive plants can emit volatiles that interfere with native insects' ability to locate their native host plants (Harvey & Fortuna 2012), affect habitat structure so that access to native hosts is restricted (Severns 2008), or alter abiotic conditions which influence oviposition (Ellingson & Andersen 2002). The cues emitted by an invader may also drive native insects to switch from ovipositing on native hosts to the invader (Singer *et al.* 1993).

(f) Construction behaviour

Constructed artefacts such as nests, traps, bowers, and tools play an important role in the life history of many species. Animals build using materials either collected from the environment or secreted by themselves (Hansell *et al.* 2014), and in both cases construction behaviour can be affected by plant invasions.

Invasive plants can become important sources of construction material (Heckscher *et al.* 2014), potentially releasing builder populations from limitations imposed by the scarcity of materials. The novel materials provided by invasive plants potentially have quite different properties to native materials, although the consequences of these differences are rarely investigated. In the only study I know to have done so (Appendix A, Table S2), Heckscher *et al*. (2014) found no relationship between use of invasive plant material and the probability of nest failure in veeries *(Catharus fuscescens)*. However, studies on other novel materials incorporated into nests raise some intriguing possibilities. For instance, some birds incorporate cigarette butts into their nests to deter parasites (Suárez-Rodríguez & Garcia 2017). Perhaps, if invasive plants carry unique and potent chemical defences (Cappuccino & Arnason 2006), then plant material could be used similarly. Social learning potentially plays a key role in transmitting preferences for novel materials throughout a population; work on nest-building in zebra finches *(Taeniopygia guttata)* has shown that first-time builders' preference for materials is influenced by social information acquired through observing a familiar conspecific building a nest (Guillette *et al.* 2016), or observing a vacant nest which has been constructed previously (Breen *et al.* 2019). While few studies have examined the role of novel materials in construction behaviour, several studies show how habitat alteration by invasive plants affects where construction – particularly nest-building – occurs. Species build nests in (Schmidt & Whelan 1999; Schmidt *et al.* 2005; Nordby *et al.* 2009; Gleditsch & Carlo 2014; Lambert *et al.* 2016) or around (Salmon *et al.* 1995) invasive plants, but invaders may be avoided where they make vegetation structure or abiotic conditions unsuitable for nest construction (Feare *et al.* 1997; Leslie & Spotila 2001; Ortega *et al.* 2006; Miller & Jordan 2011).

Invasive plants can also affect builders which secrete their own materials by altering habitat structure. For instance, changes in vegetation structure caused by invasive knapweed *(Centaurea maculosa)* allowed web-building *Dictyna* spiders to construct larger webs, improving their foraging efficiency (Pearson 2009). Furthermore, where limits on building-site availability for populations of building species may be removed by the introduction of new substrates associated with invasive plants, such as the siliques (fruit structures) of invasive Garlic mustard (*Alliaria petiolata*) which provide web-building sites for spiders (Smith-Ramesh 2017).

Impacts of behavioural change

The alteration of native animals' behaviour by invasive plants can have profound ecological effects, which range widely in scale (Fig. 1). These impacts can broadly be divided into: 1) species-level impacts on the animal species which had its behaviour altered; 2) impacts on the wider community and ecosystem; 3) impacts on humans; and 4) feedback loops which influence invasive plants. These impacts can also interact with one another, such as when species-level changes alter the interactions of one native species with other species, affecting community-level processes.

A key question from a conservation perspective is how behavioural impacts and their ecological consequences scale with invader abundance, extent and density, as the invader progresses from initial establishment to full-blown invasion (Table 1). The answer determines whether mitigation can be accomplished by reducing the invader's abundance to a lower level, or whether complete eradication is required. Some progress on this question has been made for pollinator behaviour. Two studies have observed a simple scaling effect where low densities of an invader facilitated visitation and increased the seed set of nearby native plants by attracting pollinators, while higher densities negatively affected visitation and seed set as pollinators were co-opted by the invader (Muñoz & Cavieres 2008; Iler & Goodell 2014). However, in other cases scaling can be complex, involving interplay between the scale of invader presence and individual responses of different pollinator taxa (Albrecht *et al.* 2016). Similar studies in non-pollinator systems would help us better understand how behavioural impacts scale.

(a) Species-level impacts

Where an invasive plant causes a native animal species to change its behaviour, the animal can be negatively affected. Behavioural change may pose energetic costs, for example where animals travel longer distances (Julian *et al.* 2012; Lenda *et al.* 2013), spend more time moving over foraging (Valtonen *et al.* 2006), or forage less successfully (Maerz *et al.* 2005). However, these costs are rarely quantified. Behavioural changes can also impact abundance and population dynamics (Cronin & Haynes 2004; Lenda *et al.* 2013). Importantly, these impacts are scale-dependent; even where invasive plants increase animal abundance locally, at a wider scale abundance may still decrease. For example, invasive *Mimosa pigra* protects small mammals from predators but provides little food, so although mammals are abundant beneath

Mimosa their total population will be reduced if *Mimosa* is widespread (Braithwaite *et al.* 1989).

When an environment is altered abruptly, cues which once provided information about the environment can suddenly become uninformative. Animals, constrained by their evolutionary history, respond as if these cues were still reliable, and thus make maladaptive behavioural choices – they are caught in an evolutionary trap (Box 1; Schlaepfer *et al.* 2002). Invasive plants can cause native animals to become evolutionarily trapped when their modes of impact decouple environmental cues from environmental quality (Schlaepfer *et al.* 2005). They can do this by possessing attractive cues unassociated with quality, diminishing the fitness benefits of currently preferred behavioural options without altering the associated cues, or a combination of these (Robertson *et al.* 2013). However, while several studies claim to have revealed an evolutionary trap (Appendix A, Table S2), relatively few provide evidence of preference for the lower-fitness outcome over higher-fitness alternatives (Keeler & Chew 2008; Rodewald *et al* 2011; Augustine & Kingsolver 2018; Steward & Boggs 2020; Sun *et al.* 2020), which is a prerequisite for an evolutionary trap (Robertson *et al.* 2013). One study (Hawlena *et al.* 2010) has also demonstrated an equal-preference trap, where the maladaptive option is not preferred but is treated as equal to higher-fitness alternatives (Robertson *et al.* 2013). The results of other studies, which do not examine preference (Schmidt & Whelan 1999; Borgmann & Rodewald 2004; Rodewald *et al.* 2009; Nordby *et al.* 2009; Harvey *et al.* 2010; Nakajima *et al.* 2013, Davis & Cipollini 2014), are consistent with an evolutionary trap but fall short of being diagnostic. A further issue is that studies to-date have almost exclusively focused on avian nesting and insect oviposition behaviour, making it unclear how widespread invasive-plant-induced evolutionary traps are.

Schlaepfer *et al.* (2005) recognised that the behavioural response of a native to an invader can sometimes result in increased fitness for the native, rather than maladaptation. More recently however, it has emerged that these so-called “evolutionary releases” (Schlaepfer *et al.* 2005) can pose a trap in their own right. In a long-term investigation of the interaction between invasive *Plantago lanceolata* and a population of native *Euphydryas editha* butterflies, Singer and Parmesan (2018) observed a phenomenon they termed the “eco-evolutionary trap”, and which I prefer to call the “selected dependence trap” (Box 1). *E. editha* evolved to become dependent on *P. lanceolata,* eventually leading to its local extinction when conditions changed to make oviposition on the invader unsuitable for larval survival (Box 1). The selected-dependence trap concept essentially formalises the long-standing notion that native species becoming dependent on invaders is a dangerous situation (van Riel *et al.* 2000).

Selected-dependence traps can be sprung by changes in environmental context such as agricultural practices (Singer & Parmesan 2018), but there is also a risk that conservation practitioners could unwittingly spring these traps by removing invasive plants on which native animals now depend (van Riel *et al.* 2000). Endangered species may even depend on invasive plants for their survival, as do the critically endangered Mahoenui giant wētā *(Deinacrida mahoenui)* (Ewers 2008) and the *Ogasawarana* snails (Chiba 2010). If these dependencies are selected and obligate, then the animals will be less able to adapt to removal of the invader, and attempts to translocate the animals to other habitats may be thwarted.

Two key questions emerge for conservation ecologists (Table 1). First, how do we identify selected-dependence traps, so that management of invasive plants does not inadvertently eradicate native animals? The criteria I propose in Box 1 encapsulate the key features of selected-dependence traps, and may provide a starting point for identification. Second, how do we ‘disarm’ the selected-dependence trap, freeing the native from its dependency on the invader? Strategies similar to those used for mitigating evolutionary traps (Greggor *et al.* 2019b; Robertson & Blumstein 2019) – such as reducing physical access to the invader or manipulating environmental cues to reduce preference for the invader relative to alternative options – may avoid selected-dependence traps by preventing preference for the invader from becoming fixed. Introducing native plants with similar cue sets to the invader may also be an option, provided the cues are similar enough that animals dependent on the invader are able to switch to using the native (Gosper & Vivian-Smith 2006). However, work is clearly needed to devise and test management options, particularly for animals which have already evolved dependence on invasive plants.

Box 1: Evolutionary, ecological, and selected-dependence traps

Singer and Parmesan (2018) observed that *Euphydryas editha* offspring laid on *Plantago lanceolata* experienced far higher survival than those laid on the native host plant *Collinsia parviflora.* Because *E. editha* display heritable oviposition preferences (Singer *et al.* 1988) this preference rapidly became fixed so that *Euphydryas* was completely dependent on *Plantago* and refused to oviposit on *Collinsia* (Singer *et al.* 1993, Singer & Parmesan 2018). When grazing cattle were withdrawn from the site, grasses grew to cover the *Plantago* (but not *Collinsia*), cooling the microclimate and rendering conditions unsuitable for larval survival; the *Euphydryas*, now dependent on *Plantago*, were unable to alter their behaviour and were driven to local extinction (Singer & Parmesan 2018). The authors described the phenomenon as an "eco-evolutionary trap", arguing that it is distinct from an evolutionary or ecological trap.

In an evolutionary trap, an organism prefers one behavioural option (*e.g.,* consume a resource, choose a mate) relative to other options available, even though the preferred option results in reduced fitness (Schlaepfer *et al.* 2002; Robertson *et al.* 2013). If the behaviour in question is habitat selection then the phenomenon is called an ecological trap, and therefore ecological traps are a specific type of evolutionary trap (Schlaepfer *et al.* 2002; Robertson *et al.* 2013). Evolutionary traps arise when environmental cues are decoupled from their associated fitness outcomes, so the organism's evolved response drives it to pursue now-maladaptive behaviours even when higher-fitness options are available (Schlaepfer *et al.* 2002). For example, cue similarity between invasive *Alliaria petiolata* and the native plant *Cardamine diphylla* causes late-season flights of *Pieris virginiensis* butterflies to oviposit preferentially on the invader, even though their larvae can only develop on the native (Augustine & Kingsolver 2018).

In contrast to an evolutionary trap, the "eco-evolutionary trap" described by Singer and Parmesan (2018) does not involve organisms preferring maladaptive behavioural options, nor does it involve decoupling of environmental cues from fitness outcomes. Instead, the authors observed the use of a novel resource (oviposition on *Plantago)* conferring increased fitness to a native animal *(Euphydryas)* than that conferred by the alternative (oviposition on *Collinsia).* Here, the environmental cues accurately conveyed information about the higher-quality choice, and the *Euphydryas* responded to those cues adaptively. The trap occurred because *Euphydryas* evolved complete dependence on *Plantago* and therefore on the agricultural practices suppressing grass growth at the site; when these practices ceased, *Euphydras* could not adapt and local extinction ensued (Singer & Parmesan 2018).While it could be said that, in both this case and an evolutionary trap, the animal is “trapped by its evolutionary response” (Schlaepfer *et al.* 2002), an evolutionary trap differs because the response evolved in the context of the organism’s ancestral environment, leading to maladaptation in a novel (*e.g.,* invaded) system, while *Euphydryas’* response evolved in the context of the novel system and was adaptive. Therefore, I agree that the phenomenon described by Singer and Parmesan (2018) cannot be described as an evolutionary (or ecological) trap.

Despite operating by a fundamentally different mechanism to an evolutionary trap, Singer and Parmesan’s paper has been cited as an example of an evolutionary trap (*e.g.,* Robertson & Blumstein 2019). To help prevent confusion in the future, I propose “selected-dependence trap” as a new term to replace “eco-evolutionary trap”. My rationale is as follows: *selected,* to emphasise natural selection as the mechanism underlying the dependency whilst avoiding terms like “evolutionary” that could generate confusion; *dependence,* because the relationship with the novel resource is obligate, meaning the animal cannot switch to other available resources; and *trap* because it evokes negative connotations of both hidden danger and a situation from which it is difficult to escape.

Inspired by the strict criteria for demonstrating the existence of an evolutionary trap (Robertson & Hutto 2006; Robertson *et al.* 2013), I propose that an association with a novel resource must meet the following criteria, all of which were demonstrated in the case of *E. editha* and *P. lanceolata* (Singer *et al.* 1988, 1993; Singer & Parmesan 2018), to be classified as a selected-dependence trap:

1. The novel resource must confer increased fitness (measured by a reasonable measure or index) relative to other available resource options.
2. Individuals should exhibit a preference for the novel resource, relative to other available resource options.
3. This preference must be heritable.
4. If the resource is removed or becomes unsuitable (confers decreased fitness), then individuals with a preference for the resource must not switch to other available resources.

(b) Community and ecosystem-level impacts

The effects of behavioural change can also manifest at larger scales. For instance, changes in space use can alter the patterning and dynamics of ecosystem processes (Johnson & de León 2015; Guiden & Orrock 2017) and affect biodiversity (Lambert *et al.* 2016; Sommers & Chesson 2016). Where invasive plants provide refuges (Orrock *et al.* 2010a,b; Dangremond *et al.* 2010; Pardini *et al.* 2017) or food subsidies (Orrock *et al.* 2015), the local aggregation of seed predators or other consumers can suppress the local abundance of native plants. This is a form of apparent competition between invasive and native plants (Orrock *et al.* 2010a,b) which threatens at least one endangered plant species (Dangremond *et al.* 2010). Modelling suggests that this effect will be greatest when invasive and native plants are closely matched competitors, or when productivity is high (Orrock *et al. 2010b).* Additionally, the effect may be exacerbated where native animals prefer to consume native over invasive seeds (Connolly *et al.* 2014). Behavioural changes could also influence important ecosystem functions such as carbon storage, although currently evidence for this only comes from interactions between invasive plants and invasive animals (Kourtev *et al.* 1999).

Interspecific interactions are not only influenced by interacting species' densities – traits, including behaviour, also influence the per-capita effect of one species on another (Werner & Peacor 2003). Therefore, an invasive plant's effects on a native animal's behaviour can indirectly affect other native species with which the animal interacts – a trait-mediated indirect interaction (Werner & Peacor 2003). As I described above, Pearson (2009, 2010) documented the effects of spotted knapweed *(Centaurea maculosa)* on web-building *Dictyna* spiders in North American grasslands. Knapweed transformed the grassland's physical structure, greatly increasing the availability of substrates for web construction. Consequently, the spiders altered their web-building behaviour to construct larger webs, doubling their per-capita effect on their native *Urophora* prey and driving a decline in *Urophora*'s population (Pearson 2010). Additionally, the release of spiders from constraints once imposed by competition for web sites caused their abundance to explode by 46-74 times, which was not only enough to impact *Urophora's* abundance and fecundity but also the fecundity of *Urophora's* host plant (Pearson 2010). Similarly, invasive *A. petiolata's* effects on web-building spiders in forest understories were strong enough to affect soil phosphorus availability (Smith-Ramesh 2017).

Behavioural changes can disrupt vital mutualisms between native species. Many native plants depend heavily on native pollinator mutualisms, and changes in pollinator visitation behaviour can affect native seed set, with consequences for population dynamics (Traveset & Richardson 2006). There are two potential consequences of changes in pollinators' visitation behaviour: facilitation, where the invader draws more pollinators to the area, increasing native species visitation; and competition, where invasive plants co-opt native pollinators, reducing native visitation (Bjerknes *et al.* 2007; Stout & Tiedeken 2017). Examples exist of both facilitation (Moragues & Traveset 2005; Lopezaraiza–Mikel *et al.* 2007; Bartomeus *et al.* 2008) and competition (Chittka & Schürkens 2001; Brown *et al.* 2002; Moragues & Traveset 2005; Bartomeus *et al.* 2008; Ojija *et al.* 2019) affecting native species, and also other invasive plants (Molina-Montenegro *et al.* 2008; Yang *et al.* 2011). While an early meta-analysis concluded that competition is the more common outcome (Morales & Traveset 2009), a later meta-analysis concluded that this result is probably an artefact of publication bias and certain experimental designs (Charlebois & Sargent 2017). While the outcome probably depends on environmental context (Mitchell *et al.* 2009; Bartomeus *et al.* 2016) and scaling (Muñoz & Cavieres 2008; Iler & Goodell 2014; Albrecht *et al.* 2016), certain mutualisms are likely more vulnerable to disruption than others (Traveset & Richardson 2006). For instance, mutualisms between specialist plants and generalist animals are more likely to be disrupted because the animal responds to a greater range of signals and cues, so is more readily co-opted by the invader (Traveset & Richardson 2006).

(c) Impacts on humans

Invasive plants that alter animal behaviour can have negative consequences for people. Many animals are hosts for disease, and their behaviour plays an important role in the dynamics of emerging infectious diseases (Hoverman & Searle 2016). By affecting behaviour, invasive plants can increase the risk of transmission to humans. For instance, areas with invasive *Lonicera maackii* are often used by white-tailed deer *(Odocoileus virginianus)*, which carry lone star ticks *(Amblyomma americanum)*. Consequently, in invaded areas human exposure to tick-borne ehrlichiosis is increased (Allan *et al.* 2010). Similar cases driven by other invasive plants have been documented for the vectors of malaria, trypanosomiasis, Lyme disease, Hantavirus, West Nile virus, scrub typhus, and spotted fever (Mack & Smith 2001; Gardner *et al.* 2017; Wei *et al.* 2020). Changes to daily activity patterns may also facilitate disease spread by increasing animal encounter rates disease vectors (Guiden & Orrock 2019). Finally, even if plant invasions suppress disease vectors and so reduce transmission, failing to account for the invader’s presence can undermine efforts to predict the spatial distribution of disease risk (Conley *et al.* 2011).

The behavioural impacts of invasive plants can also affect people by intensifying human-wildlife conflict. I found only one example (Appendix A, Table S2), in which several invasive plant species on Mauritius reduce fruit availability by outcompeting native plants, thus promoting the raiding of commercial fruit trees by flying foxes *(Pteropus niger*; Krivek *et al.* 2020). However, behavioural impacts likely drive conflict with other species as well. For instance, large mammalian herbivores’ space use has important implications for human-wildlife conflict (Sitati *et al.* 2003), and can be altered by plant invasions (Rozen-Rechels *et al.* 2017). Furthermore, where invasive plants drive avoidance in both livestock and native herbivores (Lym & Kirby 1987; Trammell & Butler 1995) there may be increased conflict as the two are forced to coexist in ever-smaller areas.

(d) Feedback to plant invasion

Where an invasive plant alters behaviour, the effects can feed back to affect the invader. These feedbacks may be positive, facilitating future invasion. Positive feedbacks can arise from mutualisms between invasive plants and native animals facilitating the invader’s dispersal, reproduction, and establishment in new areas (Milton *et al.* 2007; Bartuszevige & Endress 2008; Brochet *et al.* 2009), or when behavioural changes inhibit native plant species (Sommers & Chesson 2016). An invasive plant species can also facilitate other invasive plants, for instance by attracting native pollinators (Molina-Montenegro *et al.* 2008). Positive feedbacks have been invoked to explain why particular invasions succeed (Callaway *et al.* 2004), and as a possible solution (Schlaepfer *et al.* 2005) to the so-called “paradox of invasion” (Sax & Brown 2000) – that invasive plants are often able to outcompete locally adapted native plants. This is supported by theoretical work (Orrock *et al.* 2010a) which suggests that invasive plants, even those which are weaker competitors than native plants, can nevertheless spread through a feedback loop in which consumers seeking refuge in dense stands of invasive vegetation clear native seeds and vegetation from the surrounding habitat. The invader then spreads to occupy these cleared areas, and the process repeats (Orrock *et al.* 2010a).

Conversely, negative feedback loops are also conceivable, in which future invasion is inhibited by invasive plants’ behavioural effects. For instance, behavioural changes in native animals can indirectly increase the competitive ability of native plants, reducing the future spread of the invader (Smith & Schmitz 2015). Similarly, in some circumstances invader-induced changes in herbivore or seed predator behaviour may inhibit the invader's own recruitment (Orrock *et al.* 2015). As with positive feedbacks, negative feedbacks can also occur between different species of invasive plants (Yang *et al.* 2011).

Environmental context

A key theme emerging from research into the behavioural impacts of invasive plants is the moderating role of environmental context (Fig. 1), a point raised previously by reviews focusing on how invaders affect insect foraging behaviour (Mitchell *et al.* 2009; Harvey & Fortuna 2012; Bartomeus *et al.* 2016). By environmental context, I mean the characteristics of interacting invasive and native species and of the environment in which they interact, including other species, abiotic conditions, and human activities. The prevalence of context-dependence means that accounting for context is important for understanding and predicting the impacts of invasive plants on behaviour (Table 1), and recent research in other aspects of invasion ecology has progressed toward this goal. For instance, a study on invasive *Pinaceae* demonstrated how multiple measures of context can be incorporated into a modelling framework to predict (non-behavioural) impacts (Sapsford *et al.* 2020). Similar approaches could be applied to the behavioural impacts of invasive plants.

Environmental context operates at two stages in my framework (Fig. 1). First, context influences how modes of impact generated by an invader translate to behavioural changes. The characteristics of different animal species can result in different responses; thus, one invasive species often affects multiple native animal species in different ways (Braithwaite *et al.* 1989; Sogge *et al.* 2008; Kapfer *et al.* 2013; Mokotjomela *et al.* 2013; Montiel-Martínez *et al.* 2015; Rozen-Rechels *et al.* 2017; Ranyard *et al.* 2018). Comparative studies considering multiple animal species (Braithwaite *et al.* 1989; Sogge *et al.* 2008; Rozen-Rechels *et al.* 2017; Ranyard *et al.* 2018), multiple invasive plant species, or both (Trammell & Butler 1995) can provide insight into how native and invasive species' traits interact to shape the effects of invasive plants on behaviour, especially when traits are explicitly considered in predictions and analyses (Ceradini & Chalfoun 2017a; Rozen-Rechels *et al.* 2017). For instance, the responses of mammalian herbivores to *Chromolaena odorata* invasion are partly explained by whether the mammals are browsers or grazers, because *C. odorata* mostly affects food availability in the grass layer (Rozen-Rechels *et al.* 2017). The advent of comprehensive, high-quality functional trait data (Gallagher *et al.* 2020) and advances in trait-based models of species interactions (*e.g.,* Pichler *et al.* 2019) provide promising opportunities to improve our understanding of how different animals respond to plant invasion.

Differences between populations of a native species can also influence responses to invasion. For instance, naïveté can explain differences in populations' responses. Palmate newts' *(L. helveticus)* ability to detect conspecific alarm cues is impaired by eucalypt leachates, but only populations from areas where *Eucalyptus* is absent are affected; newts sourced from areas where *Eucalyptus* is present are unaffected (Iglesias-Carrasco *et al.* 2017). These differences may reflect evolutionary adaptations to the invader (Keeler & Chew 2008), or cognitive changes such as habituation to novel cues.

Context can also mean that the behavioural effects of an invasive plant vary among environments, or between times within an environment. This context can take the form of biotic (*i.e.,* other species present in the habitat; Ceradini & Chalfoun 2017b; Cheeseman *et al.* 2018) or abiotic factors (Mattos & Orrock 2010; Dutra *et al.* 2011; Johnson & de León 2015; Sommers & Chesson 2016) which moderate the effects of invaders' modes of impact. For instance, the effect of signals and cues emitted by an invasive plant depends on what signals and cues other species are emitting, and on the sensory properties of the environment (Harvey & Fortuna 2012). Additionally, human activities play an important contextual role. For instance, invasive Australian pines *(Casuarina equisetifolia)* can impede loggerhead turtle *(Caretta caretta)* nesting by affecting beach erosion so that shorelines are steeper (U.S. Congress, Office of Technology Assessment 1993). However, on beaches near towns the pines instead promote nesting by blocking lights that would otherwise illuminate the beach (Salmon *et al.* 1995).

The second role of environmental context in my framework is in influencing the ecological impacts of invader-induced changes in animal behaviour (Fig. 1), as exemplified by the context-dependency of evolutionary traps. First, the animal's characteristics can influence the strength and timing of traps. For example, early and late-season flights of *Pieris virginiensis* butterflies exhibit different oviposition preferences, with late-season females preferring the unsuitable invasive *Alliaria petiolata* while early-season females use both invasive and native hosts equally (Augustine & Kingsolver 2018). Consequently, only late-season females are caught in a severe evolutionary trap (Robertson *et al.* 2013). Second, biotic factors may influence the invader's effect on the native animal's fitness – results reported by Rodewald *et* *al.* (2009), while not diagnostic of an evolutionary trap, suggest the possibility that trap severity can change seasonally due to shifts in predation risk from native predators. Finally, abiotic factors are important, and may lead to emerging traps driven by climate change. Monarch butterflies *(Danaus plexippus)* currently thrive on invasive *Asclepias curassavica*, but fare poorly under experimental simulations of future climatic conditions (Faldyn *et al.* 2018). The monarchs will therefore become evolutionarily trapped if they continue to respond to *Asclepias'* cues as if they indicate a high-quality host.

Conclusion

Plant invasions are a conservation challenge that threaten the integrity of ecosystems worldwide, and one of the ways that they do so is by altering the behaviour of native animals. I have synthesised the disparate literature within a novel mechanistic framework, showing that the behavioural changes wrought by plant invasions, and the resulting ecological consequences, are varied and often profound. Importantly, these changes and consequences are also highly context-dependent. Priorities for future research include understanding how behavioural impacts scale with invasive plant abundance and distribution, and how different modes of impact, environmental context, and behavioural constraints affect the likelihood, magnitude, and type of behavioural impact. Progress in these areas will yield a greater ability to predict how, when, and where an invasion results in behavioural changes, enabling better targeting of management efforts to reverse, mitigate, or prevent those changes. The formation of selected-dependence traps is of particular concern and deserves further study, so that traps can be identified and carefully disarmed, or avoided in the first instance so that the survival of native animal populations and species is not jeopardised by well-meaning management of invasive plants. Tackling the key questions I have identified (Table 1) will require an interdisciplinary approach which brings together invasion ecology with the study of animal behaviour and cognition.

Appendix A: Supplementary tables

Table S1. Image credits and descriptions for Fig. 1. For full references, see reference list in main text.

Image	Credit	Description
Physical structure	Frank Vincentz	Invasive cacti *(Opuntia spp.)*, which form dense, impenetrable stands.
Resources	Matthieu Sontag	Berries of *Lonicera maackii*. In its invasive range, *L. maackii* berries are consumed by native animals (*e.g.*, Rodewald *et al*., 2011).
Abiotic characteristics	Gyrobo	A plant casts shade on the ground. Some reptiles avoid areas where invasive plants cast shade, lowering the ground temperature (Carter *et al.*, 2015; Stellatelli *et al*., 2013).
Signals and cues	Alvesgaspar	Flower of *Oxalis pes-caprae* with visiting hoverfly. In the Balearic Islands *O. pes-caprae* is invasive, and affects the visitation behaviour of native pollinators (Albrecht *et al.*, 2016).
Foraging	Jack Dykinga	An American bison *(Bos bison)* foraging. Foraging bison avoid areas invaded by leafy spurge *(Euphorbia esula)* (Trammell and Butler, 1995).
Anti-predator behaviour	BlueBreezeWiki	A wood mouse *(Apodemus sylvaticus)*, which uses patches of invasive *Rhododendron ponticum* as cover from its predators (Malo *et al*., 2013).
Movement	D. Gordon E. Robertson	A red rock crab *(Cancer productus)* moving on a rocky shore. A congeneric species, *Cancer magister*, avoids patches of invasive cordgrass *(Spartina alterniflora)* which increase the risk of stranding (Holsman *et al*., 2010).
Communication and reproduction	Minette Layne	A pair of cedar waxwings *(Bombycilla cedorum)*, apparently engaged in courtship behaviour. Consumption of ivasive n*Lonicera morrowii* fruits alters waxwing colouration and may interfere with assortative mating (Witmer, 1996).
Construction behaviour	Seney Natural History Association	A veery *(Catharus fuscescens)* nest with eggs. Some veeries incorporate invasive plant material into their nests (Heckscher *et al*., 2014).
Human activity	Phil Catterall	A tractor working in a field. A sudden shift in agricultural practices were the trigger for a selected-dependence which caused the local extinction of a population of *E. editha* (Singer and Parmesan, 2018).

Traits of invader and native	Alvesgaspar	The flowers of *Acacia saligna*, which is invasive in the Cape Floristic Region, S. Africa. Gibson *et al*. (2012) studied whether *A. saligna's* floral traits could predict its impact on visitation behaviour in native pollinators.
Spatial scale	USDA Forest Service	*Mimosa pigra* vegetation. The effects of this invader on mammals depends on spatial scale (Braithwaite *et al.* 1989).
Other native & invasive species	Ragesoss	An eastern cottontail *(Sylvilagus floridanus)*, which is invasive in the Hudson Valley, NY. Native New England cottontails *(S. transitionalis)* use invasive shrubs more often only when the eastern cottontail is present (Cheeseman *et al.*, 2018).
Native naïveté	Luis Miguel Bugallo Sánchez	A palmate newt *(Lissotriton helveticus)*. The newt's behavioural response to leachates exuded by invasive *Eucalyptus globulus* depends on whether the newt is sourced from a population where *Eucalyptus* is present *(Iglesias-Carrasco et al.*, 2017).
Surrounding habitat matrix & environmental variables	Pixabay	A moonlit night. Moonlight influences the space use of small mammals foraging in invaded areas (Johnson and de León, 2015).
Fitness and abundance	Gilles San Martin	A pair of ants *(Myrmica sp.).* Ants in areas invaded by goldenrods *(Solidago sp.)* have to travel further in search of food, negatively affecting their fitness and reducing colony sizes (Lenda *et al.*, 2013).
Evolutionary & selected-dependence traps	Fcb981	An Edith's checkerspot butterfly *(Euphydryas editha)*. A population of *E. editha* became caught in a selected-dependence trap caused by invasive *Plantago lanceolata*, and became locally extinct (Singer and Parmesan, 2018).
Biodiversity	Brett Donald	The Bell Miner *(Manorina melanophrys).* This despotic passerine nests in invasive *Lantata camara*, and causes declines in avian diversity in areas it inhabits (Lambert *et al.*, 2016).
Disrupted mutualisms & processes	Ivar Leidus	A bee *(Bombus sp.)* on purple loosestrife *(Lythrum salicaria)*. *L. salicaria* invasions in Ohio disrupt mutualisms between native pollinators and the native plant *Lythrum alatum* (Brown *et al.*, 2002).
TMII's (trait-mediated indirect interactions)	G. Kirkland	A web-building spider, species unknown. Changes in the web-building behaviour of *Dictyna* spiders caused by spotted knapweed *(Centaurea maculosa)* invasions increased the

		per-capita effect of *Dictyna* on their *Uphora* prey, driving a decline in *Uphora's* population (Pearson, 2010).
Human-wildlife conflict & disease transmission	James Gathanay	A lone star tick *(Amblyomma americanum)*, which carries ehrlichiosis. Changes in the space use of white-tailed deer *(Odocoileus virginianus)* due to honeysuckle *(Lonicera maackii)* invasions increase tick densities and disease transmission in invaded areas (Allan *et al.*, 2010).

Table S2. Results for targeted literature searches used to confirm apparent gaps in the literature. All searches were carried out on the Web of Science core collection database (www.webofknowledge.com). Results were screened manually at title and abstract level to determine relevance. Only primary research articles were included. Searches were conducted most recently on 26th August 2020 except for the search marked (*), which was conducted on 19th December 2020.

Search terms	Number of relevant results	References
TOPIC: ("invasive plant" OR "alien plant" OR "introduced plant" OR "plant invasion" OR "exotic plant" OR "weed" OR "non-native plant" OR "introduced plant") *AND* **TOPIC:** ("evolutionary trap" OR "eco-evolutionary trap" OR "ecological trap")	6	(Keeler & Chew 2008; Rodewald *et al.* 2011; Nakajima *et al.* 2013; Augustine & Kingsolver 2018; Singer & Parmesan 2018; Sun *et al.* 2020)
TOPIC: ("invasive plant" OR "alien plant" OR "introduced plant" OR "plant invasion" OR "exotic plant" OR "weed" OR "non-native plant" OR "introduced plant") *AND* **TOPIC:** ("human-wildlife conflict" OR "human wildlife conflict" OR "human-animal conflict" OR "human animal conflict")	1	(Krivek *et al.* 2020)
TOPIC: ("invasive plant" OR "alien plant" OR "introduced plant" OR "plant invasion" OR "exotic plant" OR "weed" OR "non-native plant" OR "introduced plant") *AND* **TOPIC:** (impact* OR effect* OR alter*) *AND* **TOPIC:** ("communication" OR "animal communication" OR "communication behaviour" OR "mate-finding" OR "mate search*" OR "mate locat*")	1	(Iglesias-Carrasco *et al.* 2017)
TOPIC: ("invasive plant" OR "alien plant" OR "introduced plant" OR "plant invasion" OR "exotic plant" OR "weed" OR "non-native plant" OR "introduced plant") *AND* **TOPIC:** ("construction" OR "construction behaviour" OR "nest-building" OR "plant parts") *AND* **TOPIC:** ("fitness" OR "survival" OR "fecundity" OR "failure" OR "nest failure")	1	(Heckscher *et al.* 2014)
TOPIC: ("invasive plant" OR "alien plant" OR "introduced plant" OR "plant invasion" OR "exotic plant" OR "weed" OR "non-native plant" OR "introduced plant") *AND* **TOPIC:** (impact* OR effect* OR alter*)	0	n/a

AND **TOPIC:** ("predator foraging" OR "mode of predation" OR "foraging mode" OR "hunting mode" OR "hunting strategy" OR "predation strategy")		
(*) TOPIC: ("invasive macrophyte" OR "alien macrophyte" OR "introduced macrophyte" OR "macrophyte invasion" OR "exotic macrophyte" OR "non-native macrophyte" OR "introduced macrophyte") *AND* **TOPIC:** (impact* OR effect* OR alter*) *AND* **TOPIC:** ("behaviour" OR "foraging" OR "refuge" OR "nesting").	4	(Valley & Bremigan 2002; Theel & Dibble 2008; Bogacka-Kapusta & Kapusta 2013; Figueiredo *et al*. 2015)

Chapter 3

Model Selection in Occupancy Models: Inference versus Prediction

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Abstract

Occupancy models are a vital tool for ecologists studying the patterns and drivers of species occurrence, but their use often involves selecting among models with different sets of occupancy and detection covariates. The information-theoretic approach, which employs information criteria such as Akaike's Information Criterion (AIC) is arguably the most popular approach for model selection in ecology and is often used for selecting occupancy models. However, the information-theoretic approach risks selecting models which produce inaccurate parameter estimates due to a phenomenon called collider bias, a type of confounding that can arise when adding explanatory variables to a model. Using simulations, I investigated the consequences of collider bias (using an illustrative example called M-bias) in the occupancy and detection processes of an occupancy model, and explored the implications for model selection using AIC and a common alternative, the Schwarz Criterion (or Bayesian Information Criterion, BIC). I found that when M-bias was present in the occupancy process, AIC and BIC selected models which inaccurately estimated the effect of the focal occupancy covariate, while simultaneously producing more accurate predictions of the site-level occupancy probability than other models in the candidate set. In contrast, M-bias in the detection process did not impact the focal estimate; all models made accurate inferences, while the site-level predictions of the AIC/BIC-best model were slightly more accurate. My results show that information criteria can be used to select occupancy covariates if the sole purpose of the model is prediction, but must be treated with more caution if the purpose is to understand how environmental variables affect occupancy. By contrast, detection covariates can usually be selected using information criteria regardless of the model's purpose. These findings illustrate the importance of distinguishing between the tasks of parameter inference and prediction in ecological modelling. Furthermore, my results underline concerns about the use of information criteria to compare different biological hypotheses in observational studies.

Introduction

The patterns and drivers of species occurrence are of fundamental interest to ecologists. Predicting where species occur enables ecologists to tackle key problems such as understanding the spread of invasive species (Gormley *et al.* 2011), assessing the distributions of key species within protected areas (Midlane *et al.* 2014), and estimating the range size of populations and species to evaluate their extinction risk (Breiner & Bergamini 2018) and recovery (Akçakaya *et al.* 2018). Understanding the drivers of occurrence is also important; interventions to mitigate the factors which threaten species must be informed by the diagnosis of those factors (Caughley 1994). Many studies have aimed to infer how occurrence is driven by factors including forest degradation (Zimbres *et al.* 2018), wildfires (Hossack *et al.* 2013), and anthropogenic noise pollution (Chen & Koprowski 2015).

A key challenge in studying species occurrence is that experimental manipulations of ecological systems may be physically impossible, logistically unfeasible, or unethical; consequently, ecologists are often constrained to the use of observational data. One approach to this challenge is to use a model which relates observed variation in species occurrence to one or more environmental covariates. The model can then be used to predict, or to explain (Shmueli 2010): we can predict species occurrence at new sites, or examine the effect of each covariate to explain the drivers of occurrence. Occupancy models are often used because they deal with imperfect detection (MacKenzie *et al.* 2002). They do so by modelling the probability that a species occupying the site is detected, often including environmental covariates to explain variation in detectability among sites (MacKenzie *et al.* 2002). Occupancy models therefore contain one set of covariates for occupancy probability, and a second set for detection probability; the challenge is to select suitable sets of covariates to include in the model. This challenge can be framed as a problem of model selection (Robins & Greenland 1986; Forster 2000; Burnham & Anderson 2004; Johnson & Omland 2004).

The information-theoretic approach to model selection

The information-theoretic approach (Anderson *et al.* 2000; Burnham & Anderson 2001, 2004; Lukacs *et al.* 2007; Burnham *et al.* 2011) compares models in terms of their relative Kullback-Leibler (KL) divergence – the relative distance between each model and “full reality”, in units of information entropy (Forster 2000; Burnham & Anderson 2001; McElreath 2021, p. 207). Information criteria, of which Akaike’s information criterion (AIC; Akaike 1973) is the most commonly used, estimate the relative KL divergence of each model using the sample data (McElreath 2021, p. 219). AIC is calculated by taking the in-sample deviance (a measure of how well the model fits the data), and adding an overfitting penalty proportional to the number of parameters in the model (Akaike 1973; Burnham *et al.* 2011). Consequently, AIC favours parsimonious models which balance underfitting and overfitting, with the aim of producing better out-of-sample predictions (McElreath 2021, p. 192).

Causal inference

An alternative approach to model selection which has gained recent traction in ecology and evolution (*e.g.,* Laubach *et al.* 2021; Arif & MacNeil 2022) is causal inference. Causal inference is concerned with predicting the consequences of intervening in a system, as well as inferring counterfactual outcomes – events which might have happened, under hypothetical unrealised conditions (Pearl *et al.* 2016, p. 89). Importantly, causal inference is not about ‘inferring causation from correlation’ – conclusions about causality cannot be made from the data alone, but require causal assumptions about the process which generated the data (Pearl *et al.* 2016, p. 5). To illustrate the key concepts and terminology of the causal inference approach I will discuss a hypothetical example, in which our goal is to infer how the density of an invasive plant affects the occupancy of a native animal (Fig. 1).

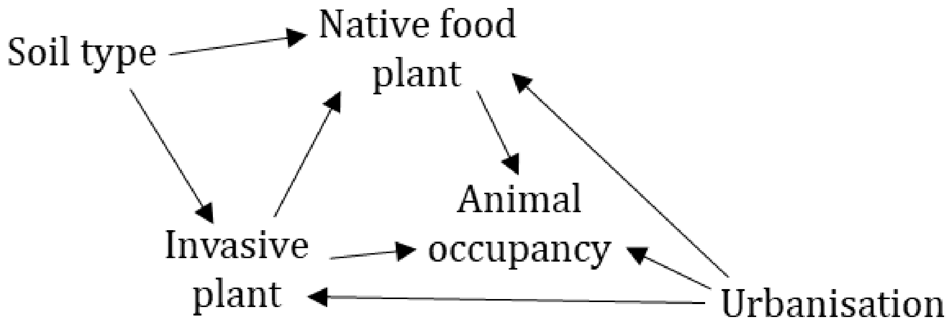


Figure 1. Directed acyclic graph for a hypothetical example in which we are interested in estimating the direct effect of the density of an invasive plant on animal occupancy.

In the causal inference approach, the first step is to employ subject expertise and the literature to identify variables which could be important in the system. This step closely resembles the “hard thinking” which is an essential part of the information-theoretic approach (Burnham *et* *al.*, 2011). In our hypothetical example, we know of a native food plant which is regularly consumed by the animal species, and may therefore influence the animal's occupancy. Furthermore, there is evidence to suggest that the invasive plant tends to outcompete the native food plant, particularly on certain soil types. Finally, as our hypothetical study is conducted along an urban-rural gradient, the degree of urbanisation is likely to be important.

The next step is to make assumptions about how these variables might be related to one another – these are known as "causal assumptions" (Pearl *et al.* 2016, p. 5). A key principle of causal inference is that these assumptions should be communicated clearly so that they are open to scrutiny, debate, sensitivity analysis, and verification (Pearl 1995). Consequently, it is common to express causal assumptions graphically, usually as a directed acyclic graph (DAG; Pearl 1995). In a DAG, variables are represented as nodes. The edges (arrows) linking each node represent the assumed mechanistic links between the variables (Pearl 1995; Greenland *et al.* 1999). The sequence of edges linking one variable to another, regardless of which direction these edges are pointing in, is called a path (Pearl 1995). In our example (Fig. 1), we have assumed that the invasive plant, the native food plant, and urbanisation all exert direct influences on the animal's occupancy. We have also assumed that the invasive plant affects the density of the native food plant through competition. Furthermore, we have assumed that urbanisation also influences the densities of both the invasive and native plants. Finally, we have assumed that soil type does not influence occupancy directly, but that it does affect the densities of both the invasive and native plants.

Once we have specified a DAG, we must identify which effects we are interested in estimating. In our example, we could estimate the direct effect (*invasive plant → animal occupancy*) or the total effect (*invasive plant → animal occupancy* and *invasive plant → native food plant → animal occupancy*) of the invasive plant; in our example, the focal effect will be the direct effect. Once we have decided on a focal effect, we can analyse the DAG directly to identify a set of variables to condition on (*i.e.,* include as covariates) which will allow us to estimate the effect. One strategy is to condition on the variables which satisfy the 'back-door criterion', in which the aim is to 'close all back-door paths' linking the focal explanatory and response variables (Pearl 1995). A back-door path is defined as any path which has an arrow entering the focal explanatory variable (Pearl 1995). Our example contains four back-door paths: 1) *invasive plant ← soil type → native food plant → animal occupancy*; 2) *invasive plant ← soil type → native food plant ← urbanisation → animal occupancy*; 3) *invasive plant ←*

urbanisation → animal occupancy; 4) *invasive plant ← urbanisation → native food plant → animal occupancy*.

Whether a path is open or closed depends on the direction in which arrows along the path are pointing. Paths which are a "fork" (*e.g.*, X ← Z → Y) or "pipe" (*e.g.*, X → Z → Y) are open by default, and conditioning on the middle variable (Z) closes them (Greenland 2003; Pearl *et al.* 2016, p. 46; McElreath 2021, p. 184-185). In contrast, paths which are a collider (*e.g.*, X → Z ← Y) are closed by default, and conditioning on the middle variable (Z) opens the path (Greenland *et al.* 1999; Greenland 2003; Pearl *et al.* 2016, p. 46; McElreath 2021, p. 185). A path with more than three variables only needs to be closed in one place to be closed overall (*e.g.,* X ← W → Z ← Y is closed by the collider at Z).

In our example, the back-door paths 1 and 2 are closed by default because *native food plant* is a collider. However, as we are interested in the direct effect *invasive plant → animal occupancy* we need to close the indirect path, *invasive plant → native food plant → animal occupancy*, by conditioning on *native food plant*. This opens paths 1 and 2, but we can close both paths again by conditioning on either *soil type* or *urbanisation*. If we condition on *urbanisation*, then doing so also closes paths 3 and 4, meaning that all four back-door paths will be closed. Consequently, we can use the model: *animal occupancy* ~ *invasive plant* + *native food plant* + *urbanisation* because it closes all of the back-door paths, satisfying the back-door criterion. We could also condition on *soil type*, but doing so is not required to estimate the direct effect. As DAG-based approaches are non-parametric in the sense that the forms of the functions represented by edges do not have to be specified (Pearl 1995; Greenland *et al.* 1999), we would also be free to incorporate linear interactions between these covariates, or model their effects as nonlinear functions.

Finally, we can explore the consequences of changing the assumptions embodied in our DAG, to see whether our inferences hold under different sets of assumptions. For instance, we could ask "what if urbanisation does not affect the density of the invasive plant?", remove the arrow *urbanisation → invasive plant,* and re-analyse the DAG. Doing so, we see that our model still satisfies the back-door criterion; our conclusions are robust to altering this assumption. We can also modify the DAG to answer questions such as "what if there was an unmeasured confounding variable affecting the densities of both the invasive and native plants?". By adding a new variable *invasive plant ← unmeasured variable → native food plant* and re-analysing the DAG, we can see again that the same model structure is supported because it satisfies the back-door criterion, and thus our conclusions still hold. Where a modified DAG supports a different model structure, we can run the new model and compare the effect estimates with those of the original model.

Collider bias and the information-theoretic approach

Proponents of the information-theoretic approach have argued that each model in the candidate set should represent a different biological hypothesis, and that the models' relative AIC scores indicate the strength of evidence for each hypothesis (Burnham *et al.* 2011). However, insights from causal inference reveal a potential problem: collider bias. Collider bias arises when back-door paths are opened due to conditioning on collider variables (Greenland 2003), and is a form of included-variable bias or "bad control" (Cinelli *et al.* 2022). This is in contrast to the classical notion of confounding (Fig. 2A), which is a form of omitted variable bias (Clarke 2005). As collider covariates and classical confounds exhibit a similar degree of correlation to the focal explanatory variable (Fig. 2A), and these correlations may be masked or otherwise distorted by the action of other variables or non-linear relationships between the covariates, it is not possible to avoid collider bias by checking the explanatory variables for multicollinearity.

As AIC and other information criteria select models based on their expected predictive performance, they are vulnerable to collider bias: including a collider covariate tends to improve a model's AIC score, while simultaneously resulting in an estimated effect which is far from the true value (Fig. 2A-C; Luque-Fernandez *et al.* 2019). Consequently, recent studies have argued that it is essential to consider whether the purpose of a model is inference (*i.e.*, explanation) or prediction when deciding on a model selection strategy (*e.g.*, Laubach *et al.* 2021; Arif & MacNeil 2022). However, the implications for models like occupancy models, which contain multiple sub-models, are unclear.

To address this topic, I investigated the consequences of a form of collider bias (using an illustrative example known as "M-bias"; Greenland 2003; Cinelli *et al.* 2022) in an occupancy modelling framework, and explored the implications for model selection using the information-theoretic approach (using AIC). I also examined the performance of a common alternative to AIC, the Schwarz criterion (or Bayesian Information Criterion, BIC; Schwarz 1978). BIC is built upon different philosophical foundations to AIC, and is not based upon information theory (Johnson & Omland 2004); some authors have suggested BIC can be used for selecting the "true" model from the candidate set (Aho *et al.* 2014). In my simulation-based approach, I generated datasets where M-bias was present in the occupancy process, the detection process, or both. I then fitted occupancy models with different sets of covariates to these datasets, and evaluated them on the accuracy of their parameter inferences, the accuracy of their site-level occupancy predictions, and their level of support from AIC and BIC.

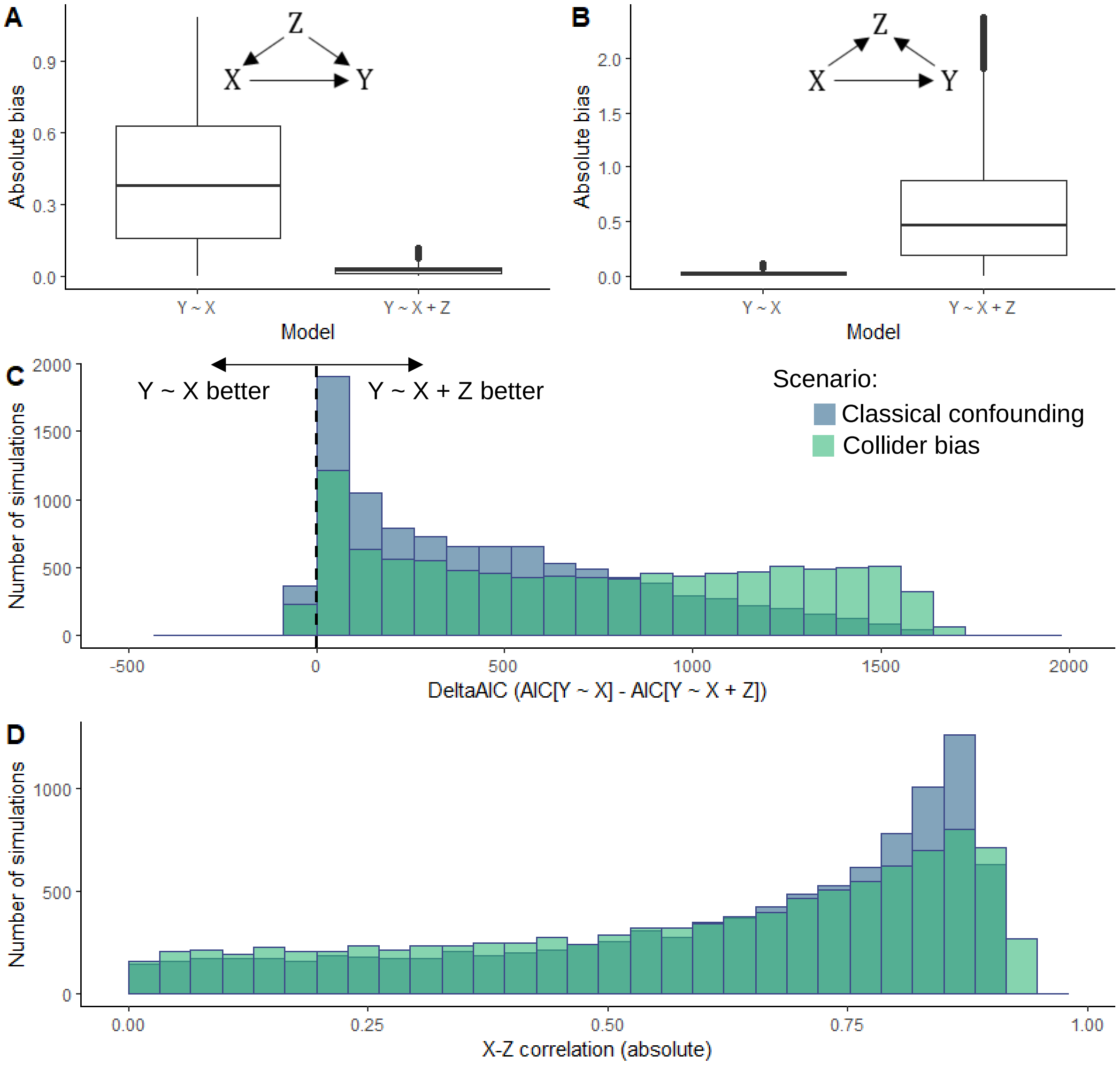


Figure 2. Luque-Fernandez *et al.* (2019) presented simulations illustrating classical confounding and collider bias in a linear model. I extended their example by conducting 10000 iterations for each example, using effect sizes drawn from a uniform distribution between -2 and 2. In classical confounding **(A)**, including the variable Z reduces the absolute bias when estimating the effect of X on Y. Conversely, in the collider example **(B)**, including Z increases the absolute bias. However, in both cases Akaike's Information Criterion (AIC) favours the model which includes Z **(C)**, illustrating that AIC does not always favour models which produce accurate parameter estimates. Furthermore, the absolute correlation between X and Z is similar in both scenarios **(D)**, meaning that checking for multicollinearity cannot reliably help to select the model which estimates β_{XY} more accurately, and that adding highly collinear explanatory variables can sometimes improve inferential accuracy. Code to reproduce the simulations is available at: https://doi.org/10.5281/zenodo.7043335

Methods

M-bias as an illustrative example

M-bias is a common illustrative example in the causal inference literature (*e.g.* Greenland 2003; Cinelli *et al.* 2022), in which an "M"-shaped back-door path (*e.g.*, Fig. 3A, left panel) is opened by conditioning on the collider variable (D in Fig. 3A), confounding the estimate of the focal effect ($X \rightarrow \psi$ in Fig. 3A). When the back-door path contains latent (unobserved) variables (A and C in Fig. 3A), it is impossible to condition on them to close the path because they are unobserved, meaning the correct approach is to not condition on the collider.

Simulation study

To explore the effects of M-bias in both the occupancy and detection components of an occupancy model, I simulated three different scenarios (Fig. 3) in which the focal effect was the effect of variable X on occupancy probability (ψ). In the first scenario (Fig. 3A), ψ was part of an M-graph while the detection probability (p) was fixed at 0.5. In the second scenario (Fig. 3B), ψ depended only on X, and p was now part of an M-graph. In the final scenario (Fig. 3C), both the occupancy and detection probabilities were part of M-graphs.

All three simulations followed the same process: **1)** generate a dataset with known parameter values, using the relationships between variables embodied in the relevant DAGs (Fig. 3); **2)** fit a number of occupancy models to the dataset (Fig. 3); **3)** evaluate each model's accuracy in parameter estimation and prediction; **4)** evaluate each model's quality under the information-theoretic framework. Each simulation was repeated 1000 times. I conducted my simulations in R (v 4.0.5; R Core Team, 2021), and provide code to reproduce my simulations and analyses at: https://doi.org/10.5281/zenodo.7043335

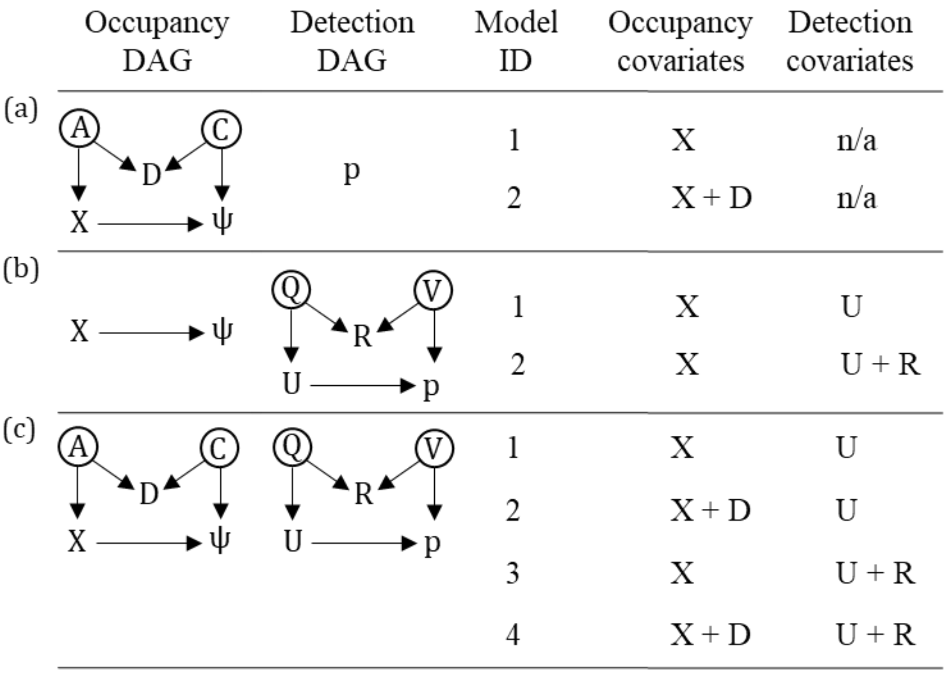


Figure 3. Data generating processes and model structures for the three scenarios: **a)** M-bias in the occupancy process, **b)** M-bias in the detection process, **c)** M-bias in both the occupancy and detection processes. Data-generating processes are represented as directed acyclic graphs (DAGs). ψ is the occupancy probability, p is the detection probability, X *is* the focal explanatory variable, and A, C, D, Q, U, R and V represent other explanatory variables. Circled variables are latent. All models included intercept terms for occupancy and detection.

1) Generating a dataset

Data were simulated for 3000 sites with two surveys each. The number of sites was deliberately high to ensure that any inaccuracy was not primarily driven by an underpowered design. Repeating the simulations with 40 simulated surveys yielded qualitatively similar results (Appendix A: Figs. S7-S9).

To generate the data, I first drew effect sizes for each arrow in the DAG from a uniform distribution (min = -1, max = 1). Values for explanatory variables with no ingoing arrows on the DAG were then drawn from a normal distribution (mean = 0, sd = 1). I then generated values for the other explanatory variables from the appropriate variables and effect sizes (*i.e.*, those from ingoing arrows on the DAG; Fig. 3), plus a “disturbance term” (*sensu* Pearl 1995) drawn from a normal distribution (mean = 0, sd = 0.025). I then calculated the log-odds of occupancy and detection as a linear combination of the effect sizes and explanatory variables with ingoing arrows on the DAG (Fig. 3), and took the inverse-logit to obtain the probability. The true occupancy state of each site was then simulated as a Bernoulli trial with probability of success equal to the occupancy probability. Finally, detection histories for each site were generated as a sequence of Bernoulli trials, with probability of success equal to the true occupancy state multiplied by the detection probability.

2) Fitting models

Occupancy models were fitted to each dataset using the *occu* function in the R package *unmarked* (v.1.0.0; Fiske & Chandler, 2011), which implements the single-season occupancy model developed by MacKenzie *et al.* (2002). The models used the logit link function. I fitted models with various combinations of observed variables (*i.e.*, excluding latent variables) for each scenario (Fig. 3).

3) Evaluating model performance

In each scenario, all models were evaluated on the accuracy of their parameter inferences and predictions. To quantify how accurately each model estimated the effect of covariate X on the occupancy probability ψ, I calculated the bias and absolute bias:

$$Bias = \hat{\beta}_{X\psi} - \beta_{X\psi}$$

$$Absolute\ Bias = \left|\hat{\beta}_{X\psi} - \beta_{X\psi}\right|$$

where $\hat{\beta}_{X\psi}$ and $\beta_{X\psi}$ are the estimated and true effects of X on ψ, respectively. Additionally, checked whether the true value, $\beta_{X\psi}$, was found within the 95% confidence interval surrounding the $\hat{\beta}_{X\psi}$ estimate, and checked whether the sign (positive or negative) of $\hat{\beta}_{X\psi}$ was the same as that of $\beta_{X\psi}$.

To evaluate each model's predictions, I used the *predict* function in R predict the occupancy probability value for each site in two datasets. I first made predictions for the data to which the model was fitted, to examine how the model retrodicted the sample. I then examined the model's performance in out-of-sample prediction by making predictions for a new dataset (also 3000 sites), which was generated using the same true parameter values as the original dataset. To assess the accuracy of the model retrodictions and predictions, I calculated the mean absolute error:

$$Mean\ absolute\ error = \frac{1}{n}\sum_{i=1}^{n}\left|\hat{\psi}_i - \psi\right|$$

where $\hat{\psi}_i$ and ψ_i are the estimated and true occupancy probabilities for site *i*, respectively, and n is the number of sites. Additionally, I calculated the proportion of sites for which the true occupancy probability was within the prediction's 95% confidence interval.

4) Evaluating models under the information-theoretic framework

To examine the degree of support for each model under the information-theoretic framework I obtained the AIC value for each model from the model's summary table. Proponents of the information-theoretic approach have advocated for multimodel inference (*e.g.*, Burnham & Anderson 2004), in which inferences are made using the entire candidate set of models, each weighted using Akaike weights derived from AIC. I calculated Akaike weights (w) for each model m as:

$$w_m = \frac{\exp\left(-0.5 \times \Delta AIC_m\right)}{\sum_{r=1}^{R} \exp\left(-0.5 \times \Delta AIC_r\right)}$$

where ΔAIC_m is the difference between the AIC of model m and lowest AIC value for the set of models in the scenario, and R is the number of models in the scenario.

I also considered BIC (Schwarz 1978) as an alternative to AIC. I calculated BIC and BIC weights for each model using the R package *AICcmodavg* (Mazerolle, 2020).

Results

Scenario 1: M-bias in the occupancy process

When M-bias was present in the occupancy process, model 1 ($\psi \sim X$) estimated the true effect of X on ψ much more accurately than model 2 ($\psi \sim X + D$) (Fig. 4A,B, Appendix A: Table S1). However, comparing the models' predictive accuracy showed the opposite picture; model 1 generally produced worse predictions than model 2 (Fig. 5A,B, Appendix A: Table S1), and similar results were observed for retrodictive accuracy (Appendix A: Fig. S1). AIC and BIC both showed clear support for model 2 in the majority of simulations (Fig. 6A,B); in 80.4% of simulations model 2 received an Akaike weight of >0.99, and in 52.2% of simulations it received the entire weight (Fig. 6B). The few simulations in which model 1 received more weight were mostly those in which $\beta_{C\psi}$ was small (Appendix A: Fig. S2). A similar pattern of results was observed for BIC (Appendix A: Fig. S2), although when BIC assigned weight to model 1 it generally assigned more weight than AIC (Fig. 6A).

Scenario 2: M-bias in the detection process

When M-Bias was present in the detection process, both models 1 ($\psi \sim X, p \sim U$) and 2 ($\psi \sim X, p \sim U + R$) accurately estimated the effect of X on ψ (Fig. 4C,D, Appendix A: Table S1). Both models also made accurate predictions, although those of model 2 were more accurate (Fig. 5C,D, Appendix A: Table S1). Similar results were observed for retrodictive accuracy (Appendix A: Fig. S1C,D). Both AIC and BIC assigned more weight to model 2 in most simulations (Fig. 6C,D).

Scenario 3: M-bias in the occupancy and detection processes

When M-Bias was present in both the occupancy and detection processes, models 1 ($\psi \sim X, p \sim U$) and 3 ($\psi \sim X, P \sim U + R$) estimated the effect of X on ψ much more accurately than models 2 ($\psi \sim X + D, P \sim U$) and 4 ($\psi \sim X + D, P \sim U + R$) (Fig. 4E-H, Appendix A: Table S1). In general, the 95% confidence interval around the estimate in models 2 and 4 only contained the true value when β_{AD} and $\beta_{C\psi}$ (and to a lesser extent β_{AX}) were relatively small (Appendix A: Figs. S4,5). In contrast, models 2 and 4 made more accurate predictions than models 1 and 3 (Fig. 5E-H, Appendix A: Table S1), and similar results were obtained for retrodictive accuracy

(Appendix A: Fig. S1E-H). Both AIC and BIC showed clear support for model 4 in the majority of simulations (Fig. 6H); the model received an Akaike weight of >0.99 in 63.0% of the simulations. While model 3 did occasionally receive weight, this mostly occurred when $\beta_{C\psi}$ was small (Appendix A: Fig. S6) and it still never received the entire weight (Fig. 6G). BIC weights were similar to the Akaike weights, although BIC assigned more weight to model 3 in some simulations (Fig.4G), again generally when $\beta_{C\psi}$ was small (Appendix A: Fig. S6).

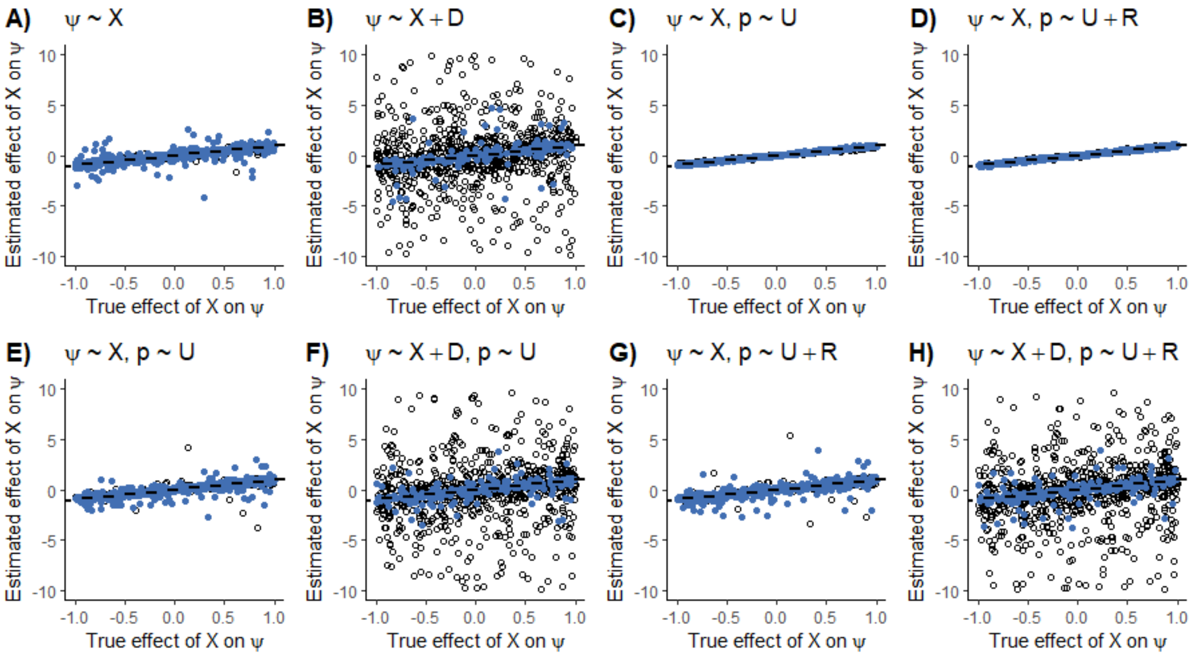


Figure 4. True versus estimated effect of *X* on occupancy probability (ψ), for the following occupancy models: **A)** scenario 1, model 1; **B)** scenario 1, model 2; **C)** scenario 2, model 1; **D)** scenario 2, model 2; **E)** scenario 3, model 1; **F)** scenario 3, model 2; **G)** scenario 3, model 3; **H)** scenario 4, model 4. Each point represents the result from one simulation, with 1000 simulations in total. The y-axis is truncated at -10 and 10; plots B, F, G and H omit 34, 33, 1 and 45 points respectively which lay outside this range. Blue points indicate that the true value was contained within the estimate's 95% confidence interval, while unfilled circles indicate that the true value was not contained within the interval. The dashed black line indicates equality between the true and estimated effect. Each model's covariates for ψ and the detection probability (p) are shown above their respective plot.

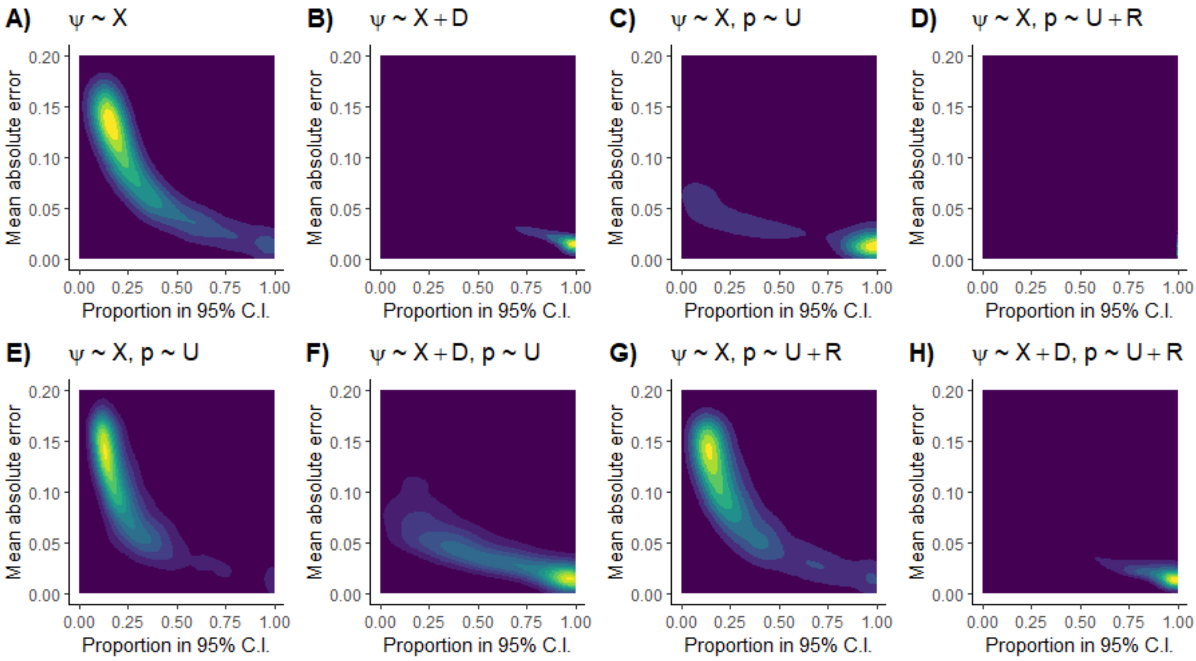


Figure 5. Kernel density estimate contours showing two measures of predictive accuracy when predicting site-level occupancy probability (*ψ*), for 1000 simulations. The x-axis shows the proportion of sites (out of 3000) for which the 95% confidence interval around the model's prediction contained the true occupancy probability. The y-axis shows the mean absolute error. Thus, the bottom right of each plot indicates higher predictive accuracy, while the top left indicates lower predictive accuracy. The density of simulations is shown by the contours, with lighter colours indicating a higher density of simulations. Results are displayed for the following occupancy models: **A)** scenario 1, model 1; **B)** scenario 1, model 2; **C)** scenario 2, model 1; **D)** scenario 2, model 2; **E)** scenario 3, model 1; **F)** scenario 3, model 2; **G)** scenario 3, model 3; **H)** scenario 4, model 4. Each model's covariates for *ψ* and the detection probability (*p*) are shown above their respective plot.

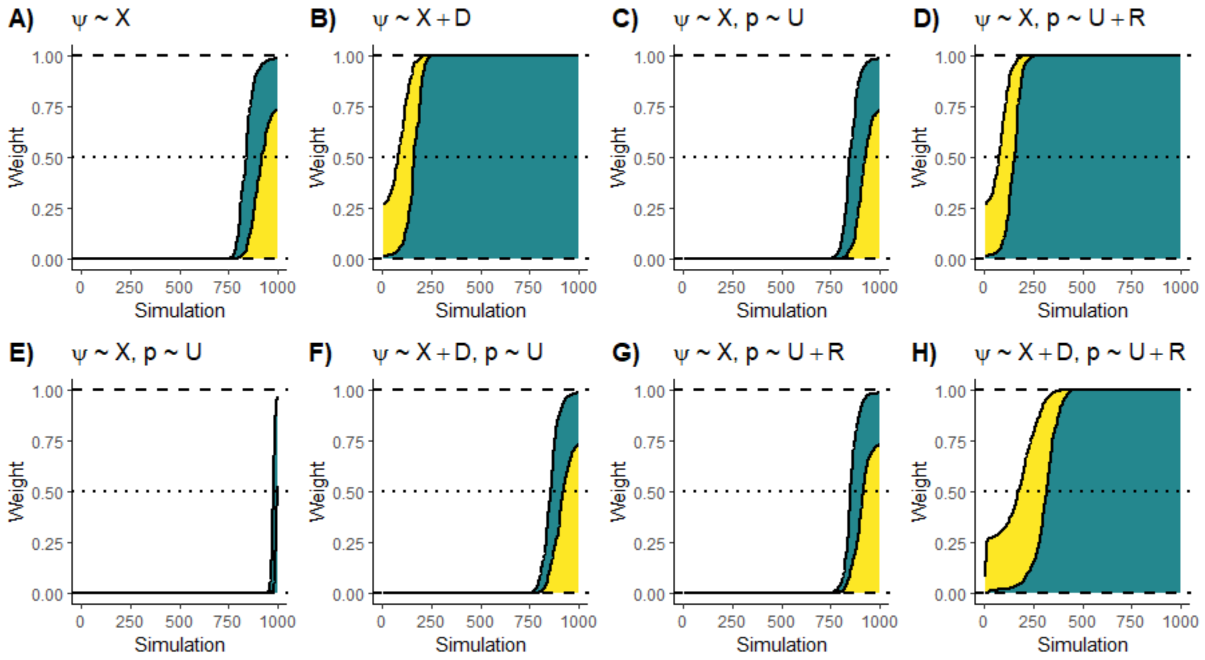


Figure 6. Akaike weight (yellow area) and BIC weight (blue area) for 1000 simulations of eight occupancy models. Simulations are shown ranked by weight, with higher Akaike and BIC weights shown on the right. The panels display: **A)** scenario 1, model 1; **B)** scenario 1, model 2; **C)** scenario 2, model 1; **D)** scenario 2, model 2; **E)** scenario 3, model 1; **F)** scenario 3, model 2; **G)** scenario 3, model 3; **H)** scenario 4, model 4. Each model's covariates for the occupancy probability (*ψ*) and the detection probability (*p*) are shown above their respective plot. Dashed horizontal lines are shown for weights of 0, 0.5, and 1.

Discussion

I investigated the consequences of M-bias (a specific form of collider bias) for occupancy modelling, and explored the implications for model selection using AIC and BIC. In my simulations, I observed that when M-bias was present in the occupancy process, AIC and BIC favoured a model which produced a highly inaccurate estimate of the focal effect but produced more accurate predictions and retrodictions of the site-level occupancy probability. This reflects the fact that AIC and BIC aim to select models which produce better out-of-sample predictions (McElreath 2021, p. 192). In contrast, M-bias in the detection process did not result in inaccurate estimates of the focal effect. However, the AIC/BIC-best models made better predictions and retrodictions. I observed the same results when M-bias was present in both the occupancy and detection processes: the model favoured by AIC and BIC produced inaccurate inferences but more accurate predictions, while models made similarly accurate inferences regardless of M-bias in the detection process. These results have important implications for model selection in occupancy models, as well as for how the information-theoretic approach is applied in ecological modelling more generally.

Information criteria select models which produce poor parameter inferences, but good predictions

When M-bias was present in the occupancy process, the model which received the greatest support from AIC and BIC produced highly inaccurate estimates of the effect of the variable of interest *(X)* on the occupancy probability (ψ). The models that received the majority of the AIC and BIC weight were only able to estimate the direction of the focal effect correctly in 65.8% of cases at best – little better than the accuracy we would expect from guessing. Such biased estimates are not informative about the drivers underlying the observed pattern, nor do they accurately predict the consequences of intervening in the system – in a real conservation problem where decisions are informed by occupancy models (*e.g.* Hossack *et al.* 2013; Chen & Koprowski 2015; Zimbres *et al.* 2018), the results could be disastrous.

While the models supported by AIC and BIC produced biased parameter estimates, they also produced more accurate predictions and retrodictions of the occupancy probability at each site. This is because these models include the variable D which has an open path to ψ; including D provides additional information about the variation in ψ, improving prediction. From the perspective of AIC and BIC, including D results in a reduced in-sample deviance which typically outweighs the penalty for adding the additional variable; this reduction must be greater to outweigh BIC's larger penalty term, which is why BIC was more conservative in its tendency to select confounded models in my simulations (Fig. 6). This also explains why AIC and BIC gave more weight to the non-confounded model (omitting *D*) when $\beta_{C\psi}$ was close to zero (Appendix A: Figs. S2, S6); the near-zero effect of *C* on ψ meant that the path from *D* to ψ through *C* was almost blocked (the other path from *D* to ψ was blocked by conditioning on *X*), and therefore *D* explained relatively little variation in ψ.

In contrast to the effects of M-bias in the occupancy process, M-bias in the detection process did not affect inferences about the effect of *X* on ψ. Additionally, including the collider variable *R* in the detection sub-model improved the accuracy of the model's predictions of the site-level occupancy probability. These results can again be explained by considering how the path structure between variables will affect the change in deviance when a variable is included; as the variable *R* has an open path to *p*, including *R* explains additional variation in the detection probability, reducing the deviance and allowing the model to better account for imperfect detection when estimating the occupancy probability. As the detection probability is generally regarded as a nuisance parameter (Karavarsamis 2015), it is inconsequential that the effect of the other detection covariate (U) will be confounded. Therefore, information criteria can be used for selecting detection covariates.

The tendency for information criteria to favour confounded models with greater predictive ability is not confined to collider bias. For example, simulations by McElreath (2021, pp. 226-228) showed that information criteria tend to select models which condition on the mediator (*M*) in a pipe (*e.g.*, $X \rightarrow M \rightarrow \psi$), inducing post-treatment bias (Rosenbaum 1984). This occurs because adding *M* explains additional variation in ψ, while also blocking the causal path which runs from *X* to ψ (McElreath, 2021, p. 228). I also expect these results to apply in other scenarios, such as case control bias (Cinelli *et al.* 2022). Finally, the M-bias example illustrates that latent variables can result in information criteria favouring confounded models, and hence that considering these variables is critical when drawing inferences.

Inference and prediction are separate tasks

The key point supported by my results is that inference and prediction are separate tasks which should not be conflated in model selection (Shmueli 2010; Laubach *et al.* 2021; McElreath 2021, p. 226). I echo Gelman and Rubin's (1995) criticism of selecting "a model that is adequate for specific purposes without consideration of those purposes”. In the context of occupancy models, both explanation and prediction are important objectives, and conflating the two does justice to neither. Furthermore, my results emphasise the importance of considering not only the model’s purpose, but also the purpose of sub-models within the model; the purpose of the occupancy sub-model depends on whether we are interested in predicting the occupancy state or inferring its drivers, while the detection sub-model’s purpose is usually prediction of the detection probability. Consequently, how occupancy covariates are chosen depends on the purpose of the model – information criteria are suitable if the purpose of the model is prediction, but are unlikely to be if the purpose is parameter inference – while detection covariates can generally be selected using information criteria. This advice also applies to cross-validation; the choice of model made by AIC is asymptotically equivalent to that made by leave-one-out cross validation (Stone 1977).

Using information criteria to compare biological hypotheses in observational studies is risky

The importance of distinguishing between inference and prediction has wider implications for how information-theoretic model selection is applied in ecology. Proponents of the information-theoretic approach have argued that it is possible to compare multiple *a priori* specified models, each representing a different biological hypothesis, with the relative AIC scores indicating the strength of evidence for each hypothesis (Johnson & Omland 2004; Richards 2005; Burnham *et al.* 2011). However, using information criteria in this way conflates inference and prediction; information criteria select models which make better predictions, but these same models can contain spurious effect sizes which hold no biological meaning, while the effects of biologically important covariates are confounded. This is not only the case for occupancy models; the occupancy models I employed are just an extension of logistic regression (Clark & Altwegg 2019), and these points apply to other forms of linear model as well (Luque-Fernandez *et al.* 2019; McElreath 2021, pp. 226-228). The implication is that using information-theoretic model selection to compare biological hypotheses in observational studies carries substantial risks.

The information-theoretic approach and causal inference are complementary

While I argue that comparing biological hypotheses using the information-theoretic approach is risky, and that I prefer a causal inference-based approach for this purpose, I must emphasise that I am not arguing that the information-theoretic approach is flawed or useless for model selection. Information criteria select models from the "predictive point of view" (Akaike 1998), while causal inference is concerned with estimating the effects of covariates, so I see the two approaches as complementary. In the case of occupancy models the two approaches may be used side-by-side in a single analysis, where occupancy covariates are chosen based on causal assumptions embodied in a DAG, while the detection covariates are selected using the information-theoretic approach.

I also argue that causal inference and the information-theoretic approach are complementary because they share philosophical underpinnings. In the information-theoretic approach, it is vital to employ subject expertise and "hard thinking" to develop hypotheses which are compared as models (Lukacs *et al.* 2007; Burnham *et al.* 2011); in causal inference, subject expertise and *a priori* thought are vital in making the causal assumptions which are embodied in the DAG (Pearl 1995; Greenland *et al.* 1999). Causal inference thus provides a framework to support the "hard thinking" required in ecological modelling (Grace & Irvine 2020). Proponents of the information-theoretic approach also recognise that "a proper analysis must consider the science context and cannot successfully be based on 'just the numbers'" (Burnham & Anderson 2004). Similarly, proponents of causal inference argue that conclusions cannot be drawn from the data alone, but require causal assumptions which come from the scientific context of the model (Pearl *et al.* 2016, p. 5).

Another feature of the information-theoretic approach is that Chamberlin's (1890) method of multiple working hypotheses is often emphasised (Burnham & Anderson 2004; Elliott & Brook 2007). I argue that causal inference is very compatible with Chamberlin's method; constructing a causal model forces us to consider multiple explanations for a phenomenon, guarding against the threat of "parental affection for a favourite theory" which concerned Chamberlin. Due to the relatively static nature of causal models, I argue they are especially suited to the case of multiple working hypotheses in parallel (Elliott & Brook 2007), in which causation operates through multiple factors simultaneously. Moreover, the tools of causal inference allow this parallel case to be extended to more complex situations with indirect effects, rather than constraining our thinking to simple additive terms and interactions.

A caveat: model selection is more than selecting covariates

I have focused on the choice of covariates, which is a key aspect of model selection, but another vital part of model selection is selecting specific mathematical functions to relate these variables to one-another (Johnson & Omland, 2004). However, as the rules of causal inference are non-parametric (Pearl 1995; Greenland *et al.* 1999) my conclusions hold irrespective of what functional forms are chosen, and I consider any role of information criteria in selecting these functions to be beyond the scope of this chapter.

Summary

I have demonstrated that when a form of collider bias known as M-bias is present in the occupancy process, occupancy models which are favoured by AIC and BIC produce inaccurate parameter estimates but accurate predictions. In contrast, M-bias in the detection process does not affect the accuracy of parameter estimates. The key conclusion supported by these results is that inference and prediction are separate tasks which should not be conflated during model selection. The correct choice of model selection procedure depends on the purpose for which the occupancy model will be used. Information-theoretic approaches are suitable for selecting occupancy covariates if the model is to be used for predicting the site-level occupancy probability. However, if the goal is instead to infer the effect of environmental covariates on occupancy, then the use of information criteria carries significant risks; I advocate for an approach based on causal inference in this situation. My results support the use of information-theoretic methods to select detection covariates regardless of the model's purpose, as long as detection probability is treated as a nuisance parameter. As single-season occupancy models are in essence a form of logistic regression, my results have wider implications for the use of information-theoretic model selection in ecology. In particular, I argue that my results, alongside those of others (Luque-Fernandez *et al.* 2019; McElreath 2021; Arif & MacNeil 2022), underscore the risks associated with using the information-theoretic approach to compare biological hypotheses in observational studies. Causal inference and the information-theoretic approach share similar philosophical underpinnings, and should be seen as complementary tools that accomplish different tasks.

Appendix A: Supplementary figures and tables

Table S1. Inferential and predictive accuracy of occupancy models across all simulations (n=1000) for each of the three scenarios (see Fig. 3).

		M-bias in occupancy process		M-bias in detection process		M-bias in occupancy and detection processes			
		$\psi \sim X$	$\psi \sim X+D$	$\psi \sim X$ $p \sim U$	$\psi \sim X$ $p \sim U+R$	$\psi \sim X$ $p \sim U$	$\psi \sim X+D$ $p \sim U$	$\psi \sim X$ $p \sim U+R$	$\psi \sim X+D$ $p \sim U+R$
Inference									
Bias	Q1	-0.07	-0.91	-0.05	-0.04	-0.10	-0.9	-0.09	-0.98
	Mean	-0.01	-0.06	0.001	-0.002	-0.02	-0.10	0.0002	-0.10
	Q3	0.08	0.90	0.04	0.04	0.10	0.80	0.09	0.82
Absolute bias	Q1	0.04	0.33	0.02	0.02	0.05	0.30	0.04	0.31
	Median	0.08	0.91	0.04	0.04	0.10	0.85	0.09	0.91
	Q3	0.17	2.70	0.08	0.07	0.20	2.55	0.18	2.70
True value in 95% C.I.		92.1%	24.7%	89%	95.6%	86.8%	26.9%	91.1%	27.2%
Sign correct		92.1%	65.4%	97.7%	97.7%	92.6%	66.0%	93.3%	65.8%
Prediction									
Mean absolute error	Q1	0.05	0.01	0.01	0.01	0.06	0.02	0.05	0.01
	Median	0.09	0.02	0.02	0.01	0.10	0.03	0.09	0.02
	Q3	0.13	0.03	0.04	0.02	0.14	0.05	0.13	0.03
Proportion of sites with true ψ in 95% C.I.	Q1	0.17	0.77	0.22	1.00	0.14	0.32	0.16	0.72
	Median	0.24	0.96	1.00	1.00	0.20	0.63	0.24	0.94
	Q3	0.47	1.00	1.00	1.00	0.32	0.95	0.43	1.00

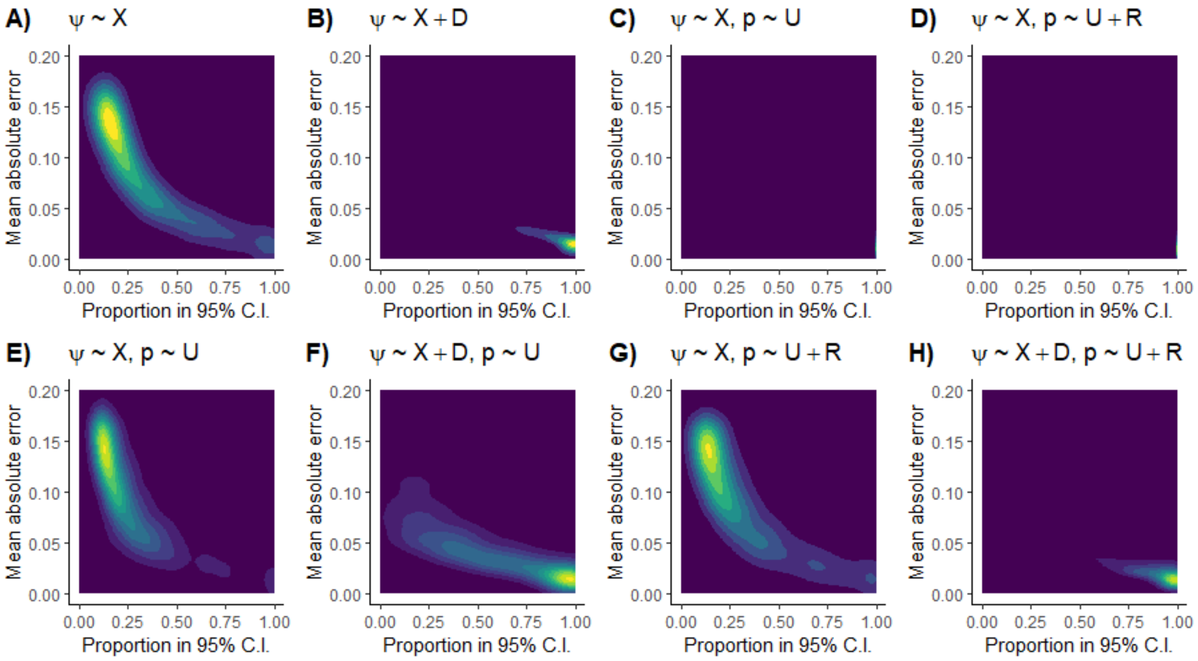


Figure S1. Kernel density estimate contours showing two measures of retrodictive accuracy when predicting site-level occupancy probability (ψ), for 1000 simulations. The x-axis shows the proportion of sites (out of 3000 total sites) for which the true occupancy probability was contained within the 95% confidence interval around the model's prediction. The y-axis shows the mean absolute error of the predictions. Consequently, the bottom right of the plot indicates higher predictive accuracy, while the top left indicates lower predictive accuracy. The density of simulations within this area is shown by the coloured contours, with lighter colours indicating a higher density of simulations. Results are displayed for the following occupancy models: **A)** scenario 1, model 1; **B)** scenario 1, model 2; **C)** scenario 2, model 1; **D)** scenario 2, model 2; **E)** scenario 3, model 1; **F)** scenario 3, model 2; **G)** scenario 3, model 3; **H)** scenario 4, model 4. Each model's covariates for ψ and the detection probability (p) are shown above their respective plot. For explanation of the scenarios, see Table 1 and main text.

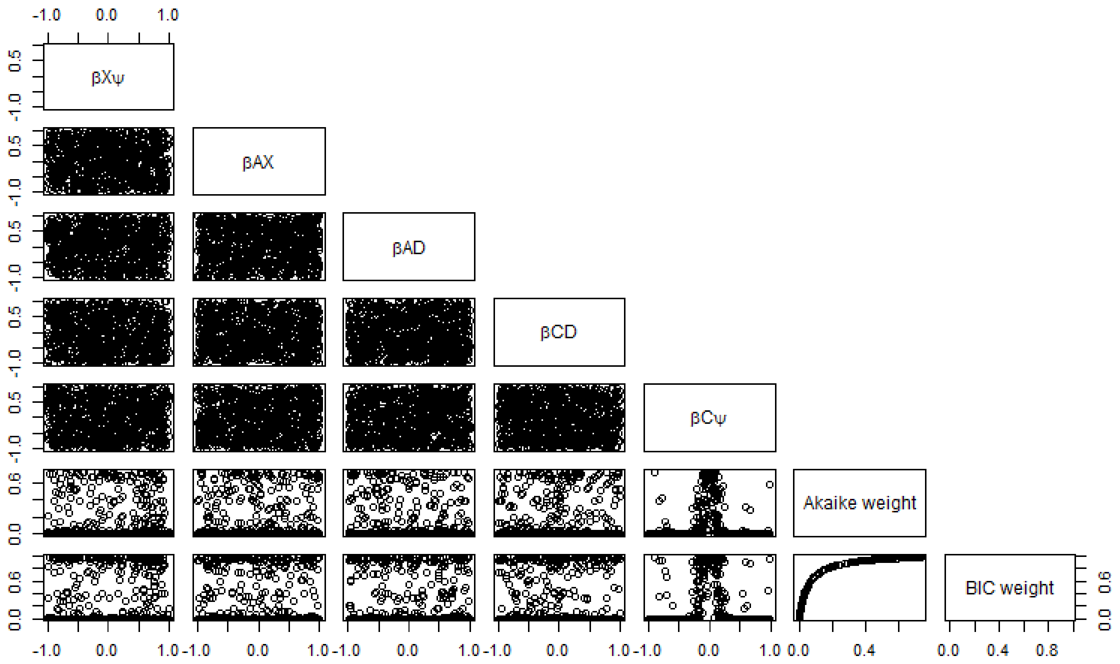


Figure S2. Pairs plot showing the relationship between the effect sizes (β values), Akaike weight, and BIC weight for model 1 in scenario 1 (see Table 1 for model definition).

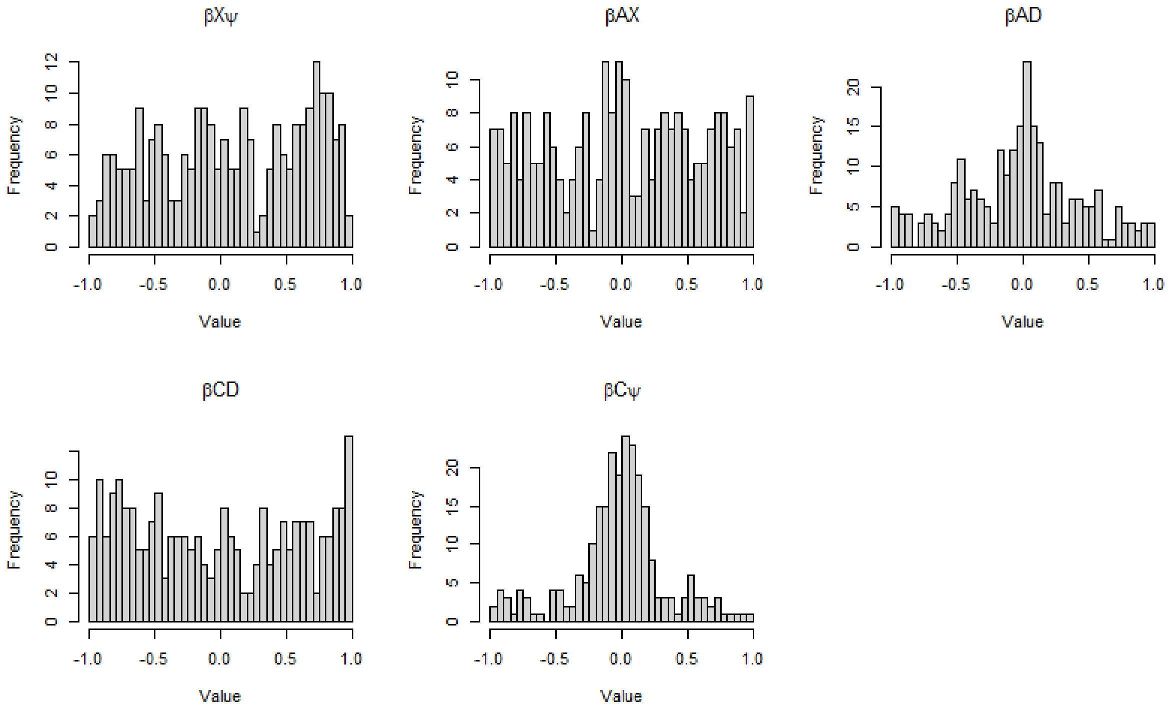


Figure S3. Histograms showing distribution of true parameter values for the simulations in scenario 1, model 2 (see Table 1 for model definition) for which the focal effect was estimated accurately (*i.e.*, the true effect of X on ψ ($\beta_{X\psi}$) was within the 95% confidence interval around the estimate).

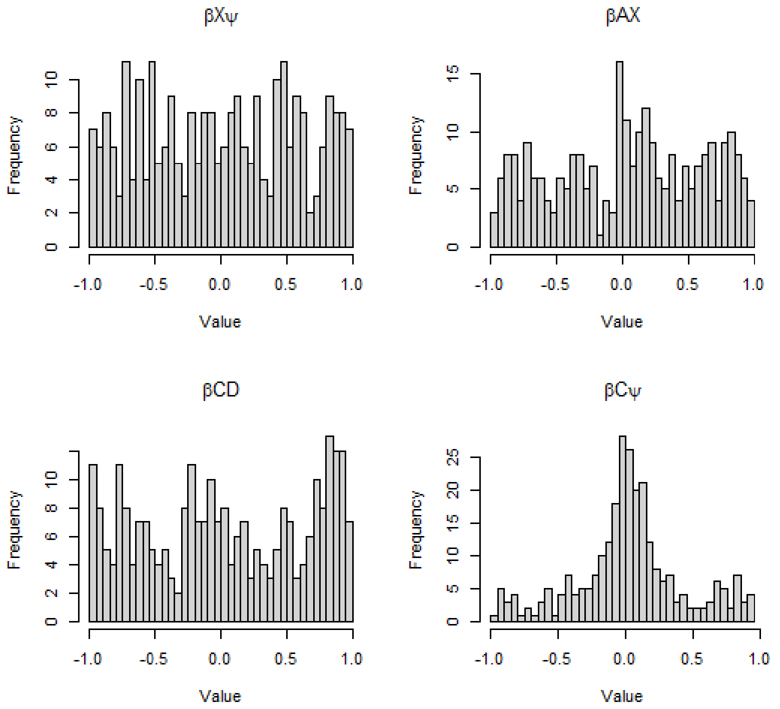


Figure S4. Histograms showing distribution of true parameter values for the simulations in scenario 3, model 2 (see Table 1 for model definition) for which the focal effect was estimated accurately (*i.e.*, the true effect of X on ψ ($\beta_{X\psi}$) was within the 95% confidence interval around the estimate).

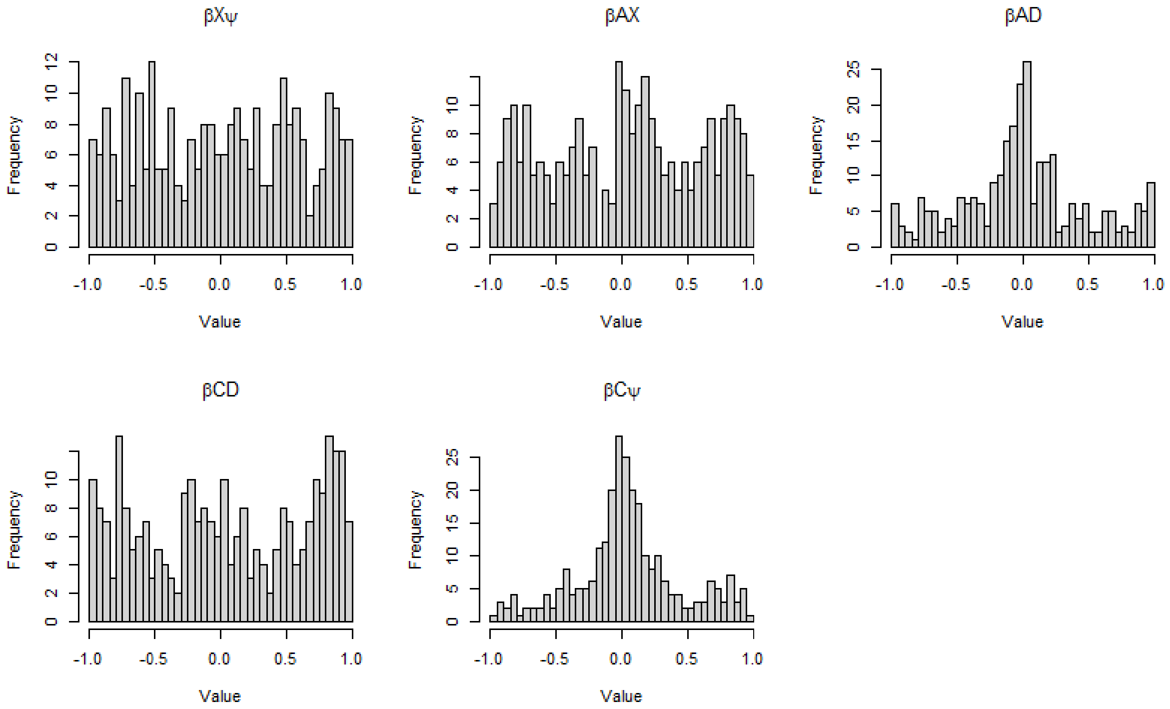


Figure S5. Histograms showing distribution of true parameter values for the simulations in scenario 3, model 4 (see Table 1 for model definition) for which the the focal effect was estimated accurately (*i.e.*, the true effect of X on ψ ($\beta_{X\psi}$) was within the 95% confidence interval around the estimate).

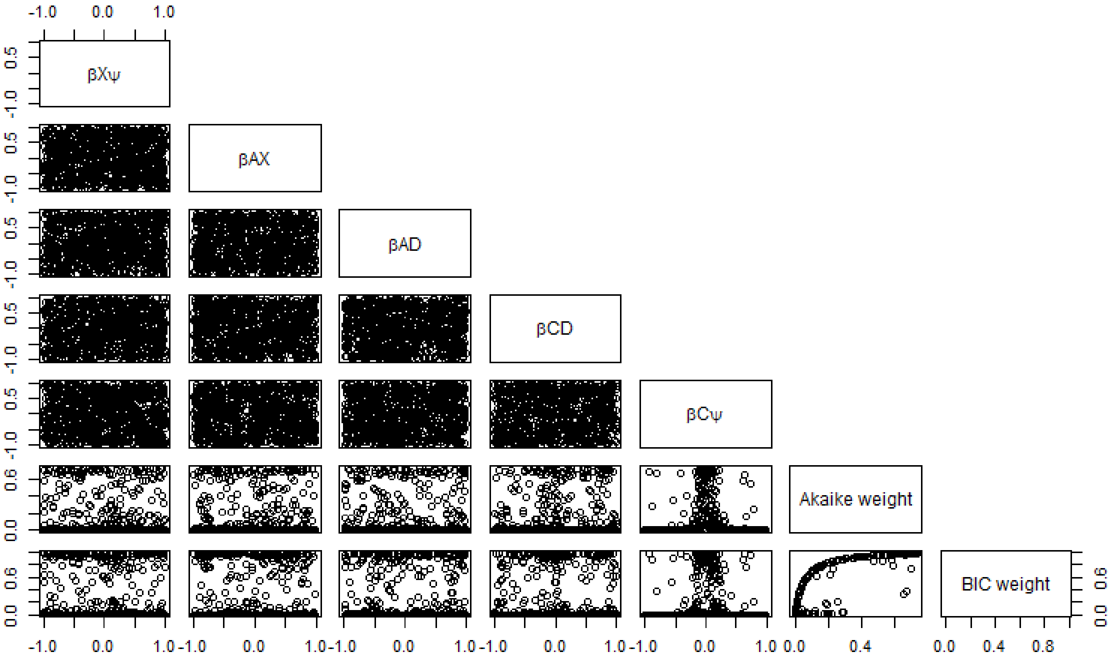


Figure S6. Pairs plot showing the relationship between the effect sizes (β values), Akaike weight, and BIC weight for model 3 in scenario 3 (see Table 1 for model definition).

Chapter 4

Impacts of invasive *Opuntia* cacti on mammalian habitat use

Abstract

Prickly pear cacti (*Opuntia spp.*) are among the world's most pervasive plant invaders, invasive in arid regions throughout the world. *Opuntia* are invasive in Laikipia County, Kenya, a key stronghold for biodiversity and vital populations of endangered mammals. Consequently, understanding *Opuntia*'s impacts on mammals in Laikipia is an urgent priority. As *Opuntia* invasions profoundly alter the physical structure and resource availability of the habitat, behavioural changes – particularly changes to habitat use – potentially comprise a key aspect of *Opuntia*'s impacts. I addressed this topic by using camera traps to explore the relationship between *Opuntia* and the occupancy and temporal patterns of activity of eight key mammal species, examining how these effects varied with spatial scale. I found that *Opuntia* exerted effects on occupancy and activity which varied among mammal species and depended on the spatial scale of the *Opuntia* cover covariate. These estimated effects were robust to altering the models' assumptions to allow for *Opuntia* to indirectly influence occupancy and activity by affecting native vegetation cover. My key findings include a negative effect of broad-scale *Opuntia* volume on the occupancy of the endangered reticulated giraffe (*Giraffa reticulata*). I also observed generally positive effects of *Opuntia* on the occupancy and activity of elephants (*Loxodonta africana*), olive baboons (*Papio anubis*), and vervet monkeys (*Chlorocebus pygerythrus*), all of which are thought to be important dispersal agents for *Opuntia*. My findings have important implications for the conservation of endangered mammal species in the region, the future spread of *Opuntia* through seed dispersal, and interactions between wildlife and local communities.

Introduction

Plant invasions are a rapidly expanding threat to ecosystems and human well-being worldwide (Dawson *et al.* 2017; Seebens *et al.* 2017). Understanding the impacts of these invasive plants is vital if we are to take informed and effective action to mitigate them. Until relatively recently, our understanding of the impacts of invasive plants has been focused on invaders' effects on biodiversity and the abundance of native species (Crystal-Ornelas & Lockwood 2020), and the evidence for these impacts is now well-established (Vilà *et al.* 2011). However, a growing body of evidence indicates that invasive plants can cause profound ecological impacts by altering the behaviour of native animals (Chapter 2; Stewart *et al.* 2021). Developing a mechanistic understanding of these behavioural impacts is a key avenue for research in invasion ecology (Chapter 2; Stewart *et al.* 2021).

Prickly pear cacti (*Opuntia spp.*) are one of the world's most pervasive plant invaders: native to the Americas, they are invasive in arid regions throughout the world, including East and Southern Africa, Australia, the Mediterranean, and parts of South-East Asia (Pasiecznik 2007, Pasiecznik & Rojas-Sandoval 2007, Pasiecznik 2015). Several species of *Opuntia* were introduced to Laikipia County, Kenya, in the latter half of the 20th century, to serve as live fences and ornamental plants (Strum *et al.* 2015; Witt 2017, Loisaba Conservancy, 2019). Since their introduction, three of these *Opuntia* species (*O. stricta*, *O. engelmannii*, and *O. ficus-indica*) have become invasive, spreading rapidly to cover large areas of the landscape (Strum *et al.* 2015; Witt 2017; Githae 2019). As Laikipia County is a key stronghold for biodiversity and hosts vital populations of endangered mammals including Grevy's zebra (*Equus grevyi*; Rubenstein *et al.* 2016), reticulated giraffe (*Giraffa reticulata*; Muneza *et al.* 2018) and African wild dog (*Lycaon pictus*; O'Neill *et al.* 2022), understanding the impacts of *Opuntia* on Laikipia's mammals is an urgent priority.

Behavioural impacts potentially comprise a key aspect of *Opuntia*'s effects on mammals in Laikipia County. In particular, *Opuntia* may alter mammalian habitat use. If these effects occur, they may have impacts on individual native species, the wider ecosystem, and local communities. For instance, restriction of movement may result in effects on individual species' population dynamics analogous to those resulting from other forms of habitat fragmentation (O'Neill *et al.* 2022). At a larger scale, changes to the movement of mammal species may affect the patterning of vital ecological processes within the system. For example, large ungulate herbivores exert powerful direct and indirect effects on the plant community and are likely to influence processes such as decomposition and nutrient cycling (Pringle *et al.* 2011). Furthermore, the movements of large mammals such as elephants (*Loxodonta africana*) are a key determinant of human-wildlife interactions (Sitati *et al.* 2003), and changes to their habitat use may exacerbate negative impacts on local communities (Shackleton *et al.* 2017). There is also the potential for impacts on wildlife tourism – a cornerstone of Laikipia's economy (Laikipia Wildlife Forum, 2012) – if charismatic species are displaced or tourists' perception of the landscape as a "natural environment" (Nzomo *et al.* 2020) is jeopardised.

Opuntia is likely to primarily alter mammalian habitat use through two non-mutually exclusive modes of impact (Chapter 2; Stewart *et al.* 2021). The first of these modes is alteration of the physical structure of the habitat; *Opuntia* forms large, impenetrable stands which may restrict the movement of some mammals around the habitat and result in their displacement from an area (Witt 2017). The dense stands may also affect patterns of actual or perceived predation risk. For small mammals, such as dik-dik (*Madoqua spp.*), which may be able to move between the stands, *Opuntia* may afford cover. By contrast, the movement of larger-bodied prey species, such as impala (*Aepyceros melampus*), might be impeded, hindering escape and thus increasing predation risk. These effects on predation risk may result in changes to mammalian habitat use.

Opuntia may also affect mammalian habitat use by altering the availability of food within the landscape. Large *Opuntia* stands provide a year-round supply of fruit which is consumed by species including elephants (*L. africana*), olive baboons (*Papio anubis*), and vervet monkeys (*Chlorocebus pygerythrus*; Strum *et al.* 2015; Witt 2017; Githae 2019). Consequently, frugivores may be attracted to heavily invaded areas (Shackleton *et al.* 2017). *Opuntia*'s effects on the physical structure of the habitat may also indirectly alter resource availability, for instance by affecting access to vegetation or water sources (Oduor *et al.* 2018; Githae 2019). The resource-mediated behavioural impacts of *Opuntia* will likely exhibit seasonal patterns of variation as the availability of other resources varies. In particular, the effects are likely to be strongest after extended dry periods when little other forage is available, making the omnipresent *Opuntia* fruit a potentially important part of frugivores' diets and strengthening the displacement of grazers and other herbivores that are unable to feed on it.

In this chapter, I explored the effects of *Opuntia* on mammalian habitat use. Using camera traps, I quantified the total effects of *Opuntia* on the occupancy and temporal patterns of activity for eight key mammal species. These total effects, which represent the probable effects of *Opuntia* invading new areas or being removed from currently invaded areas, assume that

Opuntia affects occupancy and activity through structurally mediated and resource-mediated pathways. To explore whether the estimated total effects were sensitive to this assumption, I also ran models which assumed that *Opuntia* could influence occupancy and activity indirectly, through affecting native vegetation cover. Finally, as the behavioural impacts of invasive plants can be strongly scale-dependent (Chapter 2; Stewart *et al.* 2021), I examined how the effects on occupancy and activity depended on the spatial scale of the *Opuntia* covariate.

Methods

Study system

I conducted my study at Mpala Research Centre and Loisaba Conservancy, in Laikipia County, Kenya. These two areas lie adjacent to one another immediately to the west of the Ewaso Ng'iro River and are separated by the Ewaso Narok River (Fig. 1). The study area is predominantly unfenced, except for small-scale electric fencing surrounding the Mpala ranch house and tourist accommodation at Loisaba (Crego *et al.* 2021). The area contains numerous private roads which are used to a varying degree by rangers, researchers, tourists, and other conservancy personnel. Additionally, a public road runs from the north-west corner of Mpala, traversing the Mpala plateau and exiting the property close to the research centre in the South-East. Both Mpala and Loisaba maintain working herds of cattle, sheep, and goats; camel herds are also present in the northern parts of Mpala.

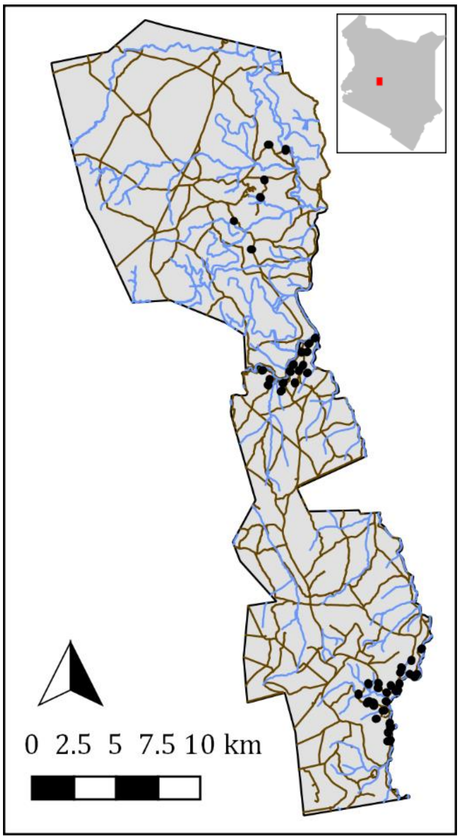


Figure 1. Map of the study region. Black points represent camera trap sites, light blue lines are rivers, and brown lines are roads. Camera trap sites are clustered within three regions: Loisaba (top), Mpala north (middle) and Mpala south (bottom). Canvas extends from longitude 244165 to 271026, latitude 28814 to 78171.

The habitat is a semi-arid savanna, with varying densities of woodland and shrubland dominated by *Vachellia* and *Senegalia* (formerly *Acacia*) species, including *V. etbaica, S. brevispica, S. mellifera, and V. gerrardii* (Young *et al.* 1995; Augustine 2003; Augustine *et al.* 2011; Mutuku & Kenfack 2019). The habitat also contains other tree and shrub species including *Boscia augustifolia, Croton dichogamus,* and *Grewia spp.* (Young *et al.* 1995; Augustine 2003; Augustine *et al.* 2011; Mutuku & Kenfack 2019). Grasses belonging to the genera *Cynodon*, *Pennisetum*, *Digitaria* and *Sporobolus* are common in the understory layer, and a variety of forbs including *Plecranthus spp*., *Pollichia campestris*, *Portulaca spp*. and *Blepharis spp*. are also present (Young *et al.* 1995). *Euphorbia nyikae* and other succulents are also present in some areas, particularly in the northern region of Mpala (Augustine 2003).

The soil is predominantly red sandy loam (Ferric and Chromic Luvisols) except for the Mpala plateau, which is dominated by black cotton soil (Pellic vertisol) (Augustine *et al.* 2011; Mutuku & Kenfack 2019; Kimuyu *et al.* 2021). The two soil types are separated by a zone of transitional soils on the Mpala escarpment and parts of the plateau (Mutuku & Kenfack 2019). As I only observed *Opuntia* on the red soils, and the red soil and black cotton soils differ substantially in their vegetation structure (Wells *et al.* 2023) and mammal assemblages, I restricted my investigation to eliminate the potential confounding effects of soil variation.

For the purposes of my investigation I divided the study area into three main regions: Mpala south, Mpala north, and Loisaba (Fig. 1). I selected these regions because they contained varying densities of *Opuntia* (from scattered individual plants to heavily invaded areas where *Opuntia* covered the majority of the ground). I further subdivided the Loisaba region into three blocks (A, B, and C) to ensure that I sampled across the breadth of this area. Due to logistical constraints imposed by the COVID-19 pandemic, the majority of my cameras were situated in the Mpala regions.

I focused my investigation on eight key mammal species. I selected elephants (*L. africana*), olive baboons *(P. anubis)* and vervet monkeys *(C. pygerythrus)* because they commonly feed on *Opuntia* fruit and are likely to be important dispersal agents (Strum *et al.* 2015; Witt 2017; Githae 2019). Impala (*A. melampus*) and dik-dik (*Madoqua spp.*) were selected because they are among the most common herbivore species in the area, particularly in red soil regions (where Grant's and Thomson's gazelles, *Nanger granti* and *Eudorcas thomsonii*, are generally absent), and thus their habitat use is likely to have important implications for herbivory in the region. I also selected Grevy's zebra (*E. grevyi*) and reticulated giraffe (*G. reticulata*) because they are of significant conservation concern (Rubenstein *et al.* 2016), Muneza *et al.* 2018). Finally, I selected spotted hyena *(Crocuta crocuta*), one of the key mammalian carnivores in the system.

Camera trap deployment

To explore the effects of *Opuntia* on mammalian occupancy, I deployed camera traps from January-April and October-November 2021. I initially deployed 30 cameras (20 × Browning Dark Ops Pro, 5 × Browning Recon Force Extreme, and 5 × Reconyx Hyperfire 2); two cameras were lost to damage, leaving 28 still operational at the end of the study period. Cameras were operational at each location for between 3 and 56 days (Q1 = 18, median = 23, Q3 = 26 days) before being moved to a new location; I aimed to leave cameras in place for at least one week before they were moved, but on a small number of occasions (n = 5) cameras were moved earlier for logistical reasons.

I defined a site as the area immediately adjacent to one camera trap. To maximise variation in *Opuntia* density while minimising variation in confounding variables, I employed a paired-site design. I divided the study area into 500 × 500m grid squares, and then randomly selected grid squares for sampling. I placed one pair of cameras within each of these grid squares; the first camera was deployed in an area visually identified as high *Opuntia* density, and the second was deployed in a random direction 50-70m away. If the second site was found to have a density of *Opuntia* equal to or higher than the first site, I generated a new random direction until the *Opuntia* density at the second site was lower. As some grid squares were sampled more than once and camera traps at some sites were lost due to damage, my total sample comprised 101 sites within 46 grid squares.

I mounted the camera traps on tree trunks, positioning them so that they had good visibility of the area 10m in front of the camera. I verified that animals in this area would be visible by taking photos of a research assistant at 2m, 4m, 6m, 8m, and 10m from the camera. I deployed the cameras at an average height of 81cm (measured from the ground to the lens), but some cameras were deployed slightly higher or lower to ensure a good view given the site's topography (min = 34cm, Q1 = 72cm, Q3 = 89cm, Q4 = 137cm). I set the camera traps to take images with a five second cool-down between captures. I used the "long range" infrared flash setting on my Browning cameras as I wanted to maximise species detections and was less concerned about blur, which could inhibit the identification of specific individuals. I set the infrared flash of the Reconyx cameras to the default “optimised” setting. To reduce the number of false detections, I cut back long grass and other vegetation close to the camera which would otherwise trigger the sensor.

Habitat and Opuntia surveys

To collect information on the local-scale habitat features that could affect site usage, I conducted habitat surveys at each camera trap site. I surveyed a circular area within a 10m radius of the camera trap. I divided this area into two parts: the field of view (FOV), defined as the area in which I could see the camera’s lens, and the rest of the area located beside and behind the camera.

Within the FOV and remaining area, I estimated the percentage of ground covered by *Opuntia stricta,* other *Opuntia* species, grasses, shrubs, forbs, succulents, trees, bare ground, and other cover (*e.g.,* rocks) with the aid of a cover estimator chart (Anderson 1986). These percentages were not required to sum to 100%, as vegetation types could grow under/over one another (*e.g.,* grass growing under shrubs). I also identified and counted the number of standing trees in the FOV and area. I defined a tree as a woody plant standing taller than 2m; woody plants shorter than 2m were classified as shrubs.

I assumed that the FOV comprised one quarter of the total site, and calculated the percentage cover for the total site by averaging the FOV and area values:

$$Total\ \%\ cover\ =\ \left(\frac{(FOV\ \%\ cover\ +\ 3(Area\ \%\ cover)}{4}\right)$$

To quantify the use of each site by livestock, I calculated the proportion of days in which livestock (cows, sheep, goats) or camels were detected by the camera trap.

I also calculated the straight-line distance from each site to the nearest river and road using QGIS (v2.28.25; QGIS Development Team, 2018).

Estimation of grid-square-level Opuntia volume

To measure the abundance of *Opuntia* across the grid squares sampled by my camera traps, I performed distance sampling (Kéry & Royle, 2015). Due to logistical constraints imposed by the COVID-19 pandemic, I only sampled 41 of the 46 grid squares in which camera traps were deployed. I performed the distance sampling along transects which ran from one edge of the square to the other, typically following a road if one was present. If no road was present, I instead walked from one side of the square to the other in as straight a line as possible. Each transect was approximately 500m long; I took GPS coordinates for the start/end points to determine the exact length. I looked for *Opuntia* lying perpendicular to the transect in either direction. When I observed a stand of *Opuntia* I recorded the species, size category (small = <1m, medium = 1-2m, large = >2m height) and whether ripe fruit was visible, and then measured the distance to the stand. I measured distances using a tape measure for stands up to 10m from the transect, and used a laser range finder (Leica Rangemaster CRF 2400-R, accurate to ±1m) for stands 10-80m from the transect. I did not count stands that lay more than 80m away to avoid accidentally counting stands situated outside of the grid square.

To obtain *Opuntia* abundance estimates for each grid square, I used a Poisson-binomial multinomial distance sampling model with half-normal detection function (Kéry & Royle, 2015), using code from Joseph (2021). I converted the resulting abundance estimates into an estimate of the total *Opuntia* volume in each grid square by first estimating the abundance of each *Opuntia* size class separately, and then combining the estimates for different size classes by assuming (based on the volume of a hemisphere where the height is equal to the radius) that the volume of a large stand ($h = 2.5$m) was 32.725 m^3, a medium stand ($h = 1.5$m) was 7.07m^3, and a small stand ($h = 0.5$m) was 0.26m^3. I multiplied the median estimated abundance for each size class by these volume values, and then added them together. I performed this calculation for the fruiting and non-fruiting *Opuntia* separately, and then summed them to get the total *Opuntia* volume per grid square. Finally, I adjusted for the unequal transect lengths by dividing each grid square's estimate by the respective transect length.

Processing of camera trap images

To process the images obtained from the camera traps, I first used the machine learning tool Megadetector (v.4.1.0, Beery *et al.* 2019) to classify images as containing an animal (any species), human, or vehicle. I manually screened all images with probability of 0.10 (the minimum probability Megadetector assigns to a classification) or higher of containing a human or vehicle, discarding all images which I identified as containing a human/vehicle and retaining images which contained animals. I also retained all images which Megadetector classified as containing at least one animal with probability of 0.98 or higher. I selected this relatively high threshold because I observed that many lower-probability classifications were in fact false detections (*e.g.*, pieces of vegetation classified as "animal"). Furthermore, my occupancy models (Appendix A) assumed no false positive classifications, but were able to account for the possibility that a species was photographed but missed by Megadetector, through modelling the imperfect detection process.

I uploaded all of the retained images to my project on the Zooniverse platform (Prickly Pear Project Kenya: https://www.zooniverse.org/projects/peter-dot-stewart/prickly-pear-project-kenya), where members of the public were able to view and classify the camera trap images (see Appendix D). Each image was classified by at least 12 volunteers before retirement from the active image pool, except for when an image was classified as "human", in which case the image was immediately retired and flagged for checking by the research team.

I generated consensus classifications for each image using a threshold-based approach. For a species to be consensus classified, at least 8 of the 12 volunteers had to classify the species as being present. I also quantified volunteer agreement by calculating the Shannon entropy (Shannon 1948) of the distribution of classifications for each image. Images with entropy values of greater than one were also discarded. Classifications made by an expert (either P.S.S. or the Prickly Pear Project Kenya moderator) were accepted automatically regardless of volunteer disagreement, and the remaining volunteer classifications were used to assess volunteer classification accuracy (Appendix D). I found that my consensus classification method resulted in highly accurate consensus classifications, with sensitivity ≥ 0.972 and specificity ≥ 0.999 for all focal species (Appendix D, Table S1).

Statistical models

To explore the effects of *Opuntia* on mammalian occupancy, I fitted occupancy models which incorporated a Gaussian process to model spatial autocorrelation in sites' occupancy probability (see Appendix A for model structure). As my objective was to infer the effect of *Opuntia* on occupancy, I selected covariates for the occupancy sub-model based on causal assumptions about the data-generating process (Chapter 3; Stewart *et al.* 2023); I represent these assumptions in Fig. 2. My assumptions imply that *Opuntia* may have a direct effect on occupancy (the structurally mediated pathway), and an indirect effect which operates through the provision of ripe fruits (the resource-mediated pathway). If *Opuntia* only affects occupancy through these pathways, then together they comprise the total effect of *Opuntia* on occupancy.

However, if *Opuntia* also affects the native vegetation (represented by the percentage cover of grasses, shrubs, forbs, and succulents, and the number of trees), then the total effect also includes this vegetation pathway. My objective was to estimate these total effects because these inform us about the likely consequences of *Opuntia* expanding to invade new areas.

To estimate the total effects of *Opuntia* on occupancy I fitted two statistical models (Table 1): one omitting the vegetation pathway, and the other assuming an indirect pathway through vegetation. For the detection sub-model, I included daily mean temperature as a covariate, as changes to the thermal environment can affect the performance of the camera's passive infrared sensor (Welbourne *et al.* 2016), and I also included a separate intercept for each model of camera trap. I standardised all covariates, including the *Opuntia* covariates, by subtracting the mean and dividing by the standard deviation. I rescaled the distances by converting them into kilometres and then dividing by 6; this placed the distances between sites on a more convenient scale for the specification of prior distributions.

I estimated the total effects of *Opuntia* on occupancy at two spatial scales, resulting in a total of four statistical models per species (Table 1). In the fine-scale models, I used the site-level *Opuntia* cover and the total number of ripe fruits. In the broad-scale models, I instead used the median estimate of the total *Opuntia* volume for each grid square.

In both the fine-scale and broad-scale models, I examined the effects of *Opuntia* on occupancy by plotting marginal effects with all other covariates set to their average value (*i.e.,* zero for standardised covariates). In my plots, I display multiple highest posterior density compatibility intervals (*i.e.*, credible intervals) ranging from 95% to 50%, as the choice of any one interval is arbitrary (McElreath 2021).

To explore the effects of *Opuntia* on the temporal patterns of animal activity, I fitted circular kernel density functions to the detection data for each species using the R package *activity* (v. 1.3.2; Rowcliffe *et al.* 2014; Rowcliffe 2022). As this approach does not allow for the inclusion of environmental covariates, I instead used two separate approaches to infer the effects of *Opuntia* on activity. First, I split the data into two parts based on my paired site design: one part contained the sites with the higher *Opuntia* density in each pair, and the other contained the sites with lower *Opuntia* density. I then qualitatively compared the activity kernels for the two datasets to examine how the timing of activity differed between high and low-*Opuntia* sites. Second, I split the activity data by site, fitted a separate kernel for each site, and then calculated the area under each kernel; this represents the total level of activity at each site

(Rowcliffe *et al.* 2014). I then fitted a log-normal hurdle model (see Appendix A for model structure) to these data to explore the effects of *Opuntia* on the total level of activity at each site. I elected to use this type of model because activity has a non-negative continuous value, but there are many sites with zero activity. I based my choice of environmental covariates (Table 1) on the same assumptions as I made for the occupancy models (Fig. 2). I used the same environmental covariates in both of the hurdle model's sub-models. Additionally, to control for differences in sampling effort among sites, I included the number of days for which the site's camera trap was deployed as a covariate. As the structure of the hurdle model does not readily allow for plotting how the posterior median/mean and compatibility intervals change over the values of a covariate, I instead explored the effect of *Opuntia* on total activity by simulating new observations using the effect sizes' (β_{OPUNTIA}, γ_{OPUNTIA}) posterior distributions and plotting the distribution of these simulated data against the *Opuntia* covariate.

I fitted all models in a Bayesian framework using Stan (Stan Development Team, 2022), implemented in R (v.4.1.2; R Core Team, 2021) with the *rethinking* (v.2.21; McElreath, 2021) and *cmdstanr* (v.2.30.1; Gabry & Cesnovar, 2021) packages. I chose weakly regularising prior distributions for my models with the aid of prior predictive simulations (Appendix B) and validated my occupancy model on synthetic data (Appendix C) to ensure that it was capable of accurately recovering parameter values. To improve the sampling of the models' Markov chains I employed a non-centred parameterisation, which uses Cholesky decomposition to break the covariance matrix down into a Cholesky factor and z-scores for sampling, which are then multiplied to give the varying intercept k_i (McElreath 2021).

I ran each occupancy and hurdle model with four Markov chains, each with 4000 iterations. For each chain, the first 3000 samples constituted the warmup phase and were not used for inference, while the following 1000 samples were used for inference; as I had four chains, a total of 4000 samples were used for inference. I ran the distance sampling models with four chains of 3500 iterations, of which the first 1500 were used for warmup, giving a total of 8000 samples across the four chains. For all models, I ensured that the chains had converged by checking that the Gelman-Rubin convergence diagnostic ($\hat{R}$; Gelman & Rubin 1992) was equal to 1.00 for all key parameters. I also assessed the performance of the Markov chain Monte Carlo (MCMC) algorithm by inspecting the effective sample size, trace plots, and trace rank plots for each parameter. Additionally, I ensured that the models did not exhibit divergent transitions and checked that histograms of the Markov chain energy transition density and marginal energy distribution showed a close match (Betancourt 2018).

Code to fully reproduce my analyses and simulations is available at https://github.com/Peter-Stewart/Zooniverse_processing, and a complete list of the R packages I used can be found in Appendix F, Table S2.

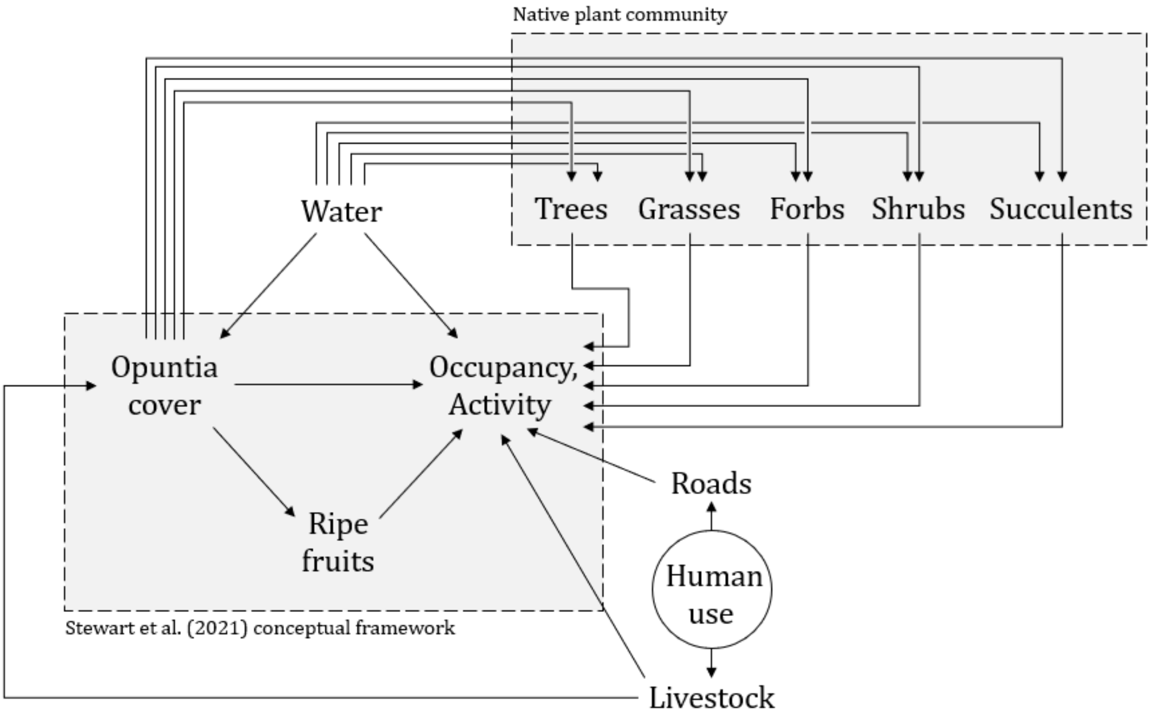


Figure 2. Directed acyclic graph representing assumptions about the ways in which *Opuntia* cover and other environmental variables might affect mammalian occupancy and activity. Nodes represent variables, while arrows represent possible mechanistic links between variables. “Human use” is a latent variable and is therefore displayed in a circle.

Table 1. Choice of habitat covariates and estimands (parameters targeted for inference) in my models. β_{OPUNTIA} represents the effect sizes for *Opuntia* percentage cover and *Opuntia* grid square volume in the fine-scale and broad-scale models respectively, while γ_{OPUNTIA} represents these effects for the zero component of my hurdle model (Appendix A). "Native plant community" is shorthand for the total percentage cover covariates for grass, shrubs, forbs and succulents, and the total number of trees.

Model	Habitat covariates	Estimands
Fine (site) scale occupancy model		
1. Total effect (assuming no vegetation pathway)	*Opuntia* cover, distance to river, distance to road, proportion of days with livestock, native plant community	β_{OPUNTIA}
2. Total effect (assuming vegetation pathway)	*Opuntia* cover, distance to river, distance to road, proportion of days with livestock	β_{OPUNTIA}
Broad (grid square) scale occupancy model		
1. Total effect (assuming no vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock, native plant community	β_{OPUNTIA}
2. Total effect (assuming vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock	β_{OPUNTIA}
Fine (site) scale activity hurdle model		
1. Total effect (assuming no vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock, native plant community	β_{OPUNTIA}, γ_{OPUNTIA}
2. Total effect (assuming vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock	β_{OPUNTIA}, γ_{OPUNTIA}
Broad (grid square) scale activity hurdle model		
1. Total effect (assuming no vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock, native plant community	β_{OPUNTIA}, γ_{OPUNTIA}
2. Total effect (assuming vegetation pathway)	*Opuntia* total volume, distance to river, distance to road, proportion of days with livestock	β_{OPUNTIA}, γ_{OPUNTIA}

Results

Effects of Opuntia on mammalian occupancy

The effects of *Opuntia* on mammalian occupancy varied among mammal species and by the spatial scale of the *Opuntia* covariate. The occupancies of olive baboons, elephants, and vervet monkeys were positively affected by *Opuntia* (Figs. 3A-C, 4A-C). For olive baboons, the effect of *Opuntia* on occupancy was stronger for the broad-scale model, with the posterior median occupancy probability for this species increasing from around 0.25 to almost 1 over the range of grid square-scale *Opuntia* volumes that I observed (Fig. 4A). The effects for elephants and vervet monkeys were also slightly stronger in the broad-scale model, but the differences were not very pronounced (Figs. 3B,C, 4B,C).

My models revealed a variety of effects of *Opuntia* on the occupancy of the non-frugivorous herbivore species. For Grevy's zebra, I did not observe a clear relationship at a fine scale (Fig. 3D), but I did find a positive relationship at the broad scale (Fig. 4D). The effects for impala were probably negative at both spatial scales (Figs. 3E, 4E), with the relationship being slightly stronger at the broad scale (Fig. 4E). By contrast, the effects for dik-dik were positive at both spatial scales (Figs. 3F, 4F), although there was more uncertainty in the broad-scale relationship, as evidenced by the wider compatibility intervals. The effects for giraffes were highly scale-dependent; the relationship between site-level *Opuntia* cover and giraffe occupancy was positive (Fig. 3G), but the effect of grid square-level *Opuntia* volume on occupancy was strongly negative (Fig. 4G). For spotted hyena, I observed that the relationship between hyena occupancy and *Opuntia* was scale-dependent; the relationship was positive for the site-level *Opuntia* cover (Fig. 3H), but negative for the grid square-level *Opuntia* volume (Fig. 4H).

For all my focal species, the results were qualitatively similar for models which included measures of the native plant community (Figs. 3, 4) and for models which omitted them (Appendix E, Figs. S18, S19).

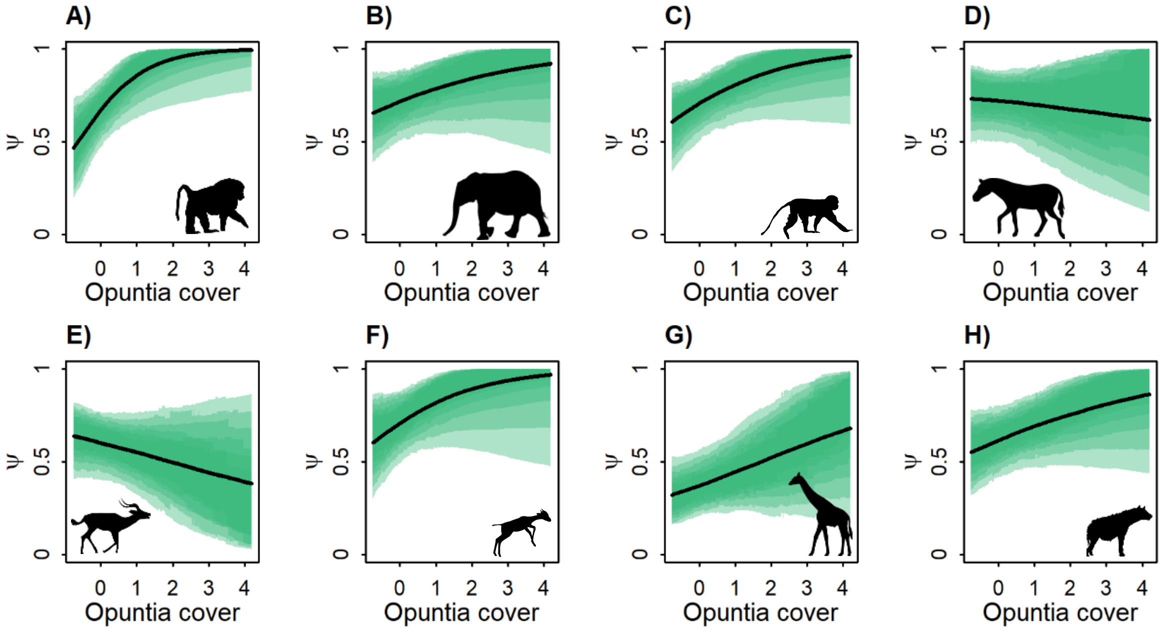


Figure 3. Marginal total effect of site-level *Opuntia* percentage cover (standardised) on occupancy probability (ψ) for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* does not indirectly affect occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Black lines indicate the posterior median marginal effect.

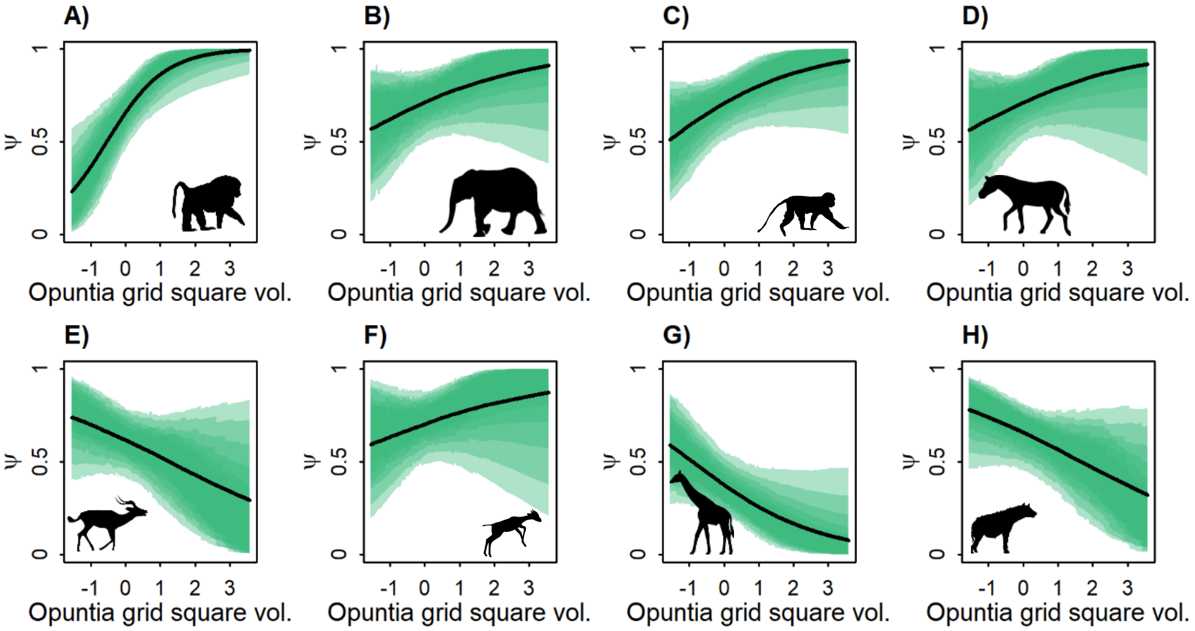


Figure 4. Marginal total effects of grid square-level *Opuntia* volume (standardised) on occupancy probability (ψ) for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* does not indirectly affect occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Black lines indicate the posterior median marginal effect.

Effects of Opuntia on mammalian temporal activity

Some of my focal species had different activity patterns in the high-*Opuntia* and low-*Opuntia* site pairs (Fig. 5). Olive baboons tended to have a higher level of activity in the morning in high-*Opuntia* sites (Fig. 5A). Elephants tended to be more active at high-*Opuntia* sites at night, while low-*Opuntia* sites had more elephant activity during the day (Fig. 5B). Impala were less active at high-*Opuntia* sites at night (Fig. 5E). Likewise, dik-dik were less active at high-*Opuntia* sites at night but were also more active at high-*Opuntia* sites during the day (Fig. 5F). Finally, I observed a spike in giraffe activity at high-*Opuntia* sites in the early afternoon (Fig. 5G).

The effects of site-level *Opuntia* cover on total activity levels were generally small and, for some species, the distribution of observations predicted by my model did not closely match the observed data (Fig. 6). However, the median site-level activity predicted by my models did slightly increase for olive baboons (Fig. 6A), elephants (Fig. 6B), and vervet monkeys (Fig. 6C), and slightly decrease for impala (Fig. 6E), dik-dik (Fig. 6F), and giraffe (Fig. 6G), as *Opuntia* cover increased.

In contrast to the effects of site-level *Opuntia* cover, the effects of grid square-level *Opuntia* volume were apparent for several of my focal species (Fig. 7). I observed clear increases in the median predicted activity with increasing *Opuntia* volume for olive baboons (Fig. 7A) and elephants (Fig. 7B), and for both of these species the distribution of observations predicted from the model closely matched the observed data. I also observed a positive effect of *Opuntia* on dik-dik activity (Fig. 7F), but this effect was weaker than for baboons and elephants. Conversely, my models revealed a negative relationship between *Opuntia* volume and activity for Grevy’s zebra (Fig. 7D), impala (Fig. 7E), and spotted hyena (Fig. 7H). There was also a slight decrease in the distribution of predicted activity for vervet monkeys (Fig. 7C), but the median predicted activity for this species remained at zero over the whole range of observed *Opuntia* volumes and the model’s predictions exhibited a poor fit to the observed data. I did not observe any clear relationship between *Opuntia* volume and activity for giraffe (Fig. 7G).

I observed qualitatively similar relationships between *Opuntia* and activity for models which included measures of the native plant community (Figs. 6, 7) and for models which did not include these covariates (Appendix E: Figs. S20, S21).

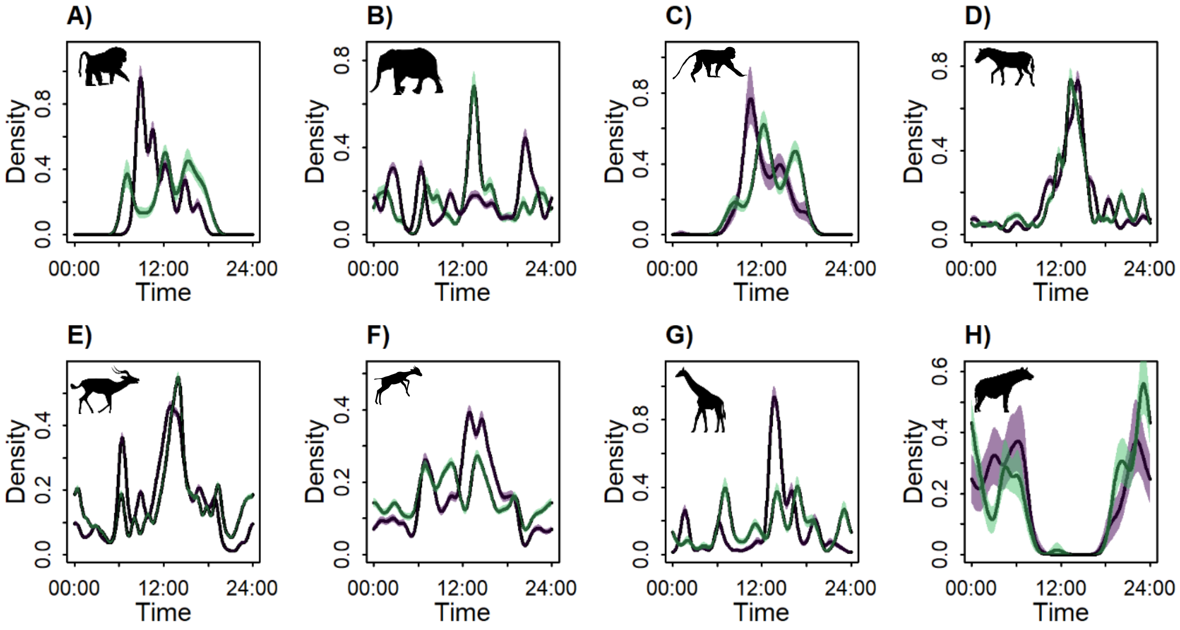


Figure 5. Activity kernels for species detections at high-*Opuntia* (dark green) and low-*Opuntia* (light green) sites, for: **A)** olive baboon (n = 1930, 610), **B)** elephant (n = 2884, 1457), **C)** vervet monkey (n = 273, 515), **D)** Grevy's zebra (n = 3114, 3141), **E)** impala (n = 17192, 24059), **F)** dik-dik (n = 6978, 6835), **G)** giraffe (n=1735, 1244), and **H)** spotted hyena (n = 132, 270). Shaded areas represent 95% confidence intervals. Sample sizes (n) represent the number of detections at high and low sites respectively.

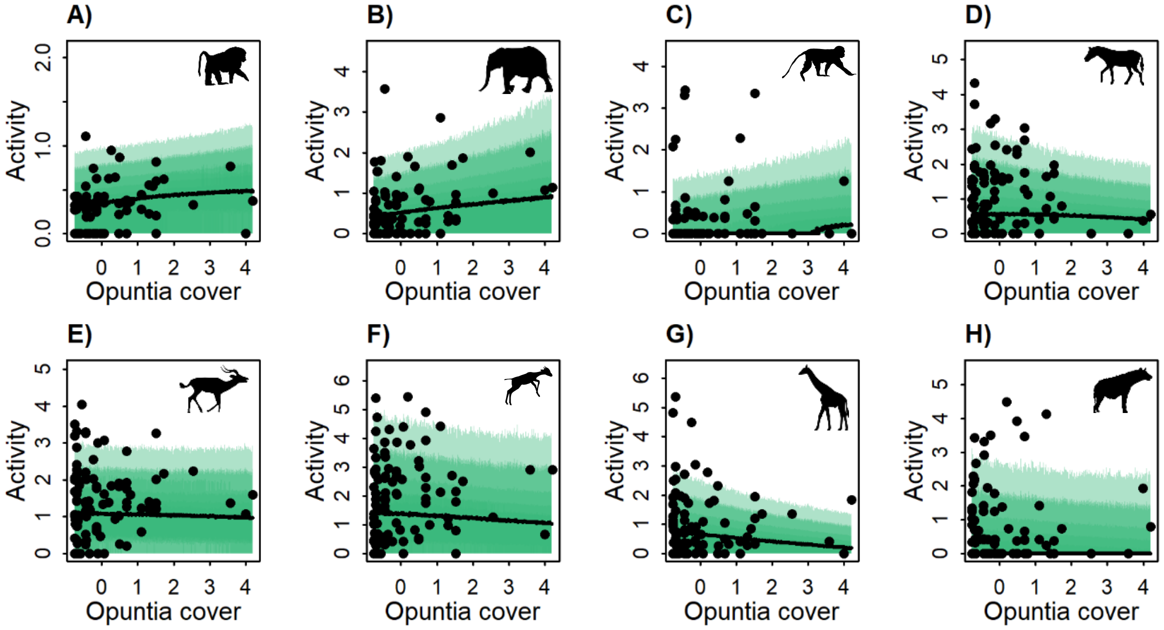


Figure 6. Relationships between total activity (rescaled) and site-level *Opuntia* percentage cover (standardised), for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* does not indirectly affect occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas encompass (from outside) 95%, 89%, 80%, 70%, 60%, and 50% of observations simulated from the posterior distribution. The black line represents the median value of these simulated observations. Points represent individual sites.

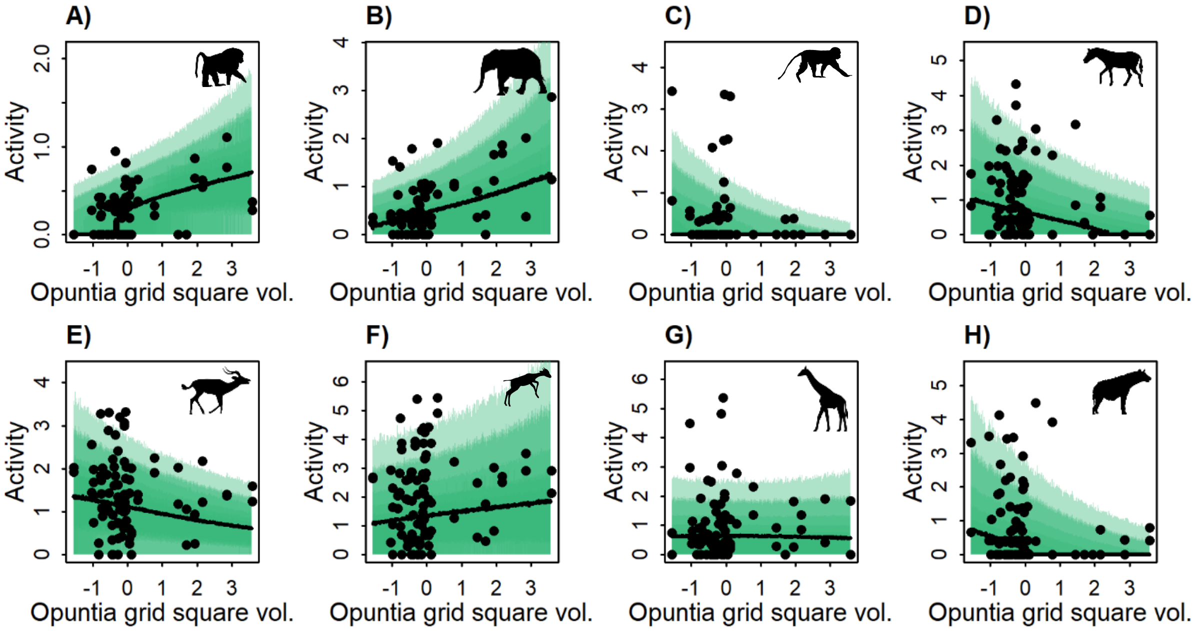


Figure 7. Relationships between total activity (rescaled) and grid square-level *Opuntia* volume (standardised), for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* does not indirectly affect occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas encompass (from outside) 95%, 89%, 80%, 70%, 60%, and 50% of observations simulated from the posterior distribution. The black line represents the median value of these simulated observations. Points represent individual sites.

Discussion

I aimed to measure the impacts of invasive *Opuntia* cacti on the occupancy and activity of eight key mammal species in Laikipia County. I found that the direction and magnitude of *Opuntia*'s effects on occupancy and activity varied among mammal species and depended on the spatial scale of the *Opuntia* covariate. These results have important implications for the conservation of key mammal species in the region, as well as for the future spread of *Opuntia* through seed dispersal.

A key finding was the negative effect of grid square-level *Opuntia* volume on the occupancy of the endangered reticulated giraffe (Muneza *et al.* 2018). This relationship may be due inhibited foraging, as I rarely observed giraffes feeding on vegetation growing in or around *Opuntia* stands (Chapter 5). Another possible explanation is that heavily invaded areas offer few suitable resting sites; recumbency is an important part of giraffes' daily activities (Saito & Idani 2020). Invaded sites could be unsuitable for recumbency due to a lack of physical space, or due to increased predation risk. Furthermore, mothers with calves are known to avoid closed habitats, presumably because dense vegetation reduces visibility and thus increases the risk of the calf being predated (Young & Isbell 1991). Habitat loss and fragmentation are thought to be the key drivers of population decline in the reticulated giraffe (Muneza *et al.* 2018). I argue that my findings support the conclusion that *Opuntia* invasion is contributing to this habitat loss; over the range of grid square-level *Opuntia* volumes that I observed, the median posterior probability of a site being occupied by giraffes decreased from 0.59 to 0.08. Given that Laikipia and the neighbouring Isiolo and Samburu Counties host approximately 25% of the reticulated giraffe's global population (see Supplementary Table 3 in Muneza *et al.* 2018), I argue that the rapid and continued expansion of *Opuntia* in the region poses a threat to the continued existence of this species. Consequently, strengthening the ongoing efforts to slow and reverse the spread of *Opuntia* through mechanical removal and biological control is critical.

In contrast to the effects of *Opuntia* on reticulated giraffe, I observed positive effects of *Opuntia* on the occupancy of elephants, olive baboons, and vervet monkeys; the relationship between grid square-level *Opuntia* volume and occupancy for olive baboons was especially strong. I also observed positive effects of *Opuntia* on olive baboon and elephant activity, particularly in my broad-scale models. These findings are not surprising; baboons, elephants, and vervet monkeys all regularly consume *Opuntia* fruit (Chapter 5) and are thought to be important dispersal agents for the *Opuntia* (Strum *et al.* 2015; Witt 2017; Githae 2019). My findings for elephants are also consistent with local communities' observation that elephants are attracted to *Opuntia* fruit, resulting in elephants encroaching with increased frequency on grazing areas near *Opuntia* stands (Shackleton *et al.* 2017). The fact that I generally observed more pronounced effects of grid square-level *Opuntia* than site-level *Opuntia* is also consistent with the explanation that these species are attracted by fruit, as grid square-level *Opuntia* is likely to be more representative of the overall availability of fruit resources.

The positive effects of *Opuntia* on the occurrence of mammalian frugivores may generate a positive feedback loop which facilitates the spread of the invasion. Frugivores are drawn to invaded areas, where they consume *Opuntia* fruits, and deposit the seeds in their faeces; this dispersal further increases the density or extent of the invaded area, which in turn attracts more frugivores. However, understanding how the habitat use of frugivores feeds back to influence the dynamics of the *Opuntia* invasion requires information which is currently lacking. In particular, it is unclear how far seeds are carried before they are deposited, or the proportion of deposition which occurs in currently invaded areas versus adjacent uninvaded habitat. This knowledge gap could be addressed by studying the habitat use of specific individuals or groups of frugivores to understand their movements in the hours following fruit consumption. If the frugivores generally remain within invaded areas, then seed dispersal will primarily increase the density of *Opuntia* in areas which are already invaded. However, if frugivores travel into uninvaded areas after feeding, then they will increase the invasion's spatial extent. Identifying the species that are responsible for transporting *Opuntia* seeds into uninvaded areas, and then estimating the distance over which this transportation occurs, would allow for more effective monitoring of currently uninvaded areas to detect and remove plants before they begin to produce their own fruit.

I also examined *Opuntia*'s effects on two of the most abundant herbivores in the region – impala and dik-dik – and found contrasting effects for the two species. For impala, I found negative relationships between *Opuntia* and occupancy at both spatial scales. One possible explanation for these effects is that *Opuntia* affects the foraging behaviour of the impala; *Opuntia* stands are not consumed by impala (Chapter 5), and the dense physical structure of *Opuntia* stands may prevent impala from accessing much of the other vegetation in an area. However, when I compared models with and without measures of the native plant community (percentage cover of grass, shrubs, forbs and succulents, and the number of trees), I observed similar results. This suggests that the effects on impala occupancy and activity are not driven by *Opuntia* affecting the native plant community. An important caveat is that I only examined broad categories of native plants; for logistical reasons, I did not record all species of plants which were present. This may obscure any effects which are due to *Opuntia* altering composition within vegetation classes (*e.g.,* by facilitating one species of forb over another) or effects mediated through key individual plant species (*e.g.,* key food plants). Further insights could be gained by investigating how *Opuntia* invasion alters the local plant community, and by examining the diet of individual animals inhabiting areas with different levels of *Opuntia*.

Another explanation for the effects of *Opuntia* on impala is that the effects are mediated by changes in actual or perceived predation risk. The presence of large *Opuntia* stands may block sightlines – reducing the distance at which an impala can detect an approaching predator – and impede escape, resulting in impala avoiding invaded areas. This explanation is supported by research which demonstrates that the interplay between habitat structure and predation risk is a key determinant of impala habitat use. Ford *et al.* (2014) found that impala at Mpala Research Centre tended to avoid closed wooded areas in favour of open glades, especially at night; notably, I also observed that impala activity was lower at night in high-*Opuntia* sites than in low-*Opuntia* sites. The authors also found that impala were more likely to encounter and be killed by predators in wooded areas, and used experimental manipulations of habitat structure to demonstrate that differences in forage quality between wooded areas and open glades could not explain the observed patterns (Ford *et al.* 2014). More recently, Epperly *et al.* (2021) not only confirmed the preference of impala for open habitats, but also showed that impala exhibit stronger antipredator responses in dense shrubby areas than in experimental clearings. Together, these findings strongly suggest that the effects of *Opuntia* on impala occupancy and activity are driven by changes in predation risk. Future research could confirm this mechanism through experimentally removing *Opuntia* stands, or by using the current *Opuntia*-removal programme as a natural experiment and examining the resulting changes in impala occurrence and antipredator behaviour. If changes to patterns of predation risk are found to be the main mechanism underlying *Opuntia*'s effects on impala habitat use, this suggests that *Opuntia* can moderate the trophic cascade through which impala influence native vegetation in the ecosystem (Ford *et al.* 2014). Investigating these potential herbivore-mediated impacts of *Opuntia* on native plants represents an important avenue for future research.

In contrast to the results for impala, dik-dik occupancy was positively related to *Opuntia* in both my fine-scale and broad-scale models, and I also observed a positive relationship between total dik-dik activity and *Opuntia* in my broad-scale model. A plausible explanation for this result is that *Opuntia* stands afford dik-dik protection from predators; dik-dik are much smaller than impala, meaning they may be able to move through and hide within *Opuntia* stands where impala cannot. Dik-dik are generally thought to prefer relatively closed habitats because they perceive open areas as risky (Otieno *et al.* 2019). Although dik-dik are known to decrease their short-term use of overstory cover (*i.e.,* trees and shrubs) in response to exposure to predator scent cues, this may represent a relatively brief increase in vigilance behaviour and is not incompatible with a preference for closed habitats (Ford & Goheen 2015). However, it is unclear whether dik-dik perceive *Opuntia* stands as safe or risky, and whether this perception matches the actual level of predation risk in invaded areas. To mechanistically link *Opuntia* invasion, predation risk, and dik-dik habitat use, methods similar to those previously applied to impala (*e.g.,* Ford *et al.* 2014; Epperly *et al.* 2021) could be employed to test whether predator encounter rate, predation rate, and dik-dik anti-predator responses are influenced by *Opuntia*. It will also be important to consider the role of territoriality, which may constrain changes in dik-dik habitat use (Ford & Goheen 2015). Investigating the constraints imposed by territoriality may also provide more general insights into the role of constraints in the behavioural impacts of invasive plants, which is a key outstanding research question in the field (Chapter 2; Stewart *et al.* 2021).

Opuntia-driven changes to predation risk may also explain why dik-dik were more active during the day at high-*Opuntia* sites, and at night in low-*Opuntia* sites; I speculate that dik-dik are able to venture further from the cover of *Opuntia* stands under the cover of darkness. This hypothesis could be tested by examining how the relationship between *Opuntia* and dik-dik activity is moderated by moonlight and cloud cover. If predation risk explains the observed activity patterns, then I would expect the effect to be weaker on moonlight nights and when cloud cover is low – as is observed in small mammals such as rodents (*e.g.,* Guiden & Orrock 2019)

The occupancy of my focal carnivore, the spotted hyena, was positively related to site-level *Opuntia* cover but negatively related to grid square-level *Opuntia* volume. I also observed that increasing grid square-level *Opuntia* had a negative effect on the total level of hyena activity but did not observe any clear relationship in my fine-scale activity model, nor did I observe any difference in activity timing between high-*Opuntia* and low-*Opuntia* site pairs. It is unclear whether these results are primarily driven by direct effects of *Opuntia* on spotted hyena hunting behaviour, or indirect effects through changes in the distribution of prey. Spotted hyenas are primarily cursorial predators (Périquet *et al.* 2015), so negative effects of broad-scale *Opuntia* volume on occupancy and activity may be due to *Opuntia* impeding the ability of hyenas to pursue prey. However, these negative relationships could also be due to changes in the occupancy of prey species – particularly impala – which I also observed. Furthermore, spotted hyenas live in groups which undergo complex fission-fusion dynamics which are influenced by ecological factors such as prey availability (Smith *et al.* 2008); these group dynamics could conceivably manifest as changes in occupancy or activity as individuals disperse to different areas around the landscape. Consequently, resolving the specific mechanisms underlying *Opuntia*'s effects on spotted hyena habitat use will require further study, likely involving the detailed tracking of specific individuals and groups (*e.g.,* using GPS tags).

A potential limitation of my study is that I was unable to disentangle the structurally mediated and resource-mediated pathways (Fig. 2) through which *Opuntia* alters mammalian habitat use. While in principle it is possible to separate these pathways by conditioning on the quantity of ripe fruits present in a site or grid square, in practice this does not work in an observational setting. This is because *Opuntia* size and fruiting are very closely related; there are too few observations of small fruiting plants or large non-fruiting plants for the model to estimate the effects reliably. While this problem could possibly be addressed by experimental manipulation (*e.g.,* removal of fruits from *Opuntia* stands) this is likely to be logistically infeasible for an invasion of this scale. Furthermore, an experimental approach may not work if the presence of large *Opuntia* stands, rather than presence of visible fruit, is the primary cue that drives the foraging behaviour of frugivorous mammals. This explanation is plausible since ripe fruits are commonly obscured among cladodes or have fallen to the ground, and are thus only visible at close range. More fundamentally, I argue that separating the structurally mediated and resource-mediated pathways is less important from a conservation perspective than estimating the total effect of *Opuntia*, which represents the expected effect of *Opuntia* expanding in range to invade new areas, as well as the likely effects of intervening to remove *Opuntia* from an area. Therefore, I do not believe that this limitation undermines the results of my investigation.

A key assumption of my approach is that the relationship between *Opuntia* and mammalian habitat use is due to *Opuntia* affecting habitat use, and not habitat use affecting the distribution of *Opuntia* (Fig. 2). In the long-term, this assumption may not be strictly true. For instance, long-term herbivore exclosure plots have a higher density of *Opuntia stricta* than control sites which are accessible to herbivores, implying that wild herbivores suppress *Opuntia* growth either directly by feeding on *Opuntia*, or indirectly by influencing *Opuntia*'s interactions with the native plant community (Wells *et al.* 2023). However, these effects likely operate on much longer timescales – months to years – than changes in animal behaviour, which can occur over a matter of hours and days. Therefore, I argue that the effects I observed over the relatively short timescale of my study are best interpreted as *Opuntia*'s effects on mammalian habitat use. However, it is clear that deepening our understanding of the complex interplay between the wild mammal community and *Opuntia* is an important avenue for future research; this is especially true for *O. engelmannii*, which has remained relatively unstudied to-date. These longer-term studies could aim to establish whether feedback loops – which are a common feature of the behavioural impacts of invasive plants (Chapter 2; Stewart *et al.* 2021) – are an important feature of the *Opuntia* invasion in Kenya.

As *Opuntia* species continue to spread across the landscape of Laikipia County the potential for them to exert ecological impacts will increase. By using camera traps to investigate the effects of *Opuntia* on mammalian habitat use, I have provided new insights into these ecological impacts. Specifically, my results show that *Opuntia* affects the occupancy and activity of key mammal species; the strength and direction on these effects varies among mammal species and depends on the spatial scale of the *Opuntia* covariate. Notably, my results suggest that a species of key conservation concern – the endangered reticulated giraffe (*G. reticulata*) – is being threatened by the *Opuntia* invasion. My findings underscore the need for current management efforts to be intensified, to slow and ultimately reverse the spread of *Opuntia* in Laikipia County.

Appendix A: Model notation

Gaussian process occupancy model

I assume that a site i (defined as the area surrounding one camera trap) is either occupied ($z_i = 1$) or unoccupied ($z_i = 0$) by a given species, with probability ψ_i of being occupied. However, the species is detected imperfectly – on a given visit t (defined as one day of camera trap deployment) the probability that a species is detected, conditional on its presence at the site, is $p_{i,t}$. If a species is absent from a site, then it is never detected (*i.e.,* I assume no false positives). Consequently, over a series of visits (a site receives v_i visits) the observed data at a site (y_i) follow a binomial distribution with v_i trials and probability $p_{i,t}$ z_i of success.

The probabilities of occupancy (ψ_i) and detection ($p_{i,t}$) at a site may depend on one or more environmental covariates – indeed, the objective of my study was to understand the relationship between *Opuntia* and the occupancy probability. To model these relationships I used a logistic regression framework, where logit(ψ_i) and logit($p_{i,t}$) are equal to a linear combination of measured environmental covariates (represented here by the generic covariates X and W) and their respective effect sizes (β_X and β_W), as well as intercept ($\bar{k}$, k_i, and α_{det}) parameters.

I defined occupancy covariates at the site level (*e.g.,* X_i), which I consider to be reasonable as variables such as vegetation structure are unlikely to change dramatically over the relatively short timescale over which my cameras were deployed. However, I defined detection covariates at the visit level (*e.g.,* $W_{i,t}$) to allow for rapidly changing environmental conditions (*e.g.,* weather) which may affect the probability that a species is detected on a given day.

The simplest occupancy models assume that the occupancy states at different sites are independent of one another. However, patterns of species occupancy often display spatial autocorrelation: the occupancy state for nearby sites tends to be more similar than for sites which are further apart. To model this spatial autocorrelation, I used a Gaussian process (McElreath 2021). This technique assumes that the covariance between a pair of sites i and j is a function of the distance between them. Two parameters control the shape of this relationship – η^2 defines the maximum covariance between a pair of sites, and ρ^2 defines the rate at which covariance declines with increasing distance. I then used a multivariate normal distribution to turn the resulting covariance matrix into a varying intercept, k_i, which I incorporated into my occupancy sub-model. This varying intercept can be viewed as an offset from the average intercept across all sites, $\bar{k}$.

This narrative description corresponds to the following model structure:

$$y_i \sim \text{Binomial}(v_i, p_{i,t}\, z_i)$$

$$z_i \sim \text{Bernoulli}(\psi_i)$$

$$\text{logit}(\psi_i) = \ln\left(\frac{\psi_i}{1-\psi_i}\right) = \bar{k} + k_i + \beta_X X_i$$

$$\begin{pmatrix} k_1 \\ k_2 \\ \vdots \\ k_i \end{pmatrix} \sim \text{MVNormal}\left(\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{K}\right)$$

$$K_{i,j} = \eta^2 \exp\left(-\rho^2 D_{i,j}^2\right)$$

$$\text{logit}(p_{i,t}) = \ln\left(\frac{p_{i,t}}{1-p_{i,t}}\right) = \alpha_{\text{det}} \; + \; +\beta_W W_{i,t}$$

Additionally, I used the following prior distributions, which I chose based on the results of prior predictive simulations (Appendix B):

$$\beta_X, \beta_W \sim \text{Normal}(0, 1)$$

$$\alpha_{\text{det}} \sim \text{Normal}(0, 0.5)$$

$$\bar{k} \sim \text{Normal}(0, 0.5)$$

$$\eta^2 \sim \text{Exponential}(2)$$

$$\rho^2 \sim \text{Log}-\text{normal}(0, 1)$$

Hurdle model

I modelled the total level of a species' activity at a site (indexed i) as a mixture of Bernoulli and normal distributions. Specifically, a site has a probability θ of showing no activity, which represents the probability that a site is not used or the site is used but the species is never detected. Consequently, a site has probability (1 – θ) of being used, in which case the level of activity is modelled as a log-normal distribution with parameters μ and σ.

Both μ and θ are modelled as functions of one or more environmental covariates (represented here by the generic covariates X and W) in a linear modelling framework. As θ is a probability, and hence must lie between zero and one, I used the logit link function for its model. In addition to environmental covariates, both linear models incorporated Gaussian processes to account for spatial autocorrelation.

$$p(A_i|\theta, \mu, \sigma) = \begin{cases} (1-\theta_i)\mathit{Log\text{-}normal}(\mu_i, \sigma) & \text{if } A_i > 0 \\ \theta_i & \text{if } A_i = 0 \end{cases}$$

$$\mu_i = \bar{k} + k_i + \beta_X X_i$$

$$logit(\theta_i) = ln\left(\frac{\theta_i}{1-\theta_i}\right) = \bar{\omega} + m_i + \gamma_W W_i$$

$$\begin{pmatrix} k_1 \\ k_2 \\ \vdots \\ k_i \end{pmatrix} \sim \text{MVNormal}\left(\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{K}\right)$$

$$K_{i,j} = \eta^2 \exp\left(-\rho^2 D_{i,j}^2\right)$$

$$\begin{pmatrix} m_1 \\ m_2 \\ \vdots \\ m_i \end{pmatrix} \sim \text{MVNormal}\left(\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{M}\right)$$

$$M_{i,j} = \tau^2 \exp\left(-\varphi^2 D_{i,j}^2\right)$$

For this model I used the following prior distributions:

$$\sigma \sim Exponential(5)$$

$$\bar{k}, \beta_X \sim Normal(0, 0.4)$$

$$\bar{\omega}, \gamma_W \sim Normal(0, 1)$$

$$\eta^2, \tau^2 \sim Exponential(2)$$

$$\rho^2, \phi^2 \sim Log-normal(0, 1)$$

I chose the priors for $\bar{k}$, β_X and σ with the aid of prior predictive simulations (Appendix B). Prior choice for the rest of the parameters was informed by the simulations I conducted for the occupancy models (Appendix B).

Appendix B: Prior predictive simulations

Introduction

Historically, ecologists have often employed extremely flat, so-called "uninformative" or "non-informative" default priors (Banner *et al.* 2020). However, the use of flat default priors is poor statistical practice; flat priors can result in overfitting and may cause Markov chain Monte Carlo (MCMC) algorithms to sample inefficiently or, in the case of more complex model structures, totally fail to adequately explore the posterior distribution (McElreath 2021). Furthermore, flat priors which appear "uninformative" on the scale at which they are specified can prove to be strongly informative on the outcome scale, such as when intercept and slope parameters in logistic regression or occupancy models are transformed to the probability scale using the logit link function (Northrup & Gerber 2018; Banner *et al.* 2020; McElreath 2021). However, specifying better priors can be challenging, particularly for hyperparameters or for parameters which interact with one another. One method for understanding the consequences of different prior distributions, and thus making informed decisions about which priors to specify, is to conduct prior predictive simulations (McElreath 2021; Wesner & Pomeranz 2021). In this appendix, I use prior predictive simulations to support the choice of prior distributions for the parameters in my models. Code to fully reproduce my simulations is available at https://github.com/Peter-Stewart/Zooniverse_processing.

Gaussian process occupancy model

Gaussian process parameters

In a Gaussian process occupancy model (see Appendix A), the covariance between a pair of sites, i and j, is related to the distance between them by the kernel function:

$$\mathrm{K}_{\mathrm{i,j}} = \eta^2 \exp\left(-\rho^2 \mathrm{D}_{\mathrm{i,j}}^2\right)$$

where $\mathrm{K}_{\mathrm{i,j}}$ is the covariance, η^2 is the maximum covariance between sites, ρ^2 is the rate at which covariance declines with distance, and $\mathrm{D}_{\mathrm{i,j}}^2$ is the squared distance between the sites (McElreath 2021). As $\mathrm{D}_{\mathrm{i,j}}^2$ is observed data, the parameters which require priors are η^2 and ρ^2.

For modelling purposes, I found it to be more convenient to re-scale the distances from their original units (metres) by first converting the distances into kilometres and then dividing by six (Fig. S1).

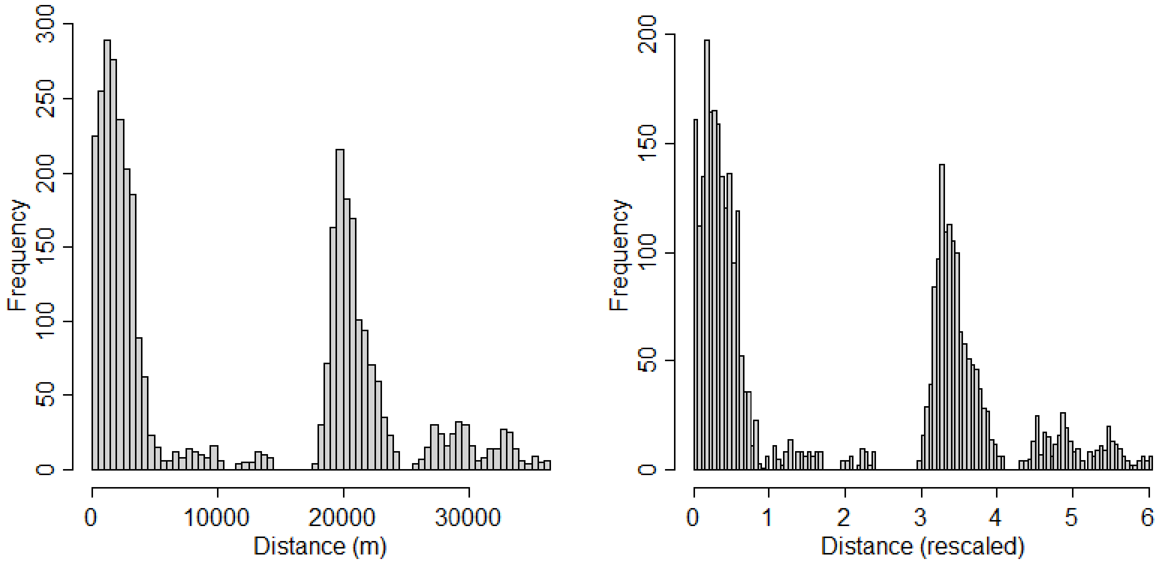


Figure S1. The distribution of distances between camera trap sites, in metres (left panel) and rescaled by dividing by 6000 (right panel).

Given that the values of the two parameters, η^2 and ρ^2, must be positive (McElreath 2021) one choice of prior is the exponential distribution. Varying the rate for these exponential priors alters the prior distribution for the relationship between covariance and distance. Based on visualisations of this relationship (Fig. S2), I concluded that an exponential(2) prior for η^2 strikes a reasonable balance, being moderately sceptical of large covariances between nearby sites while still (due to the long tail of the exponential distribution) permitting large covariances if demanded by the data. However, I also found that both choices of exponential prior for ρ^2 imply that the covariance between distant sites, such as those more than 3 units (~ 15km) apart, is high – especially relative to the covariance between neighbouring sites (Fig. S2). As the spatial autocorrelation between neighbouring sites (~ 50m apart) is likely to greatly exceed that between distant sites, I decided to consider prior distributions for ρ^2 which better encapsulated that assumption.

An alternative choice of prior for positive parameters is the log-normal distribution. When a log-normal prior is used for ρ^2, covariance decreases rapidly with distance and is lower at long distances than when an exponential prior is used (Fig. S3). Consequently, I decided on an exponential(2) prior for η^2 and a log-normal(0, 1) prior for ρ^2. These priors represent the assumption that covariance between sites may be high between nearby sites (*i.e.*, those within the same regions or in nearby parts of adjacent regions) but that there is probably little covariance between sites which are more than ~ 15km apart (Fig. S4). I emphasise that the priors do not dictate that there is no covariance between distant sites (I have added the 99% compatibility interval to Fig. S4 to further emphasise this point), meaning that the model can accommodate higher covariances between distant sites if demanded by the data. The priors are also weakly regularising (*i.e.*, slightly sceptical of very large covariances at all distances) which helps to guard against overfitting (McElreath 2021).

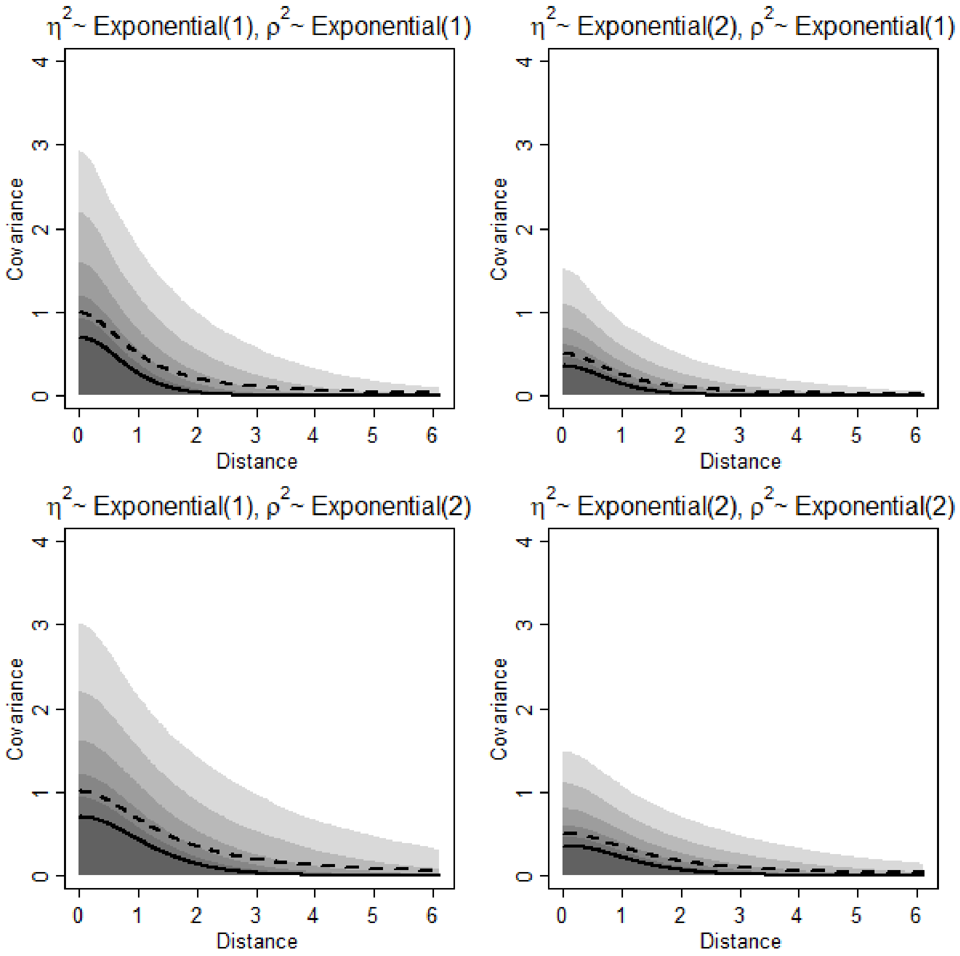


Figure S2. Prior distributions of the relationship between covariance and distance when exponential priors are specified for the parameters η^2 and ρ^2. Panels represent these prior distributions under different choices of rate parameter for the exponential distributions. Grey shaded regions show 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals (from light to dark respectively), with solid and dashed black lines indicating the prior median and mean respectively. Priors for the two covariance function parameters, η^2 and ρ^2, are displayed above each panel.

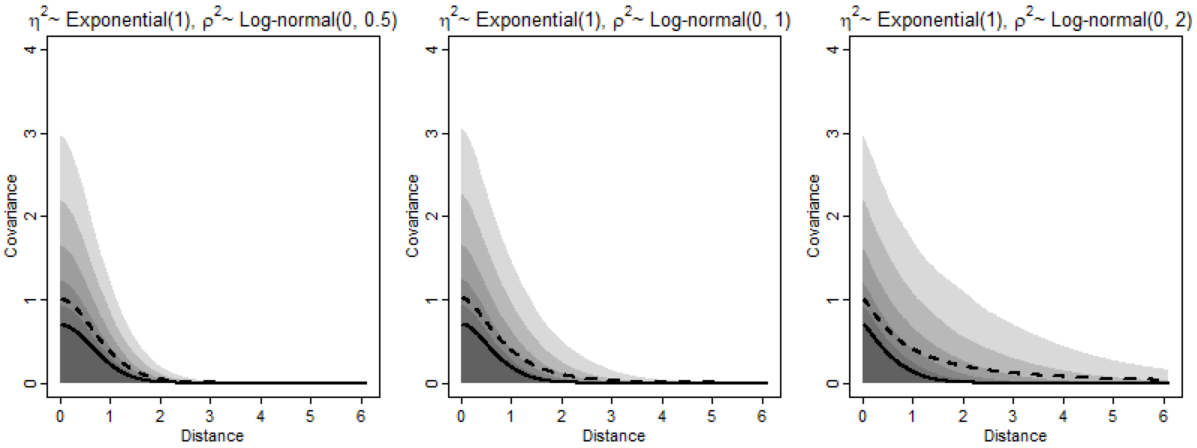


Figure S3. Prior distributions of the relationship between covariance and distance when an exponential prior is specified for η^2 and a log-normal prior for ρ^2. Panels represent these prior distributions under different choices of standard deviation parameter for the log-normal distribution. Grey shaded regions show 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals (from light to dark respectively), with solid and dashed black lines indicating the prior median and mean respectively. Priors for the two covariance function parameters, η^2 and ρ^2, are displayed above each panel.

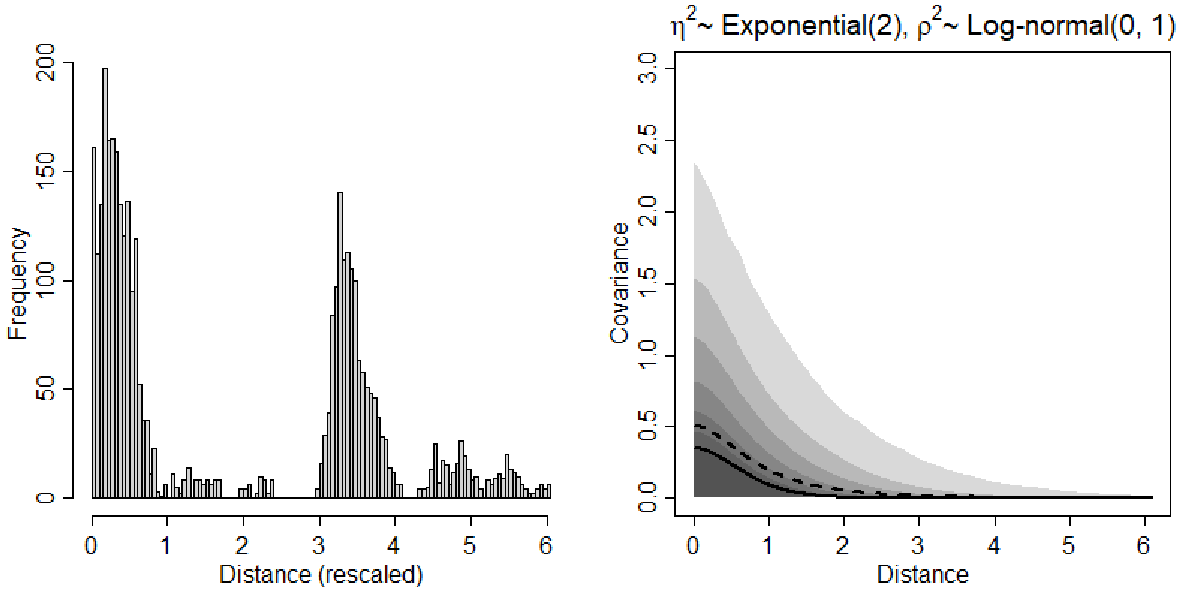


Figure S4. **Left panel:** The distribution of (rescaled) distances between camera trap sites. **Right panel:** The prior distribution of the relationship between covariance and distance which I selected for my models (see Appendix A). Grey shaded regions show 99%, 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals (from light to dark respectively), with solid and dashed black lines indicating the prior median and mean respectively. Priors for the two covariance function parameters, η^2 and ρ^2, are displayed above the panel.

Occupancy and detection sub-model parameters

The occupancy and detection sub-models of a Gaussian process occupancy model are in the form of a logistic regression. For instance, for a probability parameter q, the relationship between q and a covariate X is modelled as:

$$\mathrm{logit}(q_i) = \ln\left(\frac{q_i}{1 - q_i}\right) = \alpha + \beta X_i$$

Where i is the site index, α is the intercept and β is the slope. When covariate X has been standardised by z-transformation (*i.e.*, subtracting the mean of X from each value and then dividing by the standard deviation of X), α represents the value of $\mathrm{logit}(q_i)$ when X_i equals the average value of X, and β represents the effect of changing X by one standard deviation.

In situations where there is no prior information to suggest the direction of a covariate's effect, a normal prior with a mean of zero is sensible for the β parameter because it is agnostic about whether the effect of the covariate is positive or negative. Likewise, a zero mean for the α parameter is sensible, as it means that when a standardised X is at its average value (*i.e.*, X equals zero) the probability is 0.5.

After choosing a mean, it is then necessary to choose a standard deviation for the normal priors. As mentioned above, in logistic regression priors which are flat on the linear model scale are strongly informative on the probability scale (Northrup & Gerber 2018; Banner *et al.* 2020; McElreath 2021). For instance, when I varied the standard deviation across three orders of magnitude, I observed that priors with a larger standard deviation (*i.e.,* flat priors) result in the model assigning nearly all of the probability to values near zero and one (Fig. S5). I conducted further simulations with standard deviation values of 2, 1, and 0.5 for the α prior and a standard deviation of 1 for the β prior (Fig. S6). Based on these results, I chose a Normal(0, 0.5) prior for α_{det}, and a Normal(0, 1) prior for the β parameters in the detection sub-model.

In the detection sub-model, the above simulations are sufficient to guide the choice of priors. However, in the occupancy sub-model, the varying intercept k_i (which results from the Gaussian process) also plays a role:

$$\mathrm{logit}(\psi_i) = \ln\left(\frac{\psi}{1 - \psi}\right) = \bar{k} + k_i + \beta_X X_i$$

Consequently, setting a sensible prior for $\bar{k}$ additionally requires consideration of k_i. I therefore conducted simulations with a range of normal priors for $\bar{k}$ (Fig. S7). Based on the results of these simulations, I decided on a Normal(0, 0.5) prior for $\bar{k}$, and a Normal(0, 1) prior for the β parameters in the occupancy sub-model.

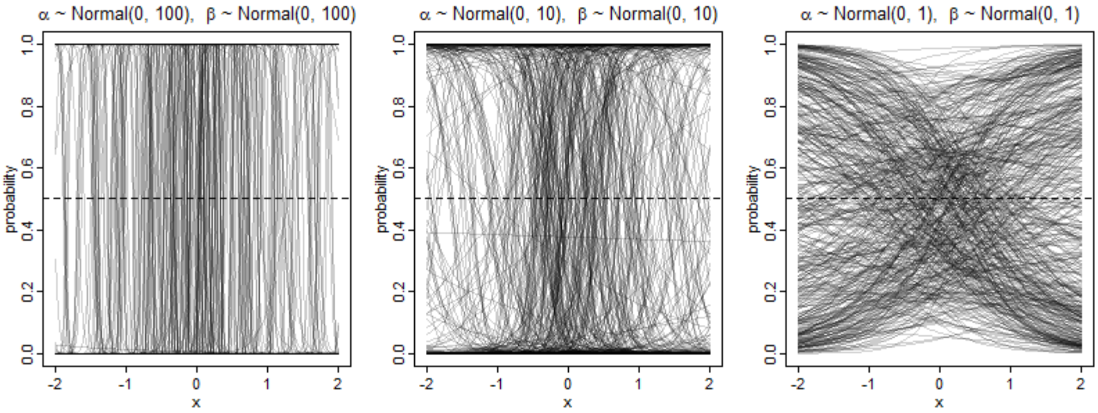


Figure S5. 500 regression lines drawn from the prior distributions of α and β for three different choices of Normal prior. Priors are defined on the log-odds scale, while the regression lines are displayed on the probability scale.

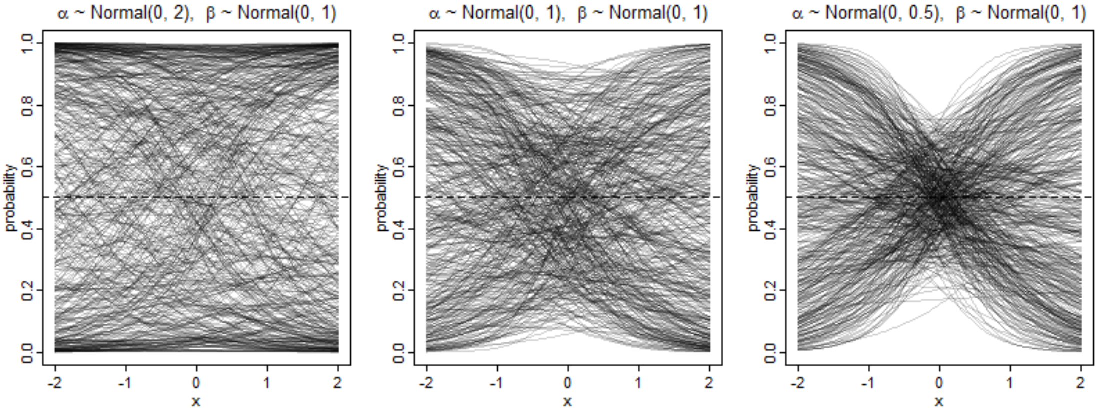


Figure S6. 500 regression lines drawn from the prior distributions of α and β for three different choices of Normal prior. Priors are defined on the log-odds scale, while the regression lines are displayed on the probability scale.

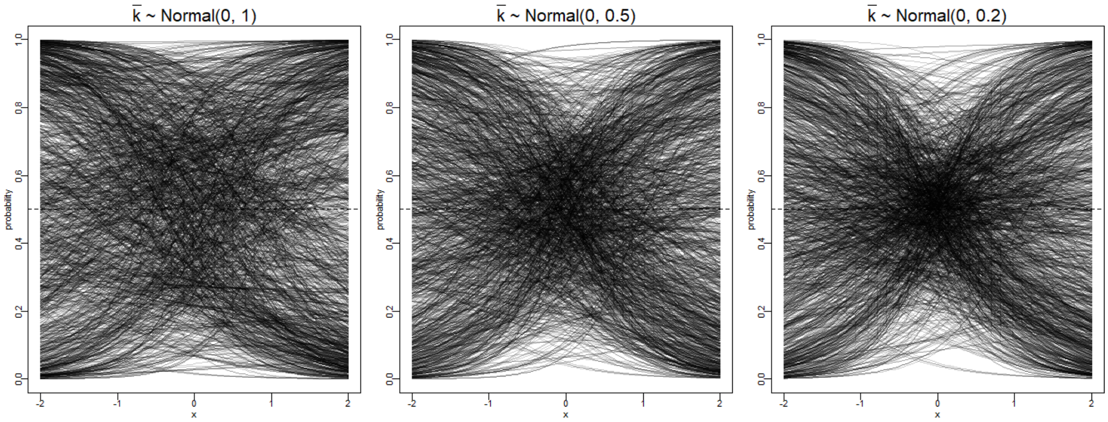


Figure S7. Regression lines drawn from the prior distributions of $\bar{k}$, k_i, and β_X, for different values of $\bar{k}$. A normal(0, 1) prior was used for β_X, while k_i was calculated using an exponential(2) prior for η^2 and a log-normal(0, 1) prior for ρ^2 in combination with the actual distances between sites. Only the first four values of k_i were retained for each value of η^2 and ρ^2 drawn from the prior distributions, to prevent the plots from becoming uninterpretable due to over-plotting. 500 values were drawn from the prior distributions of $\bar{k}$ and β_X, meaning that a total of 2000 regression lines are shown in each plot.

Hurdle model

In my hurdle model (see Appendix A), the parameter θ is modelled in a logistic regression framework, so I based my choice of priors on the results of the simulations which I conducted for the occupancy model. For the part of the model which comes into play when activity is observed (*i.e.*, when $A_i > 0$) I conducted further simulations. The structure of this section of the model is:

$$p(A_i|\theta, \mu, \sigma) = (1 - \theta_i) Log\text{-}normal(\mu_i, \sigma) \quad \text{if } A_i > 0$$

$$\mu_i = \bar{k} + k_i + \beta_X X_i$$

Where X is a covariate. I conducted my simulations using a simplified version of this model:

$$Y_i = Log\text{-}normal(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta X_i$$

Where X is a covariate and Y is the observed outcome. In this model, the parameters which require prior distributions are α, β, and σ. I checked various combinations of α, β, and σ priors, and decided on α ~ Normal(0, 0.4), β ~ Normal(0, 0.4), and σ ~ Exponential(5) as these priors allowed for both positive and negative relationships between X and Y, and the priors assigned more probability to small effects (*i.e.*, they are weakly regularising) without ruling out stronger effects if supported by the data (Fig. S8).

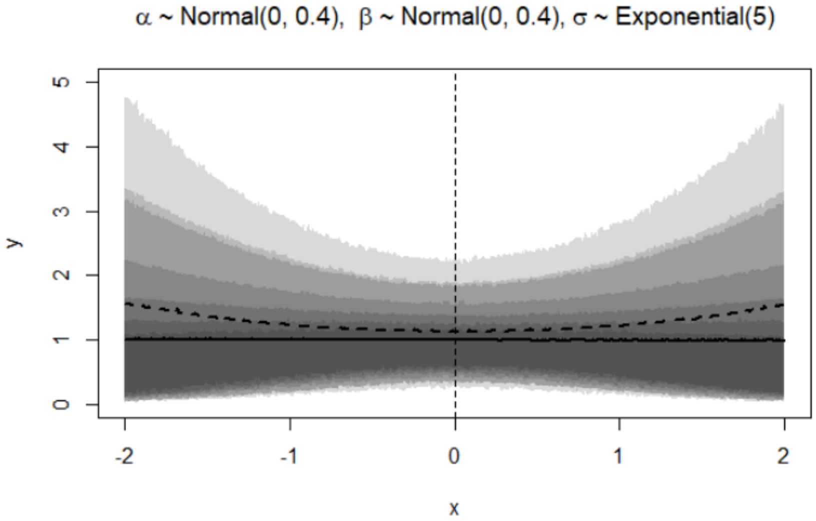


Figure S8. Prior distribution of the relationship between variables X and Y for my choice of prior distributions for α, β, and σ. Grey shaded regions show 99%, 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals (from light to dark respectively), with solid and dashed black lines indicating the prior median and mean respectively.

Appendix C: Model validation on synthetic data

My occupancy model structure (Appendix A) is justified based upon my assumptions about the underlying data-generating process, and my choice of prior distributions is supported by prior predictive simulations (Appendix B). However, implementing a model in a probabilistic programming language such as Stan is challenging, and it is important to ensure that errors are not accidentally introduced. To ensure that my occupancy model was operating as intended, and that it was capable of recovering accurate parameter estimates, I validated it by fitting it to synthetic data. Code to fully reproduce my analysis is available at https://github.com/Peter-Stewart/Zooniverse_processing.

I used the actual coordinates of the sites in my real data to construct the distance matrix used in the synthetic data, in order to diagnose any potential issues resulting from the spatial structure of the sites (*e.g.*, numerical underflow and model failure resulting from the rescaling of inter-site distances). I also used the actual number of visits (*i.e.*, camera trap days) each site received, to ensure that there were no issues resulting from some sites receiving relatively few visits. I included two covariates for occupancy, and one time-varying covariate for detection.

In my model, I used the same prior distributions as in the models which were fitted to real data (Appendix A) – these priors were chosen based on the results of prior predictive simulations (Appendix B). I ran the model with four chains each with 4000 iterations, of which 3000 were used for warmup and 1000 were used for inference. As with the models which I fitted to the real data, I employed a non-centred parameterisation to improve sampling efficiency.

Examination of my model's diagnostic plots (Figs. S9, S10) and trace rank plots for the key parameters (Fig. S11) indicated that sampling was successful. The true values for all slope and intercept parameters lay well within their respective posterior distribution (Fig. S12), and the estimated occupancy probability at each site was generally close to the true value, particularly for sites with larger numbers of visits (Fig. S13). Finally, the inferred pattern of spatial autocorrelation closely resembled the true autocorrelation between sites (Fig. S14). Based on these results, I concluded that my model was suitable to be fitted to the real data.

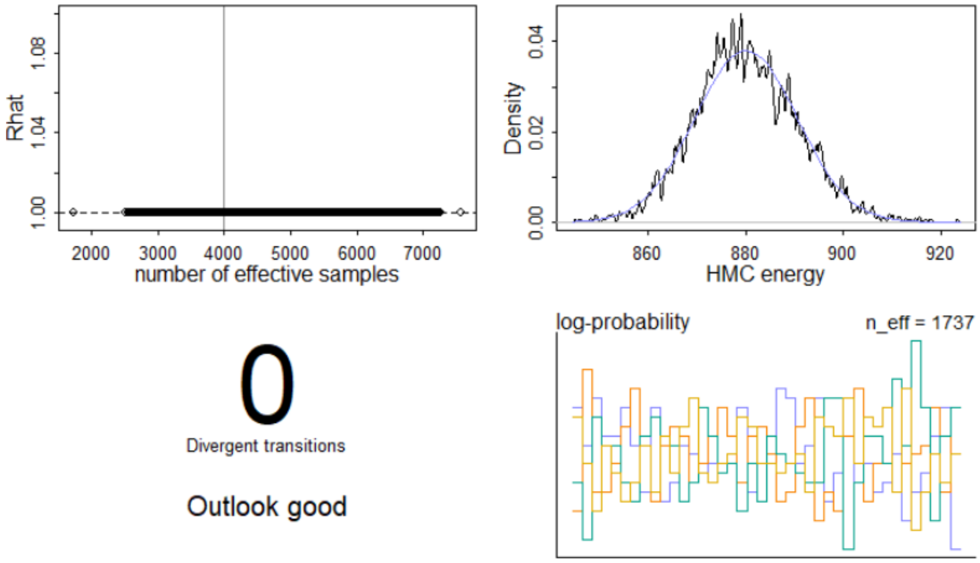


Figure S9. Diagnostic plots for the test model. **Top left:** Gelman-Rubin convergence diagnostic ($\hat{R}$; Gelman & Rubin 1992) versus number of effective sample size for all parameters in the model (n = 16807). Values of $\hat{R}$ equal to 1.00 indicate that the Markov chains have successfully converged. The vertical line indicates the actual number of Markov chain samples used for inference. **Top right:** Kernel density plot of the HMC energy diagnostic (black line), which should follow a normal distribution (blue line). **Bottom left:** Number of divergent transitions. **Bottom right:** Trace rank plot for the log-probability parameter, with number of effective samples (n_eff) displayed.

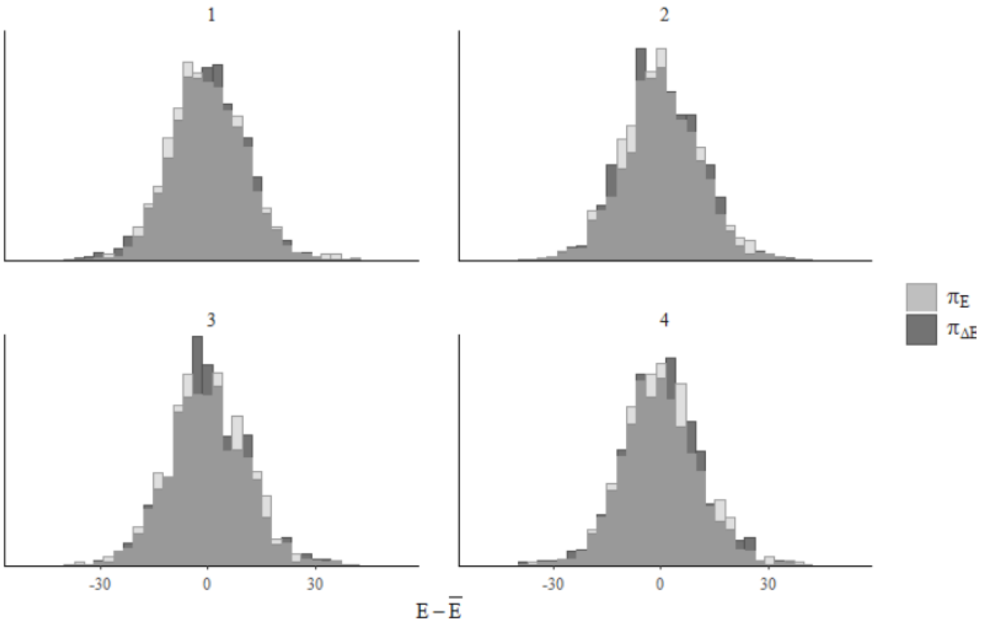


Figure S10. Histograms of the marginal energy distribution (π_E) and energy transition density ($\pi_{\Delta E}$) of the test model's Markov chains. The close match between these two distributions indicates that that the chains should effectively explore the posterior distribution (Betancourt 2018).

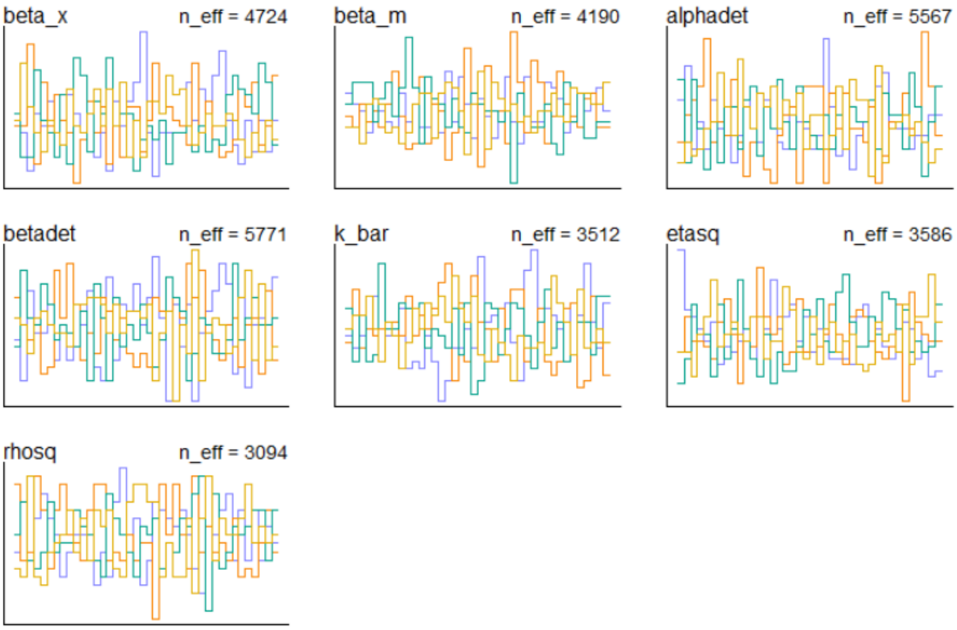


Figure S11. Trace rank plots for the test model's key parameters. Colours indicate separate Markov chains.

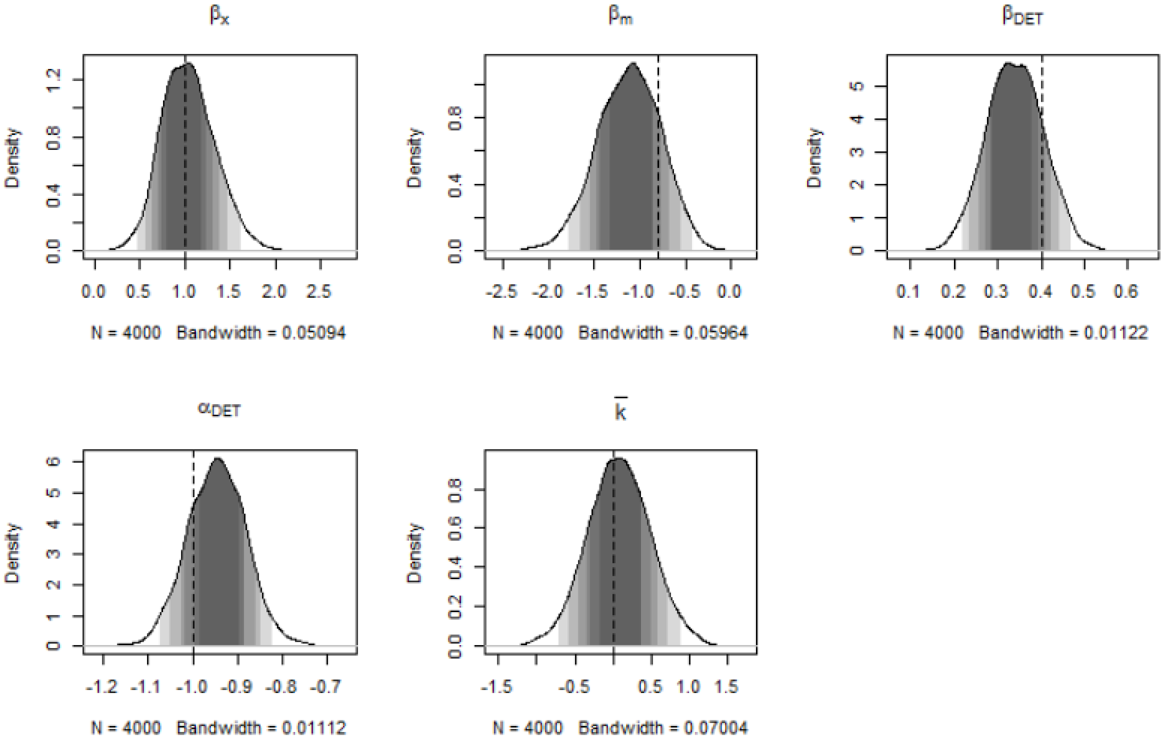


Figure S12. Kernel density plots of the posterior samples (n = 4000) for the test model's key parameters, with each parameter's true value represented as a vertical dashed line. Shaded regions represent 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals (from light to dark respectively).

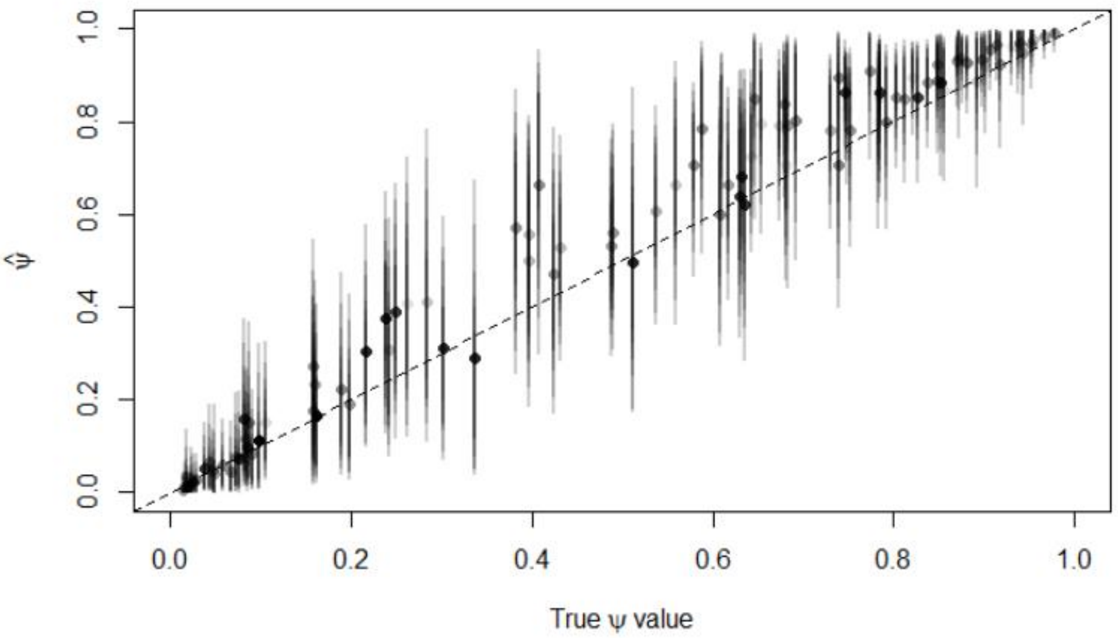


Figure S13. Estimated ($\widehat{\psi}$) versus true values for the occupancy probability (ψ) at each site. Points indicate the posterior median, and vertical lines represent compatibility intervals (at 95%, 89%, 80%, 70%, 60%, and 50% from dark to light respectively). Points which are more transparent represent sites which were visited fewer times.

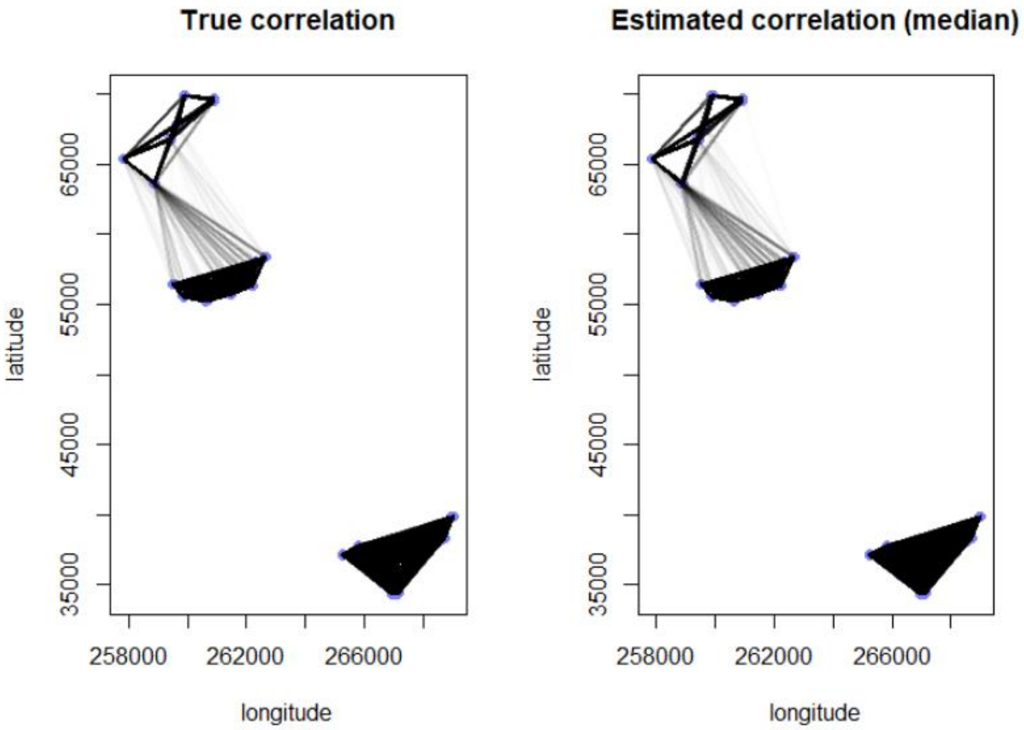
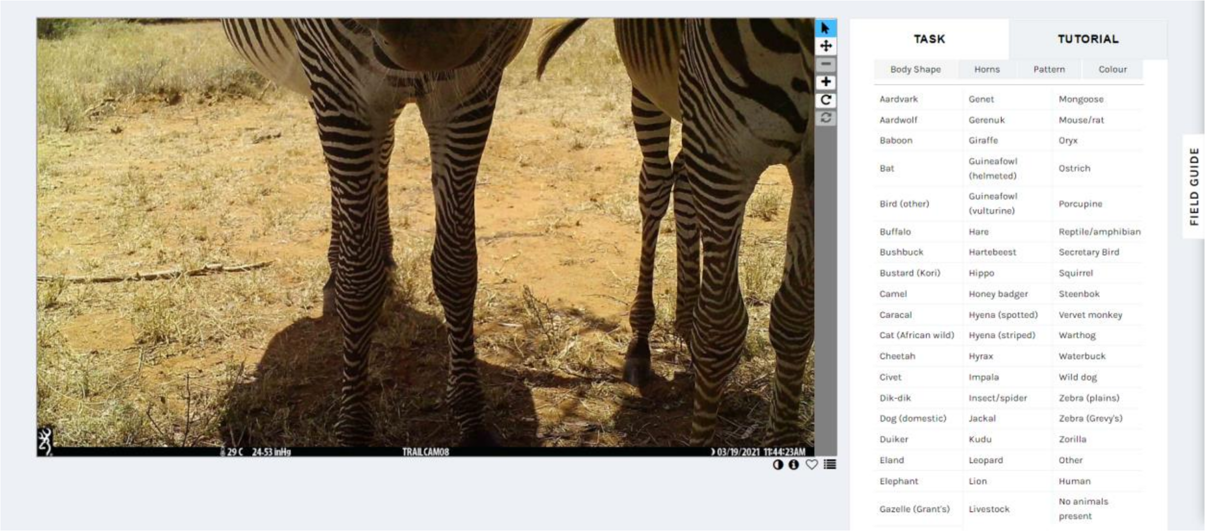


Figure S14. The true spatial autocorrelation present in the simulated dataset (left panel) and the posterior median spatial autocorrelation estimated by the model (right panel).

Appendix D: Volunteer classifications

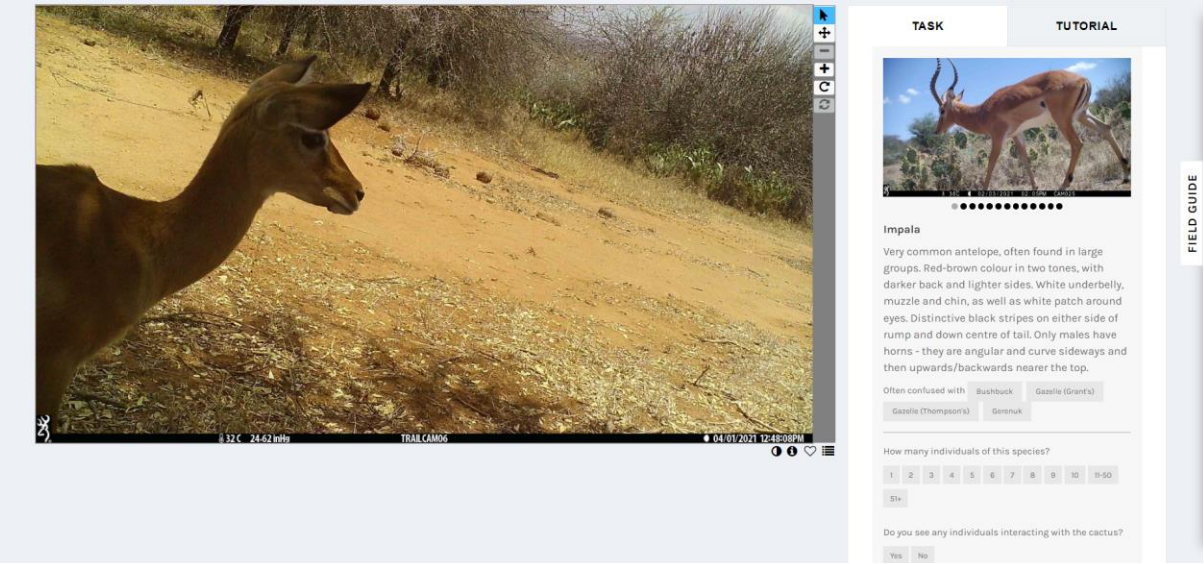
The Prickly Pear Project Kenya (project link: https://www.zooniverse.org/projects/peter-dot-stewart/prickly-pear-project-kenya) user interface (Fig. S15) presented a volunteer with a randomly selected camera trap image – the user was then asked to select from a list all of the species which were present in the image, how many individuals of each species were present, and whether any individuals appeared to be interacting with the cactus. As the purpose of the latter question was only to flag images for further expert review, "interacting" was vaguely defined, with the example in the project tutorial being "eating the cactus or its fruits". Clicking on a species in the list displayed an information panel to help the user to make their choice (Fig. S16). In addition to photos and diagnostic information for the selected species, the information panel contained the names of species which the selected species is likely to be confused with due to their physical similarity. For example, if "impala" was selected, then the user was informed that this species is often confused with bushbuck, Grant's gazelle, Thompson's gazelle, and gerenuk (Fig. S16). Clicking on these species' names would bring up further information on the key diagnostic differences between the each species and the species that the user had originally selected, along with a prompt for the user to select one of the species.

A subset (n = 23786) of my images were classified by an expert (either P.S.S. or the Prickly Pear Project Kenya moderator). I used this image subset to assess the accuracy of the volunteer classifications and the robustness of my consensus classification method by comparing the expert classification for each image to the classifications made by the other volunteers. I found that the volunteers produced highly accurate classifications, particularly once a consensus had been taken (Table S1, Fig. S17).



Aardvark
Aardwolf
Baboon
Bat
Bird (other)
Buffalo
Bushbuck
Bustard (Kori)
Camel
Caracal
Cat (African wild)
Cheetah
Civet
Dik-dik
Dog (domestic)
Duiker
Eland
Elephant
Gazelle (Grant's)
Genet
Gerenuk
Giraffe
Guineafowl (helmeted)
Guineafowl (vulturine)
Hare
Hartebeest
Hippo
Honey badger
Hyena (spotted)
Hyena (striped)
Hyrax
Impala
Insect/spider
Jackal
Kudu
Leopard
Lion
Livestock
Mongoose
Mouse/rat
Oryx
Ostrich
Porcupine
Reptile/amphibian
Secretary Bird
Squirrel
Steenbok
Vervet monkey
Warthog
Waterbuck
Wild dog
Zebra (plains)
Zebra (Grevy's)
Zorilla
Other
Human
No animals present

Figure S15. The classification panel. A randomly selected camera trap image is displayed on the left, and a list of species is displayed on the right. The user must classify an image as containing one or more species (or "no animals present") before being allowed to continue. The user has the option to zoom and pan the photo, as well as invert the colours. The "field guide" tab is visible to the right – when clicked, it brings up a species ID guide as well as information about *Opuntia* and the Ewaso ecosystem. The user is also able to access the project tutorial (which is automatically displayed to all users on their first visit to the classification panel) by clicking the "tutorial" tab at the top-right.



Impala

Very common antelope, often found in large groups. Red-brown colour in two tones, with darker back and lighter sides. White underbelly, muzzle and chin, as well as white patch around eyes. Distinctive black stripes on either side of rump and down centre of tail. Only males have horns - they are angular and curve sideways and then upwards/backwards nearer the top.

How many individuals of this species?

Do you see any individuals interacting with the cactus?

Figure S16. The information displayed when a user clicks on a species in the list (here, the user has clicked “impala”). The user is able to view different example photos by clicking the black dots under the image. Also displayed are species with which the selected species is often confused – here, the options are bushbuck, Grant’s gazelle, Thomson’s gazelle, and gerenuk. Clicking one of these options brings up an information panel with example images of the second species, and text which explains the differences between the two species – the user is then able to select which of the two species they think is correct. The user is also prompted to answer how many individuals of their selected species are present, as well as whether any individuals are interacting with the cactus – the user must answer these questions to continue.

Table S1. Classification accuracy for volunteer classifications, based on 23786 images which were classified by both an expert and volunteers. Results are shown for both consensus classifications (see main text) as well as the raw non-consensus volunteer classifications. Sensitivity and specificity are defined as Pr(classified present | truly present) and Pr(classified absent | truly absent) respectively. Species marked with an asterisk (*) were not present in the expert-classified set of images, and therefore do not have sensitivity values as they were never truly present.

	Consensus		**Raw**	
	Sensitivity	**Specificity**	**Sensitivity**	**Specificity**
Focal species				
Dik-dik *(Madoqua spp.)*	0.992	1.000	0.838	0.985
Elephant *(Loxodonta africana)*	0.995	1.000	0.942	0.999
Grevy's zebra *(Equus grevyi)*	0.972	0.999	0.761	0.995
Impala *(Aepyceros melampus)*	0.996	0.999	0.826	0.990
Olive baboon *(Papio anubis)*	0.995	1.000	0.875	0.999
Reticulated giraffe *(Giraffa reticulata)*	0.994	1.000	0.902	0.999
Spotted hyena *(Crocuta crocuta)*	0.989	1.000	0.715	1.000
Vervet monkey *(Chlorocebus pygerythrus)*	1.000	1.000	0.853	0.999
Other mammals				
Aardvark *(Orycteropus afer)**	NA	1.000	NA	0.999
Aardwolf *(Proteles cristata)**	NA	1.000	NA	1.000
African wild dog *(Lycaon pictus)**	NA	1.000	NA	1.000
African wildcat *(Felis lybica)**	NA	1.000	NA	1.000
Bat	0.941	1.000	0.500	1.000
Black-backed jackal *(Canis mesomelas)*	1.000	1.000	0.699	1.000
Buffalo *(Syncerus caffer)*	1.000	1.000	0.792	0.999
Bushbuck *(Tragelaphus sylvaticus)*	1.000	1.000	0.479	0.999
Camel *(Camelus dromedarius)*	0.991	0.999	0.857	0.999
Caracal *(Caracal caracal)**	NA	1.000	NA	1.000
Cheetah *(Acinonyx jubatus)**	NA	1.000	NA	1.000
Civet *(Civettictis civetta)**	NA	1.000	NA	1.000
Dog (domestic)*	NA	1.000	NA	1.000
Duiker (tribe Cephalophini)*	NA	1.000	NA	0.993
Eland *(Taurotragus oryx)*	0.955	1.000	0.412	0.999
Genet *(Genetta spp.)*	1.000	1.000	0.668	1.000
Gerenuk *(Lotocranius walleri)**	NA	1.000	NA	0.994
Grant's gazelle *(Nanger granti)*	0.857	1.000	0.388	0.983
Greater kudu *(Tragelaphus strepsiceros)*	1.000	1.000	0.567	0.999
Hare *(Lepus victoriae)*	0.989	1.000	0.744	0.999
Hartebeest *(Alcelaphus buselaphus)**	NA	1.000	NA	0.999

Hippopotamus *(Hippopotamus amphibius)*	1.000	1.000	0.916	1.000
Honey badger *(Mellivora capensis)*	1.000	1.000	0.788	1.000
Hyrax (family Procaviidae)*	NA	1.000	NA	1.000
Leopard *(Panthera pardus)*	1.000	1.000	0.686	1.000
Lion *(Panthera leo)*	1.000	1.000	0.642	1.000
Livestock (non-camel)	0.922	1.000	0.811	0.997
Mongoose (family Herpestidae)	1.000	1.000	0.743	0.999
Mouse/rat	1.000	1.000	0.570	1.000
Oryx *(Oryx beisa)*	1.000	1.000	0.667	0.999
Plains zebra *(Equus quagga)*	0.988	0.998	0.902	0.990
Porcupine *(Hystrix cristata)*	1.000	1.000	0.304	1.000
Squirrel (tribe Xerini)	0.973	1.000	0.729	0.999
Steenbok *(Raphicerus campestris)**	NA	1.000	NA	0.997
Striped hyena *(Hyaena hyaena)*	1.000	1.000	0.540	1.000
Thompson’s gazelle *(Nanger granti)**	NA	1.000	NA	0.997
Warthog *(Phacochoerus spp.)*	0.993	1.000	0.846	0.999
Waterbuck *(Kobus defassa)*	0.987	1.000	0.527	0.999
Zorilla *(Ictonyx striatus)*	1.000	1.000	0.472	1.000
Birds and other taxa				
Bird (other)	0.971	0.999	0.792	0.995
Helmeted guineafowl *(Numida meleagris)*	0.975	1.000	0.725	0.996
Insect/spider	0.500	1.000	0.083	0.999
Kori bustard *(Ardeotis kori)*	1.000	1.000	0.776	0.999
Ostrich *(Struthio camelus)**	NA	1.000	NA	1.000
Reptile/amphibian	1.000	1.000	0.545	1.000
Secretary bird *(Sagittarius serpentarius)*	1.000	1.000	0.848	1.000
Vulturine guineafowl *(Acryllium vulturinum)*	0.997	1.000	0.895	0.995
Special categories				
Human	1.000	1.000	0.308	1.000
Other	0.500	1.000	0.130	0.990
No animals present	0.994	0.995	0.954	0.966

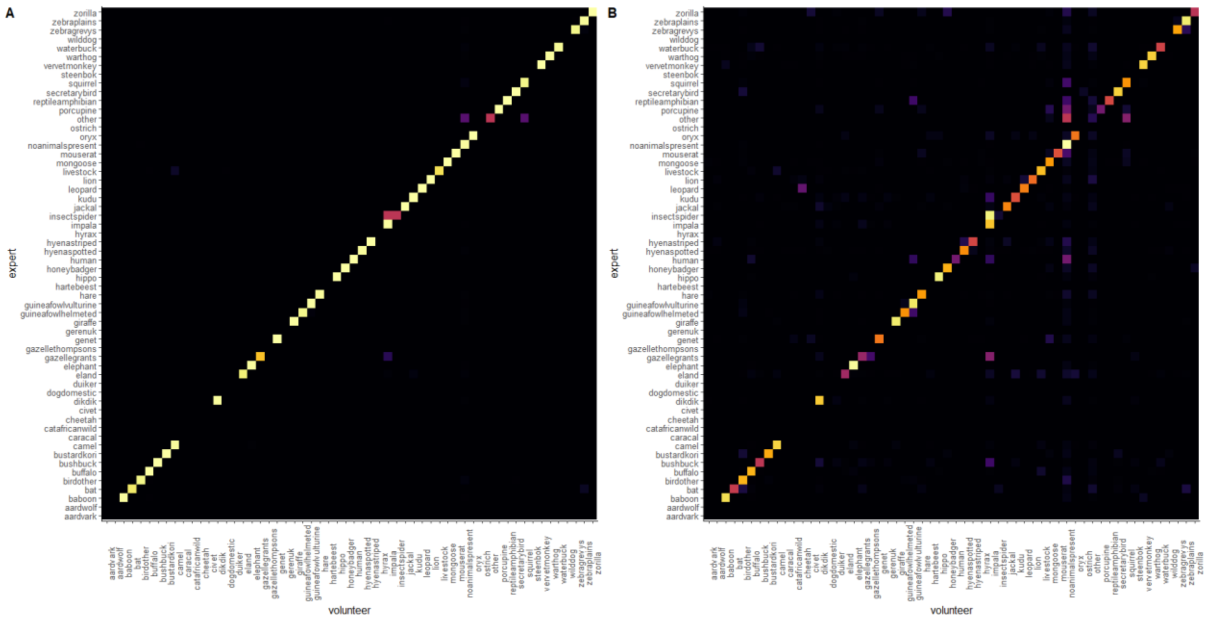


Figure S17. Confusion matrices for **A)** consensus classifications and **B)** raw volunteer classifications in the validation dataset, which comprises 23786 images which were classified by both an expert and volunteers. Lighter colours indicate a larger number of images which received each combination of expert and volunteer classifications.

Appendix E: Supplementary results

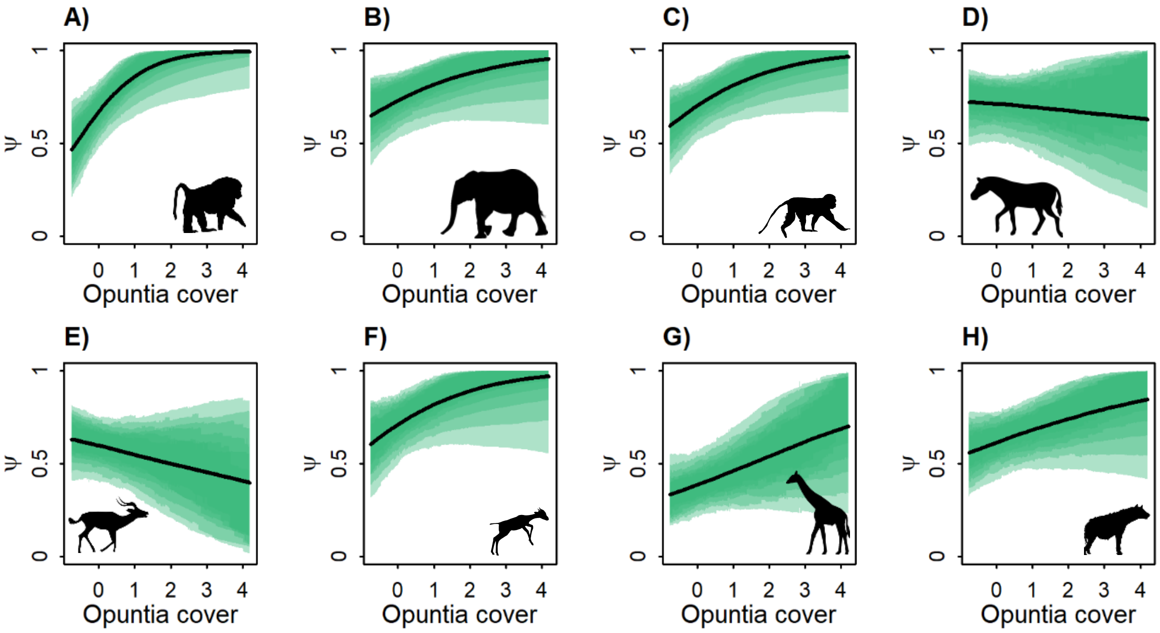


Figure S18. Marginal total effects of site-level *Opuntia* percentage cover (standardised) on occupancy probability (ψ) for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* indirectly affects occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Black lines indicate the posterior median marginal effect.

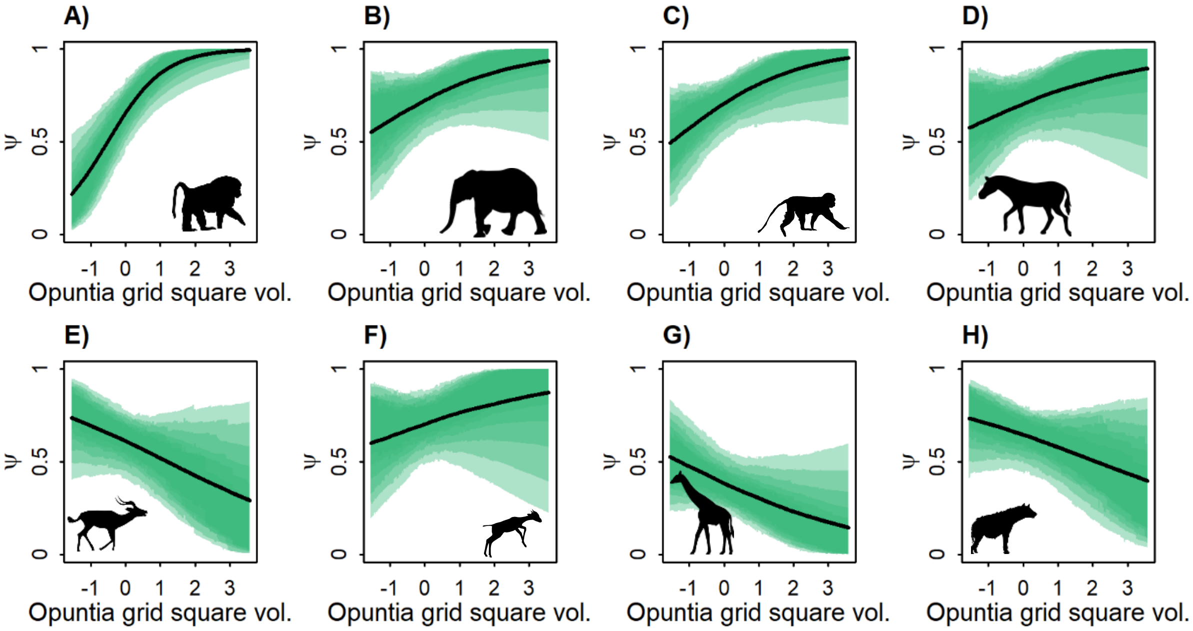


Figure S19. Marginal total effects of grid square-level *Opuntia* volume (standardised) on occupancy probability (ψ) for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* indirectly affects occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Black lines indicate the posterior median marginal effect. Points represent individual sites.

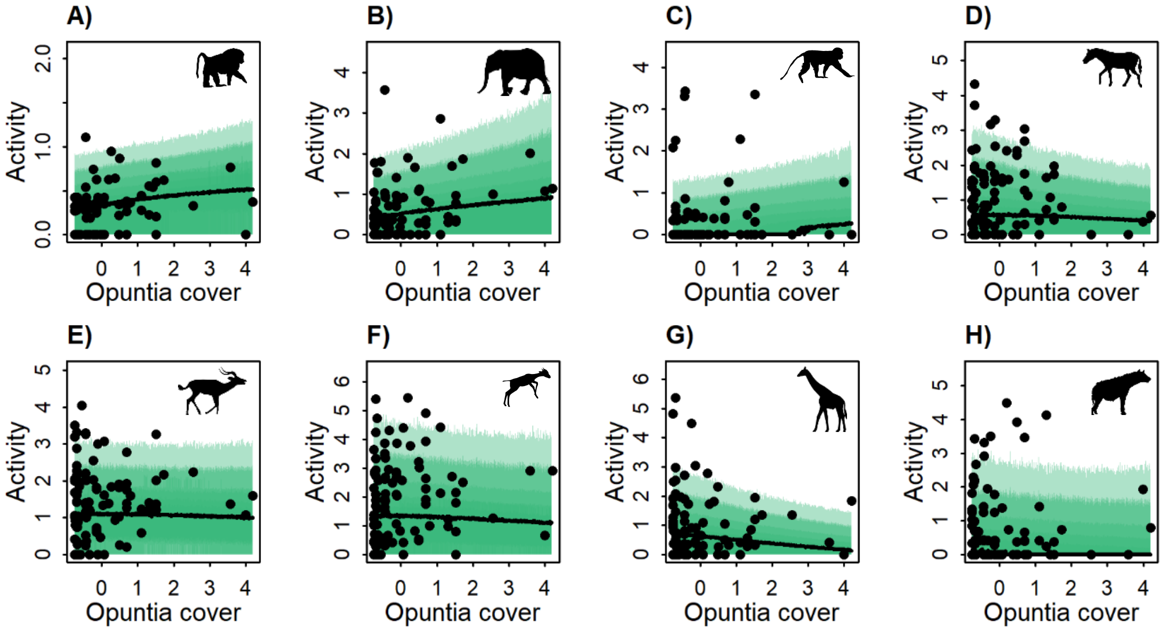


Figure S20. Relationships between total activity (rescaled) and site-level *Opuntia* percentage cover (standardised), for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* indirectly affects occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas encompass (from outside) 95%, 89%, 80%, 70%, 60%, and 50% of observations simulated from the posterior distribution. The black line represents the median value of these simulated observations. Points represent individual sites.

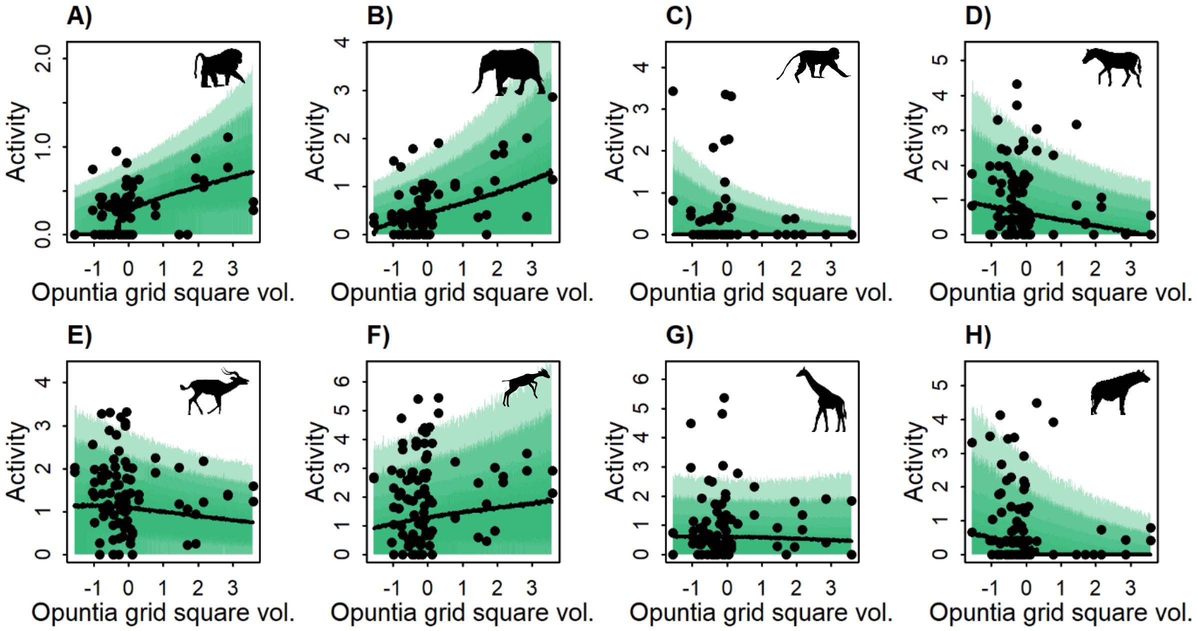


Figure S21. Relationships between total activity (rescaled) and grid square-level *Opuntia* volume (standardised), for: **A)** olive baboon, **B)** elephant, **C)** vervet monkey, **D)** Grevy's zebra, **E)** impala, **F)** dik-dik, **G)** giraffe, and **H)** spotted hyena. The models assume that *Opuntia* indirectly affects occupancy through altering the composition of the native plant community; for model structure, see Table 1. Shaded areas encompass (from outside) 95%, 89%, 80%, 70%, 60%, and 50% of observations simulated from the posterior distribution. The black line represents the median value of these simulated observations.

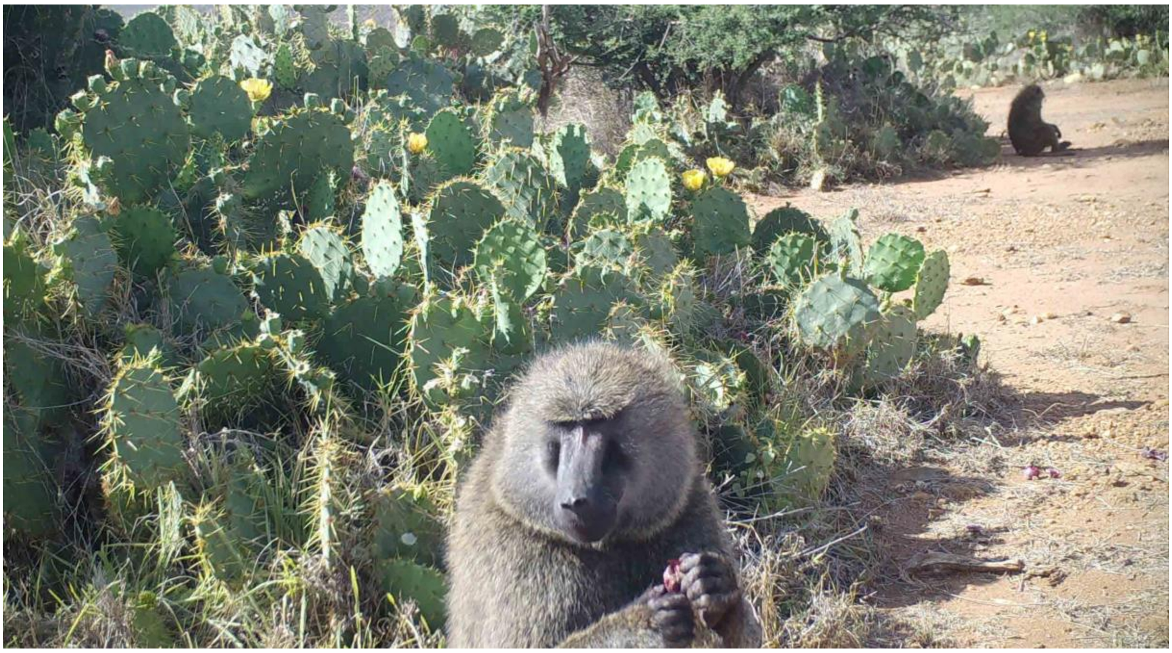
Appendix F: Software information

Table S2. R packages used in my analyses. I used R version 4.1.2 and RStudio 2022.07.1 build 554 throughout.

Name	Citation	Version	Link
rethinking	McElreath, R. (2021). rethinking: Statistical Rethinking book package.	2.21	https://github.com/rmcelreath/rethinking
cmdstanr	Gabry, J. & Cesnovar, R. (2021). cmdstanr: R Interface to 'CmdStan'.	2.30.1	https://mc-stan.org/cmdstanr
MASS	Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0	NA	https://cran.r-project.org/web/packages/MASS/index.html
dplyr	Wickham, H., François, R., Henry, L., & Müller, K. (2021). dplyr: A Grammar of Data Manipulation.	1.0.7	https://CRAN.R-project.org/package=dplyr
tidyr	Wickham, H. & Girlich, M. (2022). tidyr: Tidy Messy Data.	1.2.0	https://CRAN.R-project.org/package=tidyr
lubridate	Grolemund, G. & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, **40**(3), 1-25.	NA	https://www.jstatsoft.org/v40/i03/
bayesplot	Gabry J, Mahr T (2021). bayesplot: Plotting for Bayesian Models.	1.8.1	https://mc-stan.org/bayesplot/
viridis	Garnier, S., Ross, N., Rudis, R., Camargo, A.P., Sciaini, M. & Scherer, C. (2021). Rvision - Colorblind-Friendly Color Maps for R.	0.6.2	https://cran.r-project.org/web/packages/viridis/index.html
ggplot2	Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.	NA	https://ggplot2.tidyverse.org
ggdist	Kay, M. (2022). ggdist: Visualizations of Distributions and Uncertainty.	3.2.0	https://doi.org/10.5281/zenodo.3879620
activity	Rowcliffe, M. (2022). activity: Animal Activity Statistics.	1.3.2	https://CRAN.R-project.org/package=activity

Chapter 5

Interactions between invasive *Opuntia* cacti and native animals



Abstract

Biotic interactions are expected to play a key role in the invasion of Laikipia County, Kenya, by prickly pear cacti (*Opuntia spp.*). In particular, seed dispersal by native frugivores is thought to have been instrumental in allowing *Opuntia* to spread rapidly across the landscape, while biotic resistance imposed by native herbivores may have helped to slow the invasion in herbivore-rich areas. However, our understanding of the role of biotic interactions in *Opuntia*'s invasion of Laikipia County is limited by a lack of fundamental biological information; we know little about the fruiting dynamics of *Opuntia* under natural conditions, and the interactions between native animals and *Opuntia* have not been systematically documented. Here, I used morphological measurements and camera trap data to address these knowledge gaps for two of the main invasive *Opuntia* species – *O. engelmannii* and *O. stricta*. I found that the relationship between stand height and fruiting was positive for both *Opuntia* species, and that this relationship was stronger for *O. engelmannii*. I also found that other habitat variables affected height or fruiting in one or both *Opuntia* species. My camera trap images confirmed the importance of interactions that were previously thought to be important, such as frugivory by elephants (*Loxodonta africana*) and olive baboons (*Papio anubis*). In addition, my images revealed several interactions which have not previously been documented in the scientific literature and highlighted a potential key role for vulturine guineafowl (*Acryllium vulturinum*) as dispersers of *O. engelmannii*. These results have important implications for our understanding of the *Opuntia* invasions in Laikipia County.

Introduction

Biotic interactions are fundamentally important in determining whether biological invasions succeed or fail, and can strongly influence the resulting ecological impacts (Mitchell *et al*. 2006). Reflecting the predominant historical focus of ecologists in general (Bruno *et al.* 2003; Traveset & Richardson 2014; Valdovinos 2019), invasion ecologists have traditionally focused on the roles of competition and predation (*e.g.,* Elton 1958; Keane & Crawley 2002) in explaining the establishment and spread of invasive species. However, in parallel with the growing recognition of the importance of mutualisms in ecology (Bruno *et al.* 2003; Valdovinos 2019), it has become increasingly clear that mutualistic interactions – such as seed dispersal and pollination – can play a critical role in biological invasions (Traveset & Richardson 2014). Consequently, understanding the breadth of interactions between invasive species and the native community is a key topic for research.

Opuntia cacti, commonly called prickly pears, are invasive in arid regions worldwide (Pasiecznik 2007, Pasiecznik & Rojas-Sandoval 2007, Pasiecznik 2015). Several *Opuntia* species, including *O. stricta* and *O. engelmannii*, are invasive in Laikipia County, Kenya (Strum *et al.* 2015; Witt 2017; Githae 2019). Biotic interactions are likely to have played an important role in *Opuntia*'s invasion in Laikipia County. In particular, *Opuntia*'s ability to form seed dispersal mutualisms with a diverse range of animal species has almost certainly contributed to its rapid spread across the landscape.

Opuntia stands bear large numbers of fleshy fruits; in other regions where *Opuntia* is invasive, these fruits are consumed by a range of taxa (Mellink & Riojas-López 2002) including primates (Lotter *et al.* 1999; Dean & Milton 2000), ungulates (Gimeno & Vilà 2002), rodents (López-Darias & Nogales 2008a), mustelids (Padrón *et al.* 2011), birds (Dean & Milton 2000; Gimeno & Vilà 2002; Padrón *et al.* 2011), lizards, and tortoises (Padrón *et al.* 2011). The fruits are also consumed by a wide range of taxa in regions where *Opuntia* species are native, including birds, small and medium mammals, and tortoises (González-Espinosa & Quintana-Ascencio 1986; Mandujano *et al.* 1997; Montiel & Montaña 2000; Mellink & Riojas-López 2002; Gibbs *et al.* 2008). Furthermore, now-extinct megafauna may have once dispersed *Opuntia* in its native range, as supported by the presence of *Opuntia* seeds in Pleistocene mammoth dung from Utah (Davis *et al.* 1984). In Laikipia County, olive baboons *(Papio anubis)* and elephants *(Loxodonta africana)* are thought to be the key dispersal agents for *Opuntia*; both baboons and elephants are commonly observed feeding at *Opuntia* stands, and seeds or other fruit remains can be found in their faeces (Strum *et al.* 2015; Dyck 2017). Furthermore, *O. stricta* density is higher near baboon sleeping sites (Strum *et al.* 2015). However, it is currently unclear whether elephants and baboons are actually the main dispersers of *Opuntia* or merely the most conspicuous, and empirical data on the relative importance of different dispersal agents are sorely lacking.

Opuntia fruiting is related to size; individuals must reach a size threshold before they begin producing ripe fruit, and larger individuals tend to produce a greater number of fruits (Reyes-Agüero *et al.* 2006). Understanding the relationship between size and fruiting is useful from a management perspective; removing individuals before they reach fruiting size can prevent the *Opuntia* dispersing to new areas, thus reducing the spread of the invasion (Hoffmann *et al.* 1998a). However, the relationship between size and fruiting has not been studied for *Opuntia* in Laikipia. For *O. stricta*, data from South Africa – where the species is also invasive – show that individuals with fewer than 28 cladodes do not produce fruits, and that above this size, the number of fruits increases as the number of cladodes increases (Hoffmann *et al.* 1998b). For *O. engelmannii*, data from its native range in the Sonoran Desert show that individuals with six or more cladodes are capable of sexual reproduction (Bowers 1996). However, it is unclear whether the results for either species are applicable to the *Opuntia* invasions in Laikipia.

Other environmental variables also have the potential to influence *Opuntia* height and fruiting. For example, trees can create “fertility islands” – favourable microclimates with higher levels of soil moisture and nutrients, higher humidity, and altered microbial communities – which have been shown to facilitate *O. stricta* growth in South Africa (Novoa *et al.* 2021). Interactions with other plant species could also affect height and fruiting, for instance through competition. Finally, preliminary analyses indicate that the cochineal (*Dactylopius opuntiae*) biocontrol agent significantly reduces both the size and fruiting of *O. stricta* (Witt *et al.* 2020). Although cochineal is also found on *O. engelmannii*, its effects have yet to be quantified. However, my field observations suggest that *O. engelmannii* does not suffer the same high level of damage from cochineal as *O. stricta*.

In addition to seed dispersal, other biotic interactions with Laikipia County’s animal community may play a role in *Opuntia*’s invasion. Wells *et al.* (2023) analysed *Opuntia stricta* densities in the long-term herbivore exclusion experiments at Mpala Research Centre, and revealed that *Opuntia* densities were significantly higher in plots where wild herbivores were excluded; this effect was primarily driven by the exclusion of megaherbivores such as elephants

(*Loxodonta africana*) and giraffe (*Giraffa reticulata*). However, the relative importance of direct herbivory *versus* indirect effects, including trampling and moderating the strength of competitive interactions with native plants, is not yet understood; quantifying the interactions between *Opuntia* and native mammals may provide insight into this topic. These observations may also provide insight into any role herbivores play in *Opuntia's* vegetative dispersal. For example, herbivores may scatter cladodes while foraging (Foxcroft & Rejmánek 2007). Additionally, the dense *Opuntia* stands may provide refuge for small herbivores. For example, dik-dik (*Madoqua spp.*) site occupancy is positively related to the level of *Opuntia* in both the site and the broader landscape (Chapter 4), which may be due to dik-dik using *Opuntia* stands to hide from predators. One potential consequence of this effect is refuge-mediated apparent competition (Orrock *et al.* 2010) between *Opuntia* and native plants. Finally, there is a potential role for vertebrates in pollinating *Opuntia*; bird-pollinated *Opuntia* are common in regions such as the Galapagos (Reyes-Agüero *et al.* 2006).

In this chapter, I explored two key topics with the aim of furthering our understanding of the biotic interactions between *Opuntia* (focusing on *O. engelmannii* and *O. stricta*) and the animal community in Laikipia County. First, I used morphological measurements of individual *Opuntia* stands to quantify the relationship between *Opuntia* height and fruiting, and how both height and fruiting are jointly influenced by local habitat characteristics as well as the cochineal biocontrol agent. As these estimates have the potential to be sensitive to unmeasured site-level characteristics (*e.g.*, soil properties) I used Bayesian imputation to examine whether my results were robust to a latent site-level confound. Second, I used camera trap images to document the interactions between native animals and *Opuntia*. I identified an array of distinct interaction types and the animal species involved, and constructed interaction networks to summarise these observations.

Methods

Study system

I conducted my study at Mpala Research Centre and Loisaba Conservancy, in Laikipia County, Kenya, during the 2021 dry season (January to early April). The habitat in the region is semi-arid savanna, with woodland and shrubland dominated by *Vachellia* and *Senegalia* (formerly *Acacia*) species; other trees and shrubs including *Boscia augustifolia*, *Croton dichogamus*, and *Grewia spp*. are also present (Young *et al.* 1995; Augustine 2003; Augustine *et al.* 2011; Mutuku & Kenfack 2019). The understory layer is mainly comprised of grasses from the genera *Cynodon*, *Pennisetum*, *Digitaria* and *Sporobolus*, alongside a variety of forbs including *Plecranthus spp*., *Pollichia campestris*, *Portulaca spp*. and *Blepharis spp*. (Young *et al.* 1995).

The most common *Opuntia* species present at the study site are *O. stricta* and *O. engelmannii*; a few scattered *O. ficus-indica* individuals are also present, particularly on rocky outcrops in the central Mpala region. At the time of data collection, *O. stricta* was generally distributed at moderate densities in the southern Mpala region, with lower densities in the northern Mpala region and no individuals at Loisaba, while *O. engelmannii* was present at very high densities at Loisaba and moderate to low densities in the northern Mpala region, with no individuals present in the southern Mpala region.

Measurement of Opuntia stands

I measured *Opuntia* stands while deploying camera traps and conducting track-and-sign surveys. A camera trap site was defined as the circular area within a 10m radius of the camera trap, while each track-and-sign survey was carried out within a 20x20m square site. Sites were selected using a paired design: I first divided the study area into 500x500m grid squares, and then situated pairs of sites within a random subset of these grid squares. The first site in each pair was situated in an area visually identified as high *Opuntia* density, and the second was deployed in a random direction 50-70m away. If the second site was found to have an equal or higher density of *Opuntia* than the first site, I generated a new random direction until the *Opuntia* density at the second site was lower. In this way, I ensured that I sampled sites with a range of *Opuntia* densities.

I measured all *Opuntia* stands which lay at least partly within the site boundary. For each stand, I recorded the species and used a tape measure to determine the maximum height of the stand;

I measured maximum height rather than counting the number of cladodes because of the difficulty in accurately determining the number of cladodes for extremely large and dense *Opuntia* stands. I then counted the number of ripe fruits and estimated the percentage of cladode surface covered by the cochineal (*D. opuntiae*) biocontrol agent with the aid of a cover estimator chart (Anderson 1986). I also recorded whether the stand was at least partly under a tree; trees were defined as woody plants standing taller than 2m (shorter woody plants were classified as shrubs). Finally, I noted which vegetation types (grass, forb, or shrub) were found in the area immediately adjacent to or within the *Opuntia* stand.

Camera trap deployment and image processing

I deployed camera traps (20 × Browning Dark Ops Pro, 5 × Browning Recon Force Extreme, and 5 × Reconyx Hyperfire 2) at sites throughout the study region. The cameras were set to take photographs with a five second cool-down period. For the Browning cameras I used the "long range" infrared flash setting, while I used the default "optimised" setting for the Reconyx cameras. I mounted the cameras on tree trunks at an average height of 81cm (measured from the ground to the lens); some cameras were deployed slightly higher or lower to ensure a good view given the site's topography (min = 34cm, Q1 = 72cm, Q3 = 89cm, Q4 = 137cm). I verified that animals in the field of view would be visible by taking photos of a research assistant at 2m, 4m, 6m, 8m, and 10m from the camera. I cut back long grass and other vegetation close to the front of the camera to reduce the prevalence of false detections which would otherwise consume the memory and battery life.

To process the resulting camera trap images, I first used the Megadetector machine learning model (v.4.1.0, Beery *et al.* 2019) to classify images as containing an animal (any species), human, or vehicle. I manually screened all images with probability 0.10 (the minimum probability Megadetector assigns to a classification) or higher of containing a human or vehicle, discarding all images which I identified as containing a human/vehicle and retaining images which in fact contained animals. I also retained all images with probability 0.98 or higher of containing an animal. I then uploaded all retained images to my project, Prickly Pear Project Kenya, on the Zooniverse platform (https://www.zooniverse.org/projects/peter-dot-stewart/prickly-pear-project-kenya), where volunteers were able to classify the camera trap images. Each image was classified by at least 12 volunteers before retirement from the active image pool, except for when an image was classified as "human", in which case the image was immediately retired. I assigned consensus species classifications to each image using a threshold-based approach in which at least 8 of the 12 volunteers had to classify the species as being present, and the Shannon entropy (Shannon 1948) of all classifications on the image could not exceed one. This method for generating consensus classifications resulted in highly accurate classifications being assigned to images (Chapter 4, Appendix D). For each image, volunteers were also asked "do you see any individuals interacting with the cactus?"; this question was used to help identify images containing interactions.

Identification of candidate interaction images

I identified candidate interaction images, which were taken forward for further analysis, through two methods. First, I selected all images where three or more volunteers had answered "yes" to the question "do you see any individuals interacting with the cactus?" on the Zooniverse classifier interface. Second, I searched the project's discussion board for key terms which could signal that an image contained an interaction; my intention was to identify images with subtle or ambiguous interactions that were being discussed by the volunteers, as well as images where an animal was interacting indirectly with the *Opuntia* (*e.g.,* a squirrel carrying *Opuntia* fruit but not being adjacent to an *Opuntia* stand) which may otherwise be missed. I used the following key terms: *interact*, eating, fruit, feed*, forag**.

Coding interactions

Once candidate images had been identified, I manually viewed and coded the images. Each image was assigned an interaction identifier; images were assigned the same identifier when they contained the same individual animal or group of animals, and they interacted with the *Opuntia* over a period of time without leaving the area. Here, I refer to images with the same identifier as belonging to the same interaction event. While I did not assign a hard cut-off for the amount of temporal separation between images with different identifiers, I would generally only assign the same identifier to images after a two-minute gap if the animals were clearly the same individuals or part of the same group.

I assigned one or more interaction categories (eating fruits/eating pads or roots/eating flowers/eating other vegetation/hiding under cactus/perching/other/none) to each image, along with a confidence rating (certain/probable/unsure) which represented how sure I was that the specific interaction was occurring. For full definitions of interaction categories and examples of confidence ratings, see Table 1. Finally, for each interaction event, I calculated the maximum confidence rating for each observed category; only interactions where the maximum confidence was "certain" or "probable" were carried on for further analysis.

Table 1. Definitions of interactions and examples of confidence ratings assigned to each camera trap image. Confidence rating examples are for olive baboon (*P. anubis*) eating *Opuntia* fruits.

Behaviour	**Definition**
Eating fruits	Animal consuming ripe *Opuntia* fruit directly from the plant, or fruit which has fallen on the ground.
Eating pads or roots	Animal consuming *Opuntia* cladodes or roots.
Eating flowers	Animal consuming *Opuntia* flowers.
Eating other vegetation	Animal consuming other vegetation growing within or immediately adjacent to the *Opuntia*.
Hiding under cactus	Animal in resting posture with body wholly or partly beneath or within the *Opuntia* stand.
Perching	Animal (typically bird) perching on *Opuntia*, but not obviously eating or otherwise interacting with the fruits/cladodes/flowers.
Other	Behaviour not covered by another category (*e.g.*, mongoose apparently foraging underneath *Opuntia* stand).
None	Animal is not interacting with cactus.
Confidence	**Example**
Certain	Baboon with *Opuntia* fruit visible in hand or mouth.
Probable	Baboon standing on hind legs reaching towards *Opuntia* stand.
Unsure	Baboon sitting next to *Opuntia* stand in background, but too far away to determine what it is doing.

Data analysis

To examine the relationship between stand size (maximum height), fruiting, and other variables, I fitted two types of statistical model. First, I fitted a binomial model to explore the relationship between size and the probability of a stand producing any ripe fruit. Second, I fitted a negative-binomial (*i.e.*, gamma-Poisson) model to examine the relationship between size and the number of ripe fruits produced. I also modelled how stand height and fruiting were affected by other variables: the proportion of cladode surface covered by the cochineal biocontrol agent, whether the stand was under a tree, and whether grasses, forbs, and shrubs were found growing within or immediately adjacent to the stand.

In my models, I assumed that any effect of height on fruit is direct and operates through a single pathway (Fig. 1). I also assumed that the cochineal biocontrol agent could affect both height and fruiting (Fig. 1), as has been observed in preliminary surveys for *O. stricta* at the nearby Ol Jogi Conservancy (Witt *et al.* 2020). For the native vegetation variables – presence of grasses, forbs, and shrubs – I assumed that the effects could be on both height and fruiting (Fig.1). These effects could represent competition or other biotic interactions between the native vegetation and *Opuntia*. Likewise, I assumed that whether the *Opuntia* stand was under a tree could affect both height and fruiting (Fig. 1). One phenomenon this assumption could represent is a "fertility island" effect, in which trees create nutrient-rich microhabitats that benefit *Opuntia* stands in their vicinity; this phenomenon has been observed for *O. stricta* in Kruger National Park, South Africa (Novoa *et al.* 2021). I used an index variable approach and computed posterior contrasts to examine the effects of the binary vegetation and tree variables in my models.

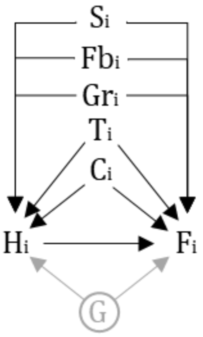


Figure 1. Directed acyclic graph representing the assumptions underlying my models of *Opuntia* height and fruiting. Nodes represent variables: H is maximum height, F is presence or number of ripe fruits, C is cochineal cover, and T, Gr, Fb, and S are tree, grass, forb and shrub presence/absence respectively. Each variable is modelled as a function of the variables which have arrows entering it. The circled variable (G) represents a latent site-level confound, and is shown in grey to indicate that it was only included in one of the two sets of models. Nodes indexed *i* represent variables measured at the level of the individual *Opuntia* stand; the latent variable (G) is not indexed *i* because it is defined at the site level.

In both the binomial and negative-binomial models, I included a site-level varying intercept term. Furthermore, to explore the potential implications of unmeasured confounding variables which could affect stands from the same site (*e.g.*, soil moisture or nutrient content) I ran a second set of models which accounted for a latent site-level confound (Fig. 1) using Bayesian imputation. I present the full notation for my models in Appendix A.

I fitted all models in a Bayesian framework using Stan (Stan Development Team, 2022), implemented in R (v.4.1.2; R Core Team, 2021) with the *rethinking* (v.2.21; McElreath, 2021) and *cmdstanr* (v.2.30.1; Gabry & Cesnovar, 2021) packages. I used prior predictive simulations to aid in my choice of prior distributions (Appendix B). To improve the models' sampling, I employed non-centred parameterisations for the site-level varying intercepts. I also standardised the maximum stand height and cochineal cover variables by subtracting the mean and dividing by the standard deviation. I ran each model with four Markov chains, each with 30000 iterations. The first 28000 samples from each chain constituted the warmup phase while the following 2000 samples were used for inference, resulting in a total of 8000 samples across the four chains. For all models, I ensured that the chains had converged by checking that the Gelman-Rubin convergence diagnostic ($\hat{R}$; Gelman & Rubin 1992) was equal to 1.00 for all key parameters. I also assessed the performance of the Markov chain Monte Carlo (MCMC) algorithm by inspecting the effective sample size, trace plots, and trace rank plots for each parameter. Additionally, I ensured that the models did not exhibit divergent transitions.

To explore the structure of the interactions between *Opuntia* and the animal community I constructed interaction networks using the R package *bipartite* (Dormann *et al.* 2008). In these networks, the upper set of nodes represent animal species, and the lower set of nodes represent behaviours (*e.g.*, eating fruit). I used unique identifier-behaviour-species combinations to construct the networks. Consequently, the width of each line between nodes represents the relative number of unique interactions, and the width of nodes represents the relative number of unique interactions in which that species or behaviour type was observed. I also constructed alternative networks in which I used all interaction observations (*i.e.*, if a behaviour was observed multiple times within one interaction identifier, then the behaviour was counted multiple times). I constructed a joint network for both *Opuntia* species, as well as separate networks for *O. engelmannii* and *O. stricta*; I present only the latter in the main text.

To quantitatively examine how the *O. engelmannii* and *O. stricta* interaction networks were structured, I calculated network metrics using the functions available in the bipartite package (Dormann *et al.* 2008). At the animal species level, I calculated the degree (*i.e.*, number of interactions) and the specialisation metric d' (Blüthgen *et al.* 2006) to examine how generalist or specialist species were in the behaviours that they exhibited. At the network level, I calculated the number of compartments (unconnected subsets of the network; Lewinsohn *et al.* 2006), the clustering coefficient (Watts & Strogatz 1998), the NODF nestedness metric weighted by interaction frequencies (Almeida-Neto *et al.* 2008), the Shannon diversity (*i.e.*, information entropy) of the network (Shannon 1948), and the H_2' specialisation metric (Blüthgen *et al.* 2006).

Code to fully reproduce my analyses can be found at https://github.com/Peter-Stewart/Zooniverse_processing, and information on the R package versions used is presented in Appendix D, Table S1.

Results

Opuntia height and fruiting

In total, I found *Opuntia* stands at 114 sites – 93 camera trap sites, and 21 track-and-sign survey sites – out of the 125 sites I surveyed. I measured a total of 876 *Opuntia* stands: 132 *Opuntia engelmannii, 742 Opuntia stricta,* and two *Opuntia ficus-indica*; only the data for *O. engelmannii* and *O. stricta* were analysed.

I found that in both *Opuntia* species, larger individuals had a higher probability of bearing ripe fruit, and also bore a larger number of fruits (Figs. 2, 3). The slope parameter relating maximum height to ripe fruit presence/absence was greater for *O. engelmannii* than for *O. stricta* (Fig. 3). This difference, coupled with the larger global intercept ($\bar{\alpha}$) for *O. engelmannii* compared to *O. stricta* (median difference = 1.12, 95% PI = -1.07 to 3.50), was reflected in a steeper relationship for *O. engelmannii* over the range of heights that I sampled (Fig. 2). With other variables in the system set to their modal (for trees, grasses, forbs, and shrubs) or mean values (for cochineal), individuals attained a posterior median probability of 0.25 of fruiting at 37cm for *O. engelmannii* and 86cm for *O. stricta*, a probability of 0.5 at 54cm for *O. engelmannii* and 107cm for *O. stricta*, and a probability of 0.9 at 87cm for *O. engelmannii* and 148cm for *O. stricta*. While the parameter relating height to the number of fruits *(i.e.,* the effect size, β) was similar for both *Opuntia* species (Fig. 3; median difference = 0.08, 95% C.I. = -0.39 to 0.53) the global intercept ($\bar{\alpha}$) was much greater for *O. engelmannii* than for *O. stricta* (median difference = 3.97, 95% C.I. = -0.01 to 7.90) which was reflected in a steeper curve for *O. engelmannii* (Fig. 2). Furthermore, the maximum height of *O. engelmannii* stands extended to higher values than for *O. stricta* stands, meaning that the largest *O. engelmannii* stands bore several times more fruit than the largest *O. stricta* stands.

The relationship between the percentage of cladodes covered by the cochineal biocontrol agent and maximum stand height was positive for *O. engelmannii*, while no relationship was observed for *O. stricta* (Fig. 3). The direct relationship between cochineal and the number of fruits (*i.e.,* conditional on height) was positive for *O. engelmannii*; the posterior median of the estimate was also positive for the probability of producing ripe fruit, but the 95% compatibility interval included negative effects (Fig. 3; lower value = -0.21). Similarly, for *O. stricta* the estimated effect was positive for the number of fruits, and likely positive but with less certainty for the probability of fruiting (Fig. 3).

The relationships between vegetation characteristics and stand height were generally positive or neutral. Specifically, there was no clear relationship between tree presence and stand height for *O. engelmannii*, and only a very weak positive relationship for *O. stricta* (Fig. 3). Similarly, I did not observe a clear relationship between grass presence and stand height for *O. engelmannii*, but I observed a clear positive relationship for *O. stricta* (Fig. 3). For both forb and shrub presence, I found a positive association with height for both *O. engelmannii* and *O. stricta* (Fig. 3). The estimates of these effects were consistent between the binomial and negative binomial models.

In contrast to the effects I observed for height, the relationships between vegetation characteristics and fruiting (conditional on height) were much more uncertain than the relationships for height (Fig. 3). The only clear relationship I observed was a strong negative relationship between tree presence and both fruiting probability and number of fruits for *O. stricta* (Fig. 3). While the posterior median estimate of the relationship between tree presence and fruiting probability was also negative for *O. engelmannii*, positive relationships were still contained within the 95% compatibility interval, and the estimated relationship for the number of fruits was centred firmly around zero (Fig. 3). For grasses, forbs, and shrubs, the estimated relationships with fruiting probability and number of fruits had consistently positive posterior medians, but in all cases there was a substantial degree of uncertainty and negative values were contained within the compatibility intervals (Fig. 3). For *O. stricta*, the estimated relationships with grasses, forbs, and shrubs were centred around zero (Fig. 3).

I observed qualitatively similar results in the models that assumed a latent site-level confound (Appendix C, Figs. S2, S3).

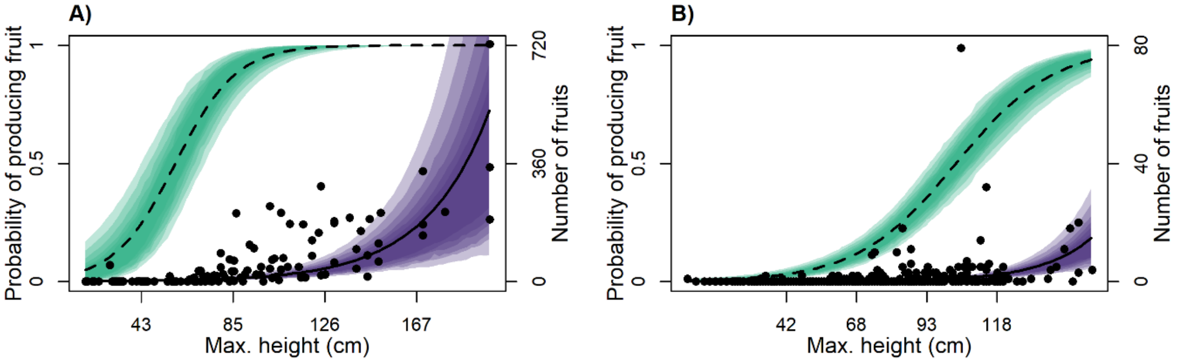


Figure 2. Relationship between maximum height and fruiting for **A)** *Opuntia engelmannii* and **B)** *Opuntia stricta*. Values for trees, grasses, forbs and shrubs are set to their respective modes (absent, present, present, and absent respectively). All plots assume that the value of cochineal cover is set to the average (*i.e.*, zero). Solid lines and purple shaded areas represent the posterior median and compatibility intervals (*i.e.*, credible intervals) for the average number of ripe fruits, while dashed lines and green shaded areas represent the posterior median and compatibility intervals for the probability of producing any ripe fruit. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Points represent maximum height and number of ripe fruit measurements for individual *Opuntia* stands.

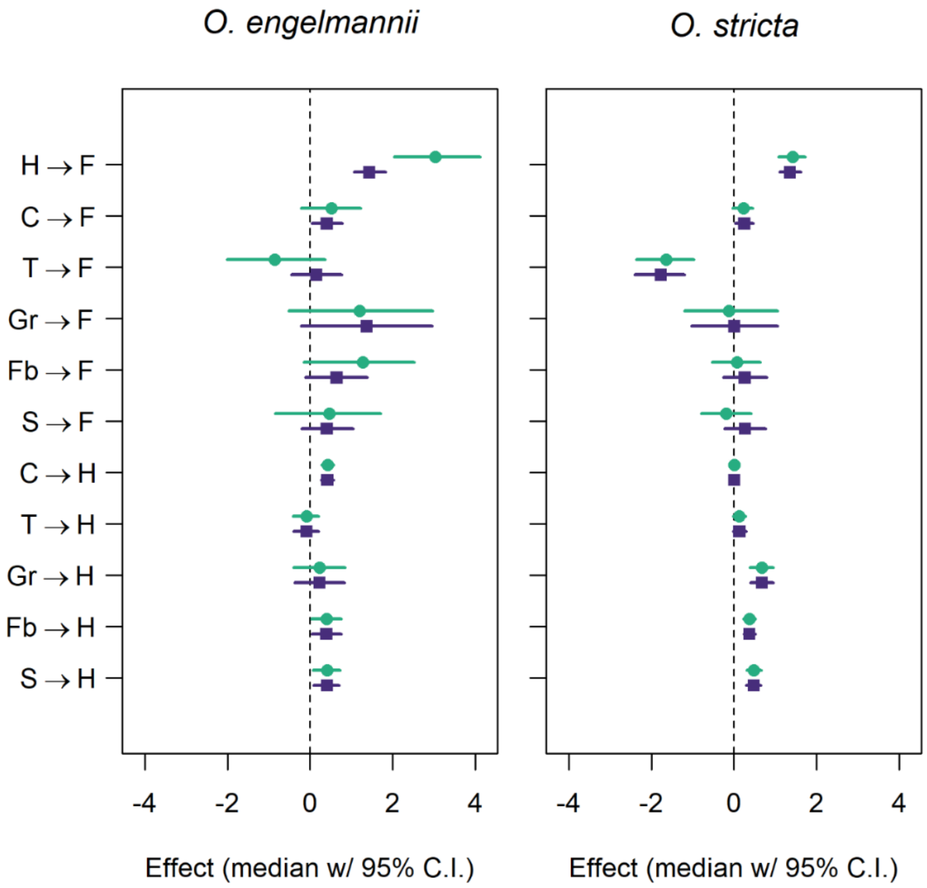


Figure 3. Effect size estimates from models of height and fruiting for *Opuntia engelmannii* (left panel) and *Opuntia stricta* (right panel). Effects are represented by the y-axis labels; for example, H → F represents the effect of height on fruiting. These effects correspond to slope (β) parameters where height (H) and cochineal (C) are the explanatory variable, and contrasts between indicator variable levels where tree (T), grass (Gr), forb (Fb) and shrub (S) presence/absence are the explanatory variable. Points and lines represent posterior median values and 95% compatibility intervals (*i.e.*, credible intervals) respectively. Points drawn as green circles represent estimates from the binomial model of fruit presence/absence, while purple squares represent estimates from the negative binomial model of the number of fruits. For full model structures, see Figure 1 and Appendix A.

Interactions between animals and Opuntia

My search identified 9699 candidate images from 1733 distinct interaction events. After removing all images where I had ascertained that no animals were interacting with the cactus, or where the maximum confidence assigned to an interaction type within a sequence was "unsure", I was left with 1542 images from 268 distinct interaction events.

The interactions that I observed contained a total of 16 animal species and six distinct behaviours (Fig. 4). Dik-dik (*Madoqua spp.*) eating other vegetation growing amongst the *Opuntia* was the most common interaction for both *O. engelmannii* (Fig. 4) and *O. stricta* (Fig. 4); impala (*Aepyceros melampus*) were also often observed feeding on other vegetation around both *Opuntia* species, as were zebra (*Equus grevyi* and *E. quagga*) for vegetation growing around *O. engelmannii*. I also observed other animals – warthog (*Phacochoerus spp.*), buffalo (*Syncerus caffer*), hippopotamuses (*Hippopotamus amphibius*), elephants (*L. africana*), and livestock – feeding on other vegetation (Fig. 4).

Frugivory also accounted for a substantial proportion of the distinct interaction events that I observed, particularly for *O. engelmannii* (Fig. 4). A variety of species – olive baboons (*P. anubis*), vulturine guineafowl (*Acryllium vulturinum*), elephants (*L. africana*), vervet monkeys (*Chlorocebus pygerythrus*), domestic camels (*Camelus dromedarius*), and small birds (*e.g.*, the superb starling, *Lamprotornis superbus*) – were observed feeding directly on *O. engelmannii* fruits. I also observed ground squirrels (either *Euxerus erythropus* or *Xerus rutilus*) carrying ripe *O. engelmannii* fruits on several occasions. Furthermore, I observed instances of elephants, dik-dik, and oryx (*Oryx beisa*) consuming the remains of *O. engelmannii* fruits which had been discarded on the ground by baboons. For *O. stricta* (Fig. 4) I observed fewer distinct frugivory events, and only olive baboons, vervet monkeys, and elephants were observed consuming *O. stricta* fruits. In networks where I used all observations (*i.e.*, regardless of whether they came from distinct interaction events), frugivory was the most commonly observed interaction for *O. engelmannii* (Appendix C, Fig. S5b), illustrating that some frugivores – particularly olive baboons and vulturine guineafowl – tended to forage on fruit for long periods without leaving a site.

I also observed a variety of other less common interactions (Fig. 4). Elephants were observed feeding on the pads and roots of *O. stricta* (Fig. 4); these feeding bouts were long, as reflected in the network for *O. stricta* which used all observations (Appendix C, Fig. S5c). I did not observe any species feeding on the pads or roots of *O. engelmannii*, but I did observe dik-dik feeding on the flowers of *O. engelmannii* on several occasions (Fig. 4). I observed a variety of small bird species perching on both *Opuntia* species and hiding under *O. stricta* on one occasion (Fig. 4). Finally, I observed a ground squirrel hiding under *O. engelmannii* on one occasion.

The network-level metrics that I calculated revealed that the network for *O. engelmannii* formed a single compartment, while the *O. stricta* network comprised two compartments (Table 2a, Appendix C, Fig. S6). Both networks exhibited the same level of clustering (Table 2a). The *O. engelmannii* network was more diverse and nested, while the *O. stricta* network displayed a higher level of specialisation (Table 2a). Species-level metrics (Table 2b) indicated that of the main frugivore species, olive baboons were the most specialised overall (*i.e.*, they exhibited few other behaviours); they were also the most specialised frugivore for the *O. engelmannii* network, and the second most specialised behind vervet monkeys for the *O. stricta* network (Table 2b). The other key frugivores were mostly relatively specialised, except for elephants, which were relatively generalised in their behaviours particularly for the *O. stricta* network (Table 2b). Most other species in the networks were relatively generalist except for dik-dik, where the majority of their interactions were eating other vegetation, and birds (not including guineafowl), which specialised almost entirely in perching on both *Opuntia* species.

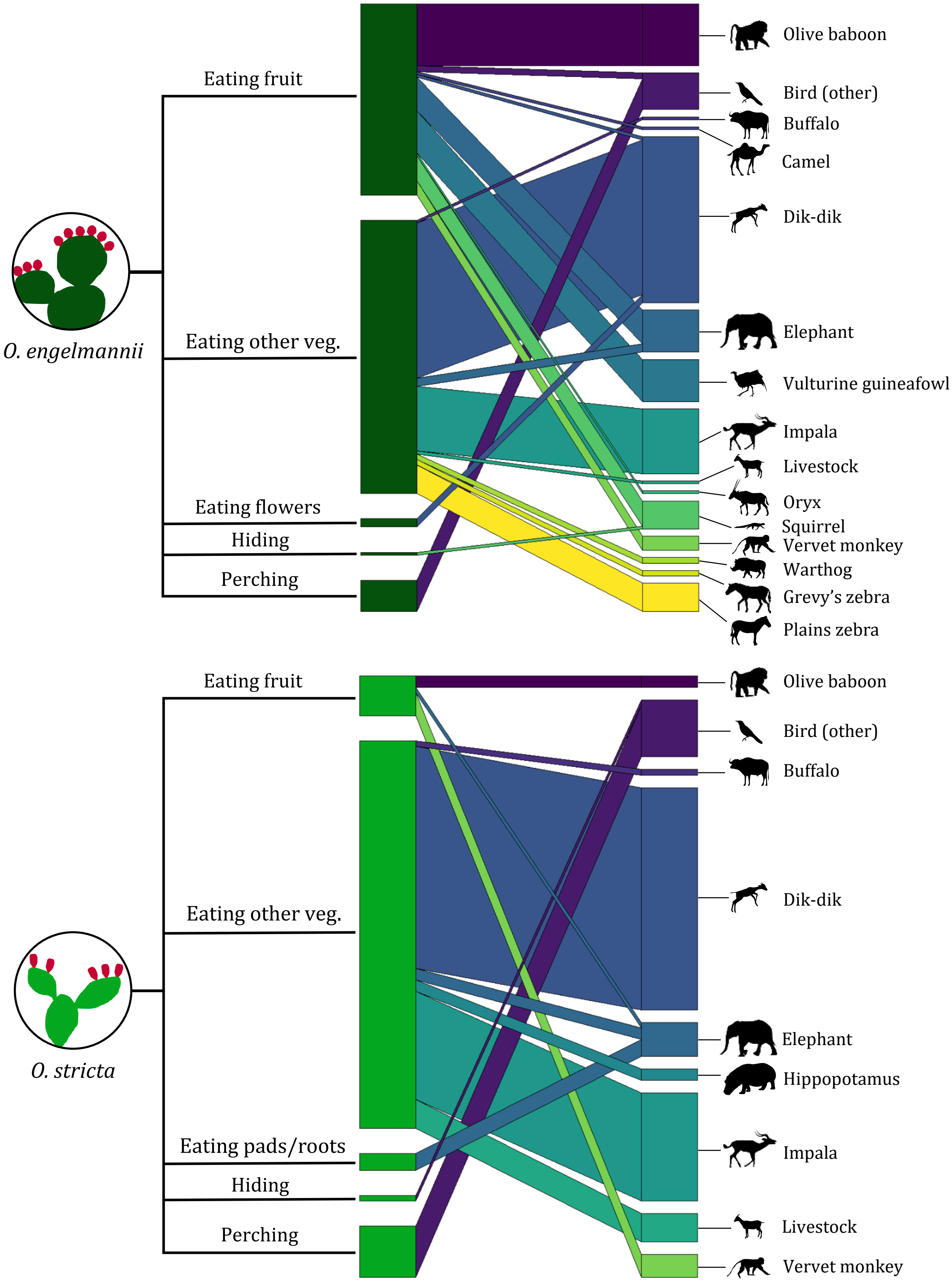


Figure 4. Interaction networks for *Opuntia engelmannii* and *Opuntia stricta*. Nodes on left represent interaction types, while nodes on right represent animal species. Edges connecting nodes represent observed interaction-species combinations. Node and edge width represents the number of independent interaction events in which a given interaction/species was observed. For interaction category definitions, see Table 1.

Table 2. Interaction network metrics at A) network level and B) species level. NA values indicate that a species was not present in a given network, and hence no value was calculated.

A) Network-level metrics

Network	Compartments	Clustering coefficient	Weighted NODF	Shannon diversity	H_2’
O. engelmannii	1	0.2	17.9	2.3	0.8
O. stricta	2	0.2	2.9	1.8	0.9

B) Species-level metrics

	O. engelmannii network		*O. stricta* network	
Species	Degree	d'	Degree	d'
Olive baboon *(Papio anubis)*	1	0.46	1	0.64
Bird (other)	2	0.79	2	1.00
Buffalo *(Syncerus caffer)*	1	0.00	1	0.00
Camel *(Camelus dromedarius)*	1	0.08	NA	NA
Dik-dik *(Madoqua spp.)*	3	0.46	1	0.31
Elephant *(Loxodonta africana)*	2	0.15	3	0.42
Vulturine guineafowl *(Acryllium vulturinum)*	1	0.39	NA	NA
Hippopotamus *(Hippopotamus amphibius)*	NA	NA	1	0.00
Impala *(Aepyceros melampus)*	1	0.29	1	0.16
Livestock	1	0.00	1	0.04
Oryx *(Oryx beisa)*	1	0.08	NA	NA
Squirrel (tribe Xerini)	2	0.36	NA	NA
Vervet monkey *(Chlorocebus pygerythrus)*	1	0.25	1	0.81
Warthog *(Phacochoerus spp.)*	1	0.12	NA	NA
Grevy’s zebra *(Equus grevyi)*	1	0.12	NA	NA
Plains zebra *(Equus quagga)*	1	0.20	NA	NA

Discussion

I aimed to address key knowledge gaps related to the biotic interactions between invasive *Opuntia* cacti and native animals in Laikipia County. Specifically, I quantified the relationship between *Opuntia* height and fruiting, measured how both height and fruiting are related to local habitat characteristics, and used camera traps to document the interactions between *Opuntia* and the animal community. I found that for both *O. engelmannii* and *O. stricta*, taller stands had a higher probability of producing ripe fruit, and also bore a greater number of fruits; these relationships were stronger for *O. engelmannii* than for *O. stricta*. Other variables – the presence of trees, grasses, forbs, shrubs, and the cochineal biocontrol agent – also affected height or fruiting in one or both *Opuntia* species. My camera trap images contained numerous instances of interactions between native animals and the *Opuntia*. Overall, the interaction network derived from these observations for *O. engelmannii* was more diverse than the network for *O. stricta*, whereas the latter displayed a higher level of specialisation. These results have important implications for the *Opuntia* invasion in Laikipia County.

I confirmed that larger *Opuntia* stands are more likely to produce ripe fruit, and also bear a larger number of ripe fruits. Under the natural conditions in which I conducted my study, *O. engelmannii* started fruiting at smaller sizes than *O. stricta*. *O. engelmannii* stands also bore more fruits at a given size than *O. stricta*, and produced several times more fruit upon reaching their maximum size. Data from the native range of *O. engelmannii* have shown that the species can grow from a single cladode to a height of over one metre within a year (Gathaara *et al.* 1989). In my results, individuals had a high probability of producing ripe fruit at this height. As differences in the climate, soil properties, and other factors may reduce the transferability of growth rate estimates from *Opuntia*'s native range, an important next step will be to measure the relationship between age and height for *Opuntia* species growing under natural conditions in Laikipia County. The information on growth rate and fruiting size can then be integrated into models to estimate the future dynamics of the *Opuntia* invasion.

My analysis of the interaction networks for *O. engelmannii* and *O. stricta* revealed differences in network structure. One difference was that the *O. engelmannii* network was more diverse than the network for *O. stricta*. A plausible explanation for this difference is that *O. engelmannii* is far more dominant in areas where it is present than *O. stricta* is; *O. engelmannnii* tends to cover a greater proportion of the habitat, forms larger stands, and bears more fruit. This may force native animals to interact with it – either directly (*e.g.*, consuming fruit) or indirectly (*e.g.,* consuming other vegetation around the *Opuntia*) – or else be displaced from the area. The *O. engelmannii* network was also more nested than the *O. stricta* network, meaning that the behaviours exhibited by relatively specialist species (*e.g.,* olive baboons) were also exhibited by more generalist species (*e.g.,* elephants). This may be due to the main behaviours in the *O. stricta* network being dominated by species which only engaged in that behaviour (*e.g.,* dik-dik eating other vegetation) while in the *O. engelmannii* network, these species engaged in multiple behaviours (*e.g.,* dik-dik also ate *Opuntia* flowers and fruit). This mechanism would also explain why the *O. stricta* network displayed a higher level of specialisation than the *O. engelmannii* network. These findings are also consistent with an explanation based on dominance; where *Opuntia* stands are larger and bear more fruit, there may be more scope for multiple interaction types (*e.g.,* both frugivory and herbivory).

My camera trap data confirmed that elephants and olive baboons are key consumers of *Opuntia* fruit; vervet monkeys were also commonly observed feeding on the fruits of both *Opuntia* species. However, my results also revealed a potentially key role for vulturine guineafowl as dispersers of *O. engelmannii*; for this *Opuntia* species, I observed more frugivory interaction events for vulturine guineafowl than for any other species except olive baboons. I also observed several instances of ground squirrels carrying *O. engelmannii* fruits, small bird species (*e.g.,* the superb starling) feeding on the fruits of both *Opuntia* species, and even domesticated camels consuming ripe *O. engelmannii* fruits on one occasion. My findings highlight key avenues for future research into the role of animals in *Opuntia*'s dispersal ecology. One immediate question is: what is the spatial patterning of *Opuntia* seed deposition for each potential disperser species? Understanding how far different species carry *Opuntia* seeds into currently uninvaded areas would be extremely useful for forecasting the future spread of the invasion and implementing proactive management to remove new stands before they begin fruiting. Additionally, it would be useful to know whether there are certain locations (*e.g.,* resting sites; Strum *et al.* 2015) or habitats where each species tends to deposit seeds. Another key research topic concerns the fate of seeds deposited by different animal species. Currently, there is no information on the germination rates of *Opuntia* seeds in Laikipia County, and how this is affected by different animal dispersers. In several *Opuntia* species, germination is facilitated by passage through an animal's gut (López-Darias & Nogales 2008b; Mokotjomela *et al.* 2013) but whether this is true for animals in Laikipia County is not yet known. Furthermore, secondary dispersal or seed predation by small mammals (Dudenhoeffer & Hodge 2018) or vulturine guineafowl

(Papageorgiou *et al.* 2019) may also influence the ultimate fate of seeds deposited in dung, and therefore of the future spread of *Opuntia* (Dudenhoeffer & Hodge 2018).

My camera trap images also revealed several images of apparent secondary consumption of fruits which had been processed by olive baboons. Some of these cases involved elephants, but others involved species – dik-dik and oryx – which are not otherwise known to consume *Opuntia* fruits. I also observed instances where warthogs and helmeted guineafowl (*Numida meleagris*) may have been feeding on baboon-processed fruits, but could not verify these interactions to an acceptable degree of certainty. In other systems, primates facilitate secondary dispersal by processing fruits so that other species can access them; this processing can involve removing outer fruit layers which other animals cannot handle, or moving fruits to more physically accessible locations (Brockelman *et al.* 2022). My observations suggest that baboons may perform the same role for *Opuntia* by removing the spiny outer skin of the fruit and dropping the fruit remains on the ground, where other species can reach them. To determine whether this behaviour results in secondary dispersal, it is first necessary to establish that the remains of fruits which have been processed contain viable seeds. If the remains do contain viable seeds, it is then necessary to determine whether the seeds survive gut passage in the species that secondarily consume them. Another possibility which merits investigation is that ants disperse seeds from fruit remains; in other systems, birds partially consume *Opuntia* fruits, allowing for secondary dispersal by ants (Montiel & Montaña 2000).

While I observed instances of elephants feeding on the pads and roots of *O. stricta*, I did not observe any species feeding on the pads or roots of *O. engelmannii*. Notably, I did not observe domestic camels feeding on *O. engelmannii*, even though I observed camels in the vicinity of *O. engelmannii* and camels are known to feed on *O. stricta* (Wells *et al.* 2023; I did not observe any camels at sites where *O. stricta* was present). This may suggest that *O. engelmannii* is less palatable to herbivores than *O. stricta*, which may explain why the former has been able to invade relatively undisturbed conservancy land with an abundance of wild herbivores. One approach to test whether wild herbivores confer biotic resistance to *O. engelmannii* invasion (either through direct herbivory or indirect interactions) would be to measure *O. engelmannii* densities in herbivore exclusion plots (as per Wells *et al.* 2023). An important caveat is that *Opuntia* are likely to be most vulnerable to herbivores while they are still seedlings (Reyes-Agüero *et al.* 2006) and as most of the *Opuntia* stands visible to my camera traps were relatively large, I may have missed cases of herbivory on these seedlings. A longitudinal study following the fates of *O. engelmannii* stands from seedling to fruiting size would be useful for addressing this knowledge gap.

Although I did not observe any species feeding on the pads or roots of *O. engelmannii*, I did observe dik-dik eating *O. engelmannii* flowers on several occasions. To my knowledge, this interaction has not previously been documented in the scientific literature. Whether these flowers form an important part of the dik-dik's diet in invaded regions is not yet known, and whether there are any implications for the reproduction of the *Opuntia* is currently unclear.

I also observed numerous instances of herbivores – mainly dik-dik, impala and zebra, occasionally warthog, buffalo, hippopotamuses, elephants, and livestock – feeding on other vegetation which was growing amongst the *Opuntia*. As *Opuntia* expands to cover a greater degree of the habitat, the ability of animals to forage on this other vegetation is likely to have implications for their ability to persist in invaded areas. For example, I did not observe giraffes feeding on other vegetation, suggesting that inhibited foraging could partly explain the strong negative relationship between *Opuntia* volume and giraffe occupancy (Chapter 4).

Surprisingly, and contrary to previous research (Witt *et al.* 2020), I did not observe negative relationships between the proportion of cladodes covered by the cochineal biocontrol agent and either height or fruiting for *O. stricta*. Instead, I observed no relationship between cochineal and height, and a weakly positive relationship between cochineal and fruiting. The likely explanation for this discrepancy is that the relationships I observed are artefacts of a selection effect. For example, if small *O. stricta* individuals are killed by cochineal – and thus not measured – more rapidly than larger individuals, then this will bias the estimated effect of cochineal on height. Viewed from a causal inference perspective, stand survival is a function of both cochineal cover and stand height, and is hence a collider; only measuring individuals which are alive conditions on survival, inducing collider bias. Such problems can be difficult to avoid in purely observational settings, and illustrate the importance of more sophisticated study designs – such as before-after control-impact (BACI) designs – in assessing the efficacy of management interventions (Christie *et al.* 2019). A further issue is that the effects of cochineal on height and fruiting may actually represent the aggregate of several biological effects. For instance, the estimated effect of cochineal on height may also capture the effect of height on the probability that an individual stand is initially infected with cochineal, and the effect of height on the spread of cochineal within the stand (and hence on the proportion of cladode coverage). Disentangling these effects could be accomplished by studying the spread of cochineal through invaded areas over time, while incorporating information on the position, size/age, and survivorship of individual *Opuntia* stands.

The observational nature of my investigation carries other limitations which also provide promising avenues for future research. For logistical reasons, I was constrained to an observational approach for my study of *Opuntia*'s morphology and how it is related to co-occurrence with native plants. This approach makes it difficult to disentangle the causal pathways through which *Opuntia* and native plants interact. For example, the positive relationships between *O. stricta* height and the occurrence of grasses, forbs, and shrubs could reflect a facilitative effect of native plants on the growth of *O. stricta*, a facilitative effect of *O. stricta* on the growth of native plants (*e.g.*, a refuge effect; Oduor *et al.* 2018), or a combination of both effects. Consequently, experimental approaches will be an important next step for disentangling the effects of *Opuntia* invasion on the composition of the native plant community, and for ascertaining whether certain native species facilitate or hinder the spread of *Opuntia* into new areas.

A further limitation was the relatively crude way in which I classified native vegetation into broad categories. An important next step will be to conduct a comprehensive survey of plant species which co-occur with *Opuntia* in the field. Surveys conducted in Kenya's Nairobi National Park have revealed high levels of native plant richness in plots invaded by *O. ficus-indica* (Oduor *et al.* 2018), but it is not yet known whether these results generalise to the *Opuntia* invasion in Laikipia. If combined with experimental approaches, these detailed surveys could provide important insights into the effects of *Opuntia* on native plant biodiversity.

Although camera traps are a powerful tool for documenting biotic interactions – particularly those involving elusive species or occurring at night – they too carry limitations. One such limitation is that the way in which a camera trap is deployed must be tailored to a given size of target species; a common rule of thumb is to deploy a camera at approximately the target species' shoulder-height (Palencia *et al.* 2022). As my camera traps were originally deployed to study the occupancy of animals ranging in size from dik-dik to elephants, with the aim being to maximise species detections and identifiability, I deployed cameras at an average height of 81cm. Consequently, my study design was not optimised for small mammals and birds, which may have been underrepresented in my sample. Conversely, in some images of giraffes and elephants, it was not possible to determine whether an interaction was occurring as only the animal’s legs were visible. In addition, camera traps often fail to trigger for slow-moving species (Hobbs & Brehme 2017), which may explain the lack of tortoises in my images, even though I observed tortoises apparently feeding on *Opuntia* fruit on several occasions while in the field. These limitations could be addressed by technical modifications, such as the use of modified camera traps (*e.g.,* Hobbs & Brehme 2017; Littlewood *et al.* 2021) or perhaps continuous video recordings, to further expand our knowledge of *Opuntia*’s interactions with native animals.

Another key set of biotic interactions which my camera traps were unable to document are those with invertebrates. To my knowledge, the pollination ecology of *Opuntia* has not been studied in Kenya. This presents an important avenue for future research not only because of the implications for *Opuntia*’s dispersal ecology, but also for the potential impacts on native pollinators and other native plant species, such as through the disruption of native mutualisms and the formation of selected-dependence traps (Chapter 2; Stewart *et al.* 2021).

Other interactions with invertebrates also present opportunities for future research. One key question is whether ants play a role in defending *Opuntia* from invertebrate herbivores. In its native range, several ant species feed at extrafloral nectaries on *O. stricta* while providing the cactus with defence against insect herbivores which translates into increased fruit production (Oliveira *et al.* 1999). In the field, I often observed ants crawling on the *Opuntia* and appearing to feed on the extrafloral nectaries, which suggests that a similar phenomenon may be occurring in areas where *Opuntia* is invasive. There is also the possibility that ants impede the cochineal biocontrol agent; investigating these interactions presents a promising avenue for future research.

Finally, a complete picture of the interactions between *Opuntia* and Laikipia’s animals cannot be obtained without considering the interactions that occur belowground. These interactions can involve a wide range of invertebrates, vertebrates, and non-animal taxa (*e.g.*, fungi) and can exert important influences on processes, including biotic interactions, that occur aboveground (Pendergast *et al.* 2013; Bardgett & van der Putten 2014). Whether belowground interactions play an important role in the *Opuntia* invasion in Laikipia County is not yet known, and investigating these interactions is a key topic for future research.

Through a combined approach of morphological measurements and camera trap data, I have filled key knowledge gaps related to the biotic interactions between invasive *Opuntia* cacti and animals in Laikipia County. In particular, I have quantified the relationship between stand height and fruiting for *O. engelmannii* and *O. stricta* under natural conditions. Using camera trap data, I have also confirmed the importance of biotic interactions – including frugivory by olive baboons and elephants – which were thought to be important in explaining the dynamics of the *Opuntia* invasion. I have also revealed interactions which were previously underappreciated or undocumented in the scientific literature, including the key role of vulturine guineafowl as frugivores and potentially dispersers of *O. engelmannii*. My findings suggest numerous avenues for future research to improve our understanding of *Opuntia*'s dispersal ecology, enabling forecasting and proactive management to halt the spread of this invasive species.

Appendix A: Model notation

In my models, observations (*Opuntia* stands) are indexed i. F is the presence/absence (for binomial models) or number (for negative-binomial models) of ripe fruit. H is the maximum height. C is the proportion of cladode surface covered by the cochineal biocontrol agent. T is the presence/absence of a tree at least partially covering the stand. Gr, Fb, and S are the presence/absence of grasses, forbs, and shrubs respectively.

Binomial model

$$F_i \sim Bernoulli(\theta_i)$$

$$logit(\theta_i) = ln\left(\frac{\theta_i}{1-\theta_i}\right) = \overline{\alpha}_F + \alpha_{SITE[i]} + \beta_{HF}H_i + \beta_{CF}C_i +$$

$$\alpha_{TF[T[i]]} + \alpha_{GrF[Gr[i]]} + \alpha_{FbF[Fb[i]]} + \alpha_{SF[S[i]]}$$

$$H_i \sim Normal(\mu_i, \sigma_H)$$

$$\mu_i = \alpha_H + \beta_{CH}C_i + \alpha_{TH[T[i]]} + \alpha_{GrH[Gr[i]]} + \alpha_{FbH[Fb[i]]} + \alpha_{SH[S[i]]}$$

$$\alpha_{SITE} \sim Normal(0, \sigma_F)$$

$$\sigma_F \sim Exponential(1)$$

$$\overline{\alpha}_F, \alpha_{TF}, \alpha_{GrF}, \alpha_{FbF}, \alpha_{SF}, \alpha_{TH}, \alpha_{GrH}, \alpha_{FbH}, \alpha_{SH} \sim Normal(0,1)$$

$$\beta_{HF}, \beta_{CF}, \beta_{CFH} \sim Normal(0,1)$$

Negative-binomial model

$$F_i \sim Negative\text{-}binomial(\lambda_i, \phi)$$

$$ln(\lambda_i) = \overline{\alpha}_F + \alpha_{SITE[i]} + \beta_{HF}H_i + \beta_{CF}C_i +$$

$$\alpha_{TF[T[i]]} + \alpha_{GrF[Gr[i]]} + \alpha_{FbF[Fb[i]]} + \alpha_{SF[S[i]]}$$

$$H_i \sim Normal(\mu_i, \sigma_H)$$

$$\mu_i = \alpha_H + \beta_{CH}C_i + \alpha_{TH[T[i]]} + \alpha_{GrH[Gr[i]]} + \alpha_{FbH[Fb[i]]} + \alpha_{SH[S[i]]}$$

$$\phi \sim Exponential(1)$$

$$\alpha_{SITE} \sim Normal(0, \sigma_F)$$

$$\sigma_F \sim Exponential(1)$$

$$\overline{\alpha}_F \sim Normal(0, 0.5)$$

$$\alpha_{TF}, \alpha_{GrF}, \alpha_{FbF}, \alpha_{SF}, \alpha_{TH}, \alpha_{GrH}, \alpha_{FbH}, \alpha_{SH} \sim Normal(0,1)$$

$$\beta_{HF}, \beta_{CF}, \beta_{CFH} \sim Normal(0,1)$$

Binomial model with latent site-level confound

$$F_i \sim Bernoulli(\theta_i)$$

$$logit(\theta_i) = ln\left(\frac{\theta_i}{1-\theta_i}\right) = \overline{\alpha}_F + \alpha_{SITE[i]} + \beta_{HF}H_i + \beta_{CF}C_i +$$

$$\alpha_{TF[T[i]]} + \alpha_{GrF[Gr[i]]} + \alpha_{FbF[Fb[i]]} + \alpha_{SF[S[i]]} + \beta_{GF}G_i$$

$$H_i \sim Normal(\mu_i, \sigma_H)$$

$$\mu_i = \alpha_H + \beta_{CH}C_i + \alpha_{TH[T[i]]} + \alpha_{GrH[Gr[i]]} + \alpha_{FbH[Fb[i]]} + \alpha_{SH[S[i]]} + \beta_{GH}G_i$$

$$\alpha_{SITE} \sim Normal(0, \sigma_F)$$

$$\sigma_F \sim Exponential(1)$$

$$\overline{\alpha}_F, \alpha_{TF}, \alpha_{GrF}, \alpha_{FbF}, \alpha_{SF}, \alpha_{TH}, \alpha_{GrH}, \alpha_{FbH}, \alpha_{SH} \sim Normal(0,1)$$

$$\beta_{HF}, \beta_{CF}, \beta_{CFH}, \beta_{GF}, \beta_{GH} \sim Normal(0,1)$$

$$G_i \sim Normal(0,1)$$

Negative-binomial model with latent site-level confound

$$F_i \sim Negative\text{-}binomial(\lambda_i, \phi)$$

$$ln(\lambda_i) = \overline{\alpha}_F + \alpha_{SITE[i]} + \beta_{HF}H_i + \beta_{CF}C_i +$$

$$\alpha_{TF[T[i]]} + \alpha_{GrF[Gr[i]]} + \alpha_{FbF[Fb[i]]} + \alpha_{SF[S[i]]} + \beta_{GF}G_i$$

$$H_i \sim Normal(\mu_i, \sigma_H)$$

$$\mu_i = \alpha_H + \beta_{CH}C_i + \alpha_{TH[T[i]]} + \alpha_{GrH[Gr[i]]} + \alpha_{FbH[Fb[i]]} + \alpha_{SH[S[i]]} + \beta_{GH}G_i$$

$$\phi \sim Exponential(1)$$

$$\alpha_{SITE} \sim Normal(0, \sigma_F)$$

$$\sigma_F \sim Exponential(1)$$

$$\overline{\alpha}_F \sim Normal(0, 0.5)$$

$$\alpha_{TF}, \alpha_{GrF}, \alpha_{FbF}, \alpha_{SF}, \alpha_{TH}, \alpha_{GrH}, \alpha_{FbH}, \alpha_{SH} \sim Normal(0,1)$$

$$\beta_{HF}, \beta_{CF}, \beta_{CFH}, \beta_{GF}, \beta_{GH} \sim Normal(0,1)$$

$$G_i \sim Normal(0,1)$$

Appendix B: Prior predictive simulations

I used prior predictive simulations to aid my choice of priors for the α and β parameters in my negative-binomial models for fruit abundance. In my models, the relationship between a covariate (*e.g.*, height, H_i) and the number of fruits (F_i) is given by:

$$F_i \sim Negative\text{-}binomial(\lambda_i, \phi)$$

$$log(\lambda_i) = \alpha + \beta H_i$$

I used simulations to explore the consequences of selecting different priors for α and β (Fig. S1), which informed the choice of priors in my final models (Appendix A).

Code to fully reproduce my simulations is available: at https://github.com/Peter-Stewart/Zooniverse_processing.

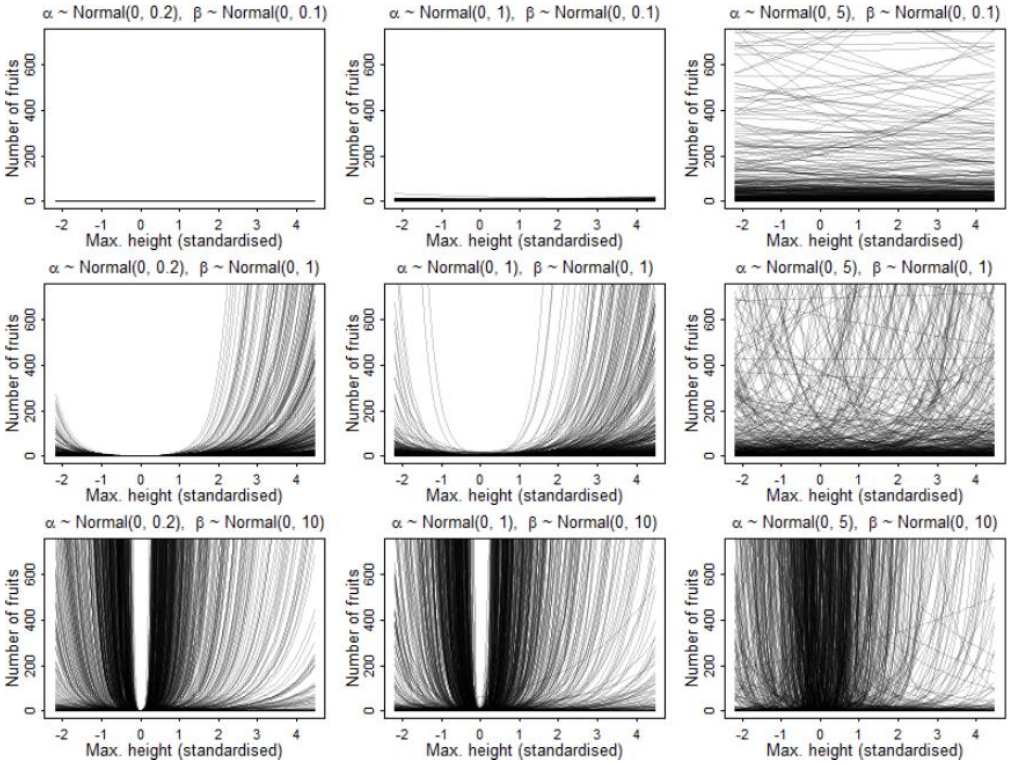


Figure S1. 1000 regression lines drawn from the prior distributions of α and β for three different choices of normal prior.

Appendix C: Supplementary results

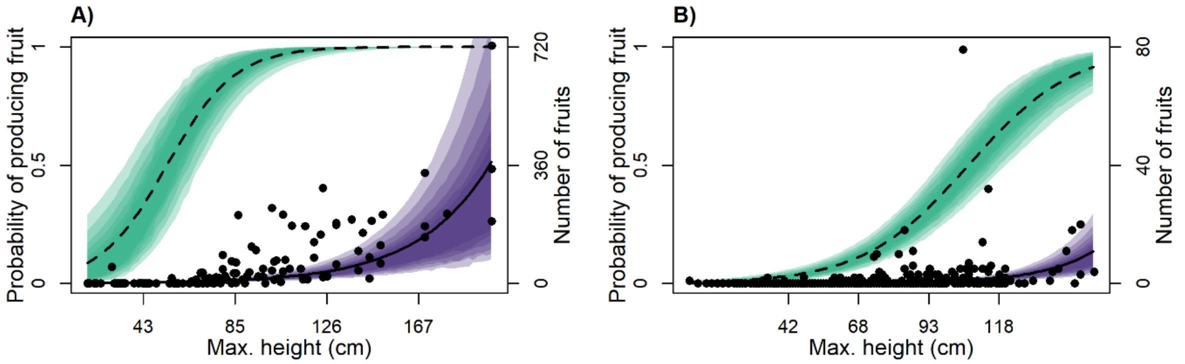


Figure S2. Relationship between maximum height and fruiting for **A)** *Opuntia engelmannii* and **B)** *Opuntia stricta*, assuming a latent site-level confound. Values for trees, grasses, forbs and shrubs are set to their respective modes (absent, present, present, and absent respectively). All plots assume that the value of cochineal cover is set to the average (*i.e.*, zero). Solid lines and purple shaded areas represent the posterior median and compatibility intervals (*i.e.*, credible intervals) for the average number of ripe fruits, while dashed lines and green shaded areas represent the posterior median and compatibility intervals for the probability of producing any ripe fruit. Shaded areas represent (from outside) 95%, 89%, 80%, 70%, 60%, and 50% compatibility intervals. Points represent maximum height and number of ripe fruit measurements for individual *Opuntia* stands.

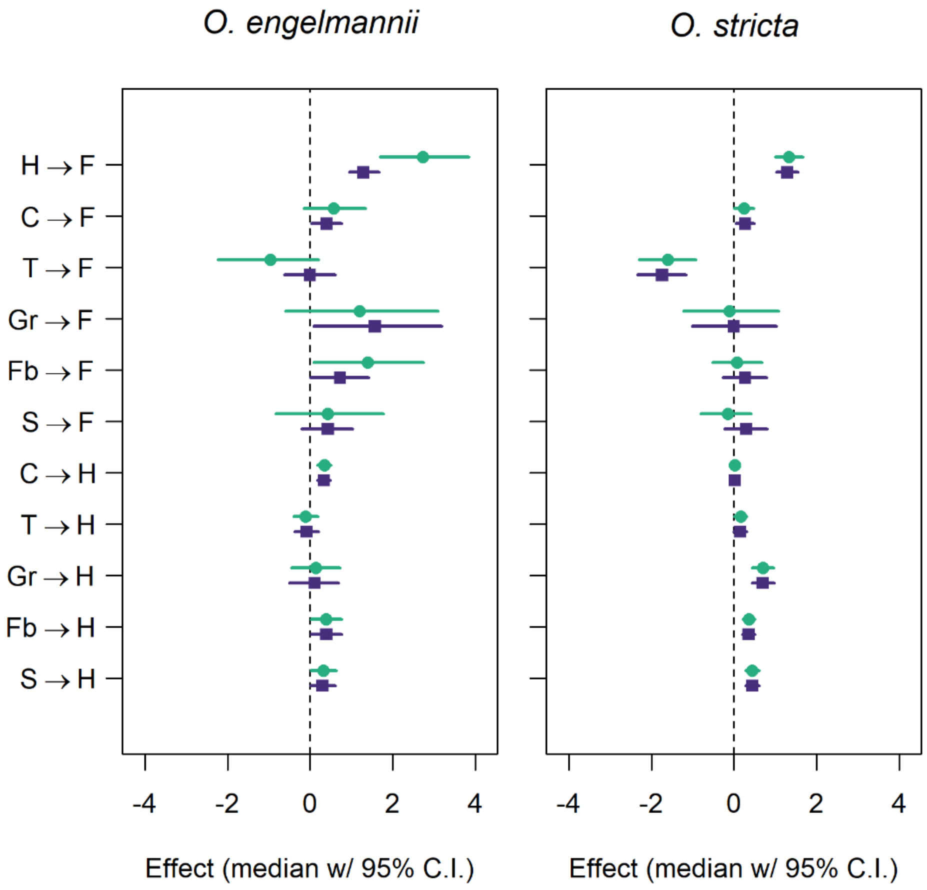


Figure S3. Effect size estimates from models of height and fruiting for *Opuntia engelmannii* (left panel) and *Opuntia stricta* (right panel), assuming a latent site-level confound. Effects are represented by the y-axis labels; for example, H → F represents the effect of height on fruiting. These effects correspond to slope (β) parameters where height (H) and cochineal (C) are the explanatory variable, and contrasts between indicator variable levels where tree (T), grass (Gr), forb (Fb) and shrub (S) presence/absence are the explanatory variable. Points and lines represent posterior median values and 95% compatibility intervals (*i.e.*, credible intervals) respectively. Points drawn as green circles represent estimates from the binomial model of fruit presence/absence, while purple squares represent estimates from the negative binomial model of the number of fruits. For full model structures, see Figure 1 and Appendix A.

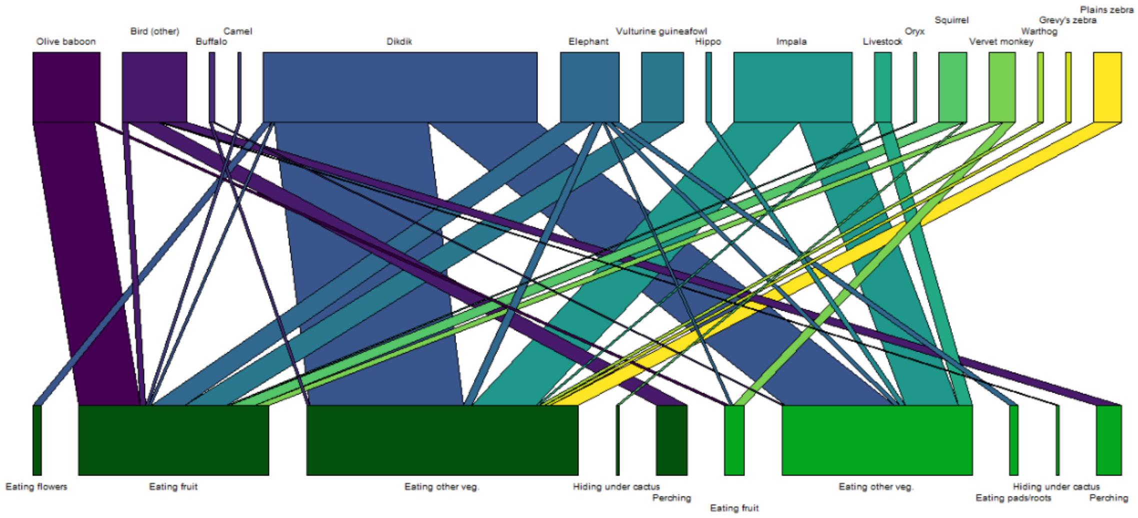


Figure S4. Joint interaction network for *Opuntia engelmannii* and *Opuntia stricta*. Upper-level nodes represent animal species, while lower-level nodes represent interaction types observed for *O. englelmannii* (dark green) and *O. stricta* (light green). Edges connecting nodes indicate observed species-behaviour combinations. Node and edge width represents the number of independent interaction events in which a given species/interaction was observed. For interaction category definitions, see main text table 1.

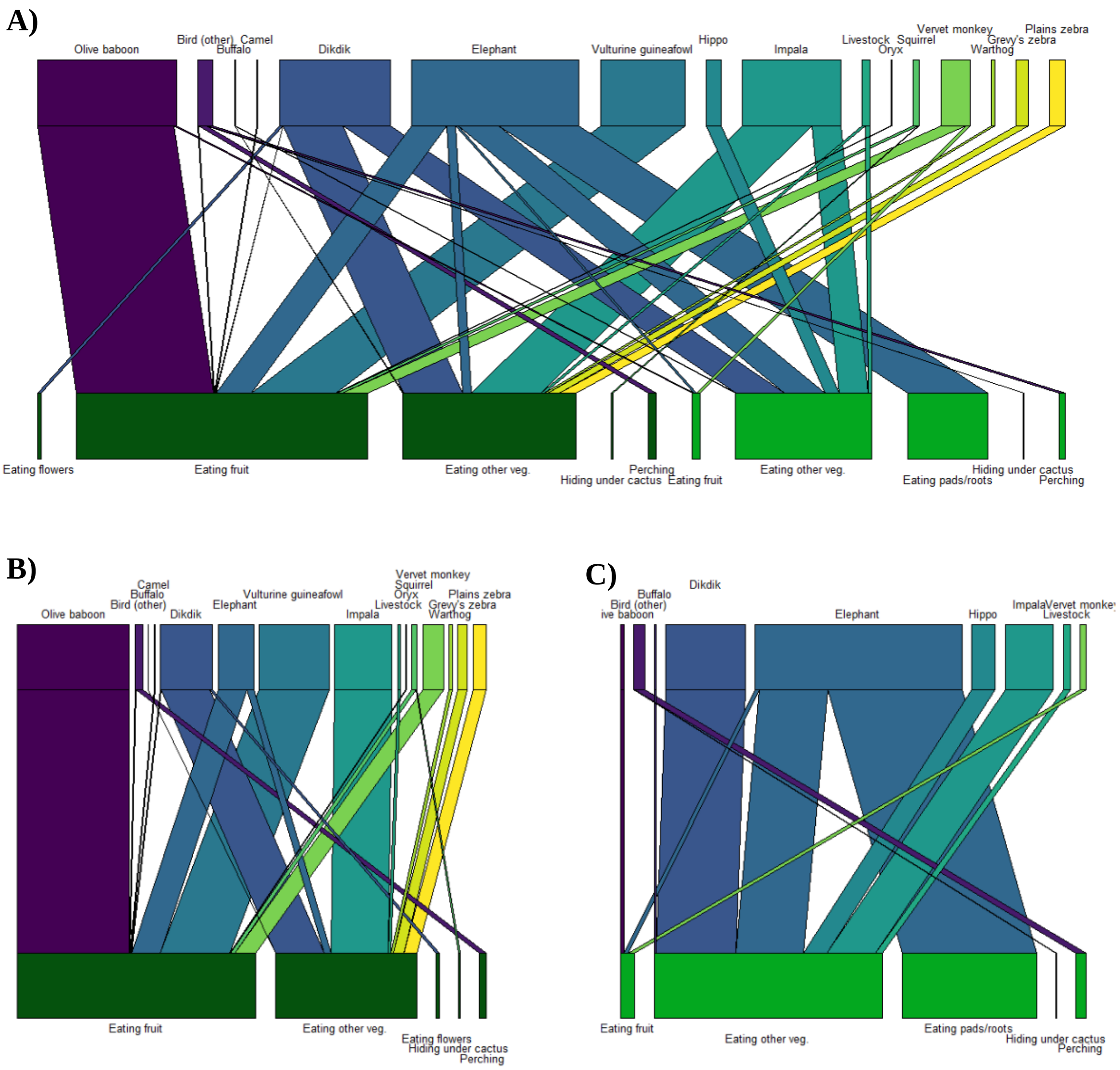


Figure S5. Interaction networks for **A)** both *Opuntia engelmannii* and *Opuntia stricta*, **B)** *O. engelmannii* only, and **C)** *O. stricta* only. Upper-level nodes represent animal species, while lower-level nodes represent interaction types observed for *O. englelmannii* (dark green) and *O. stricta* (light green). Edges connecting nodes indicate observed species-behaviour combinations. Node and edge width represents the number of camera trap images in which a given species/interaction was observed. For interaction category definitions, see main text table 1.

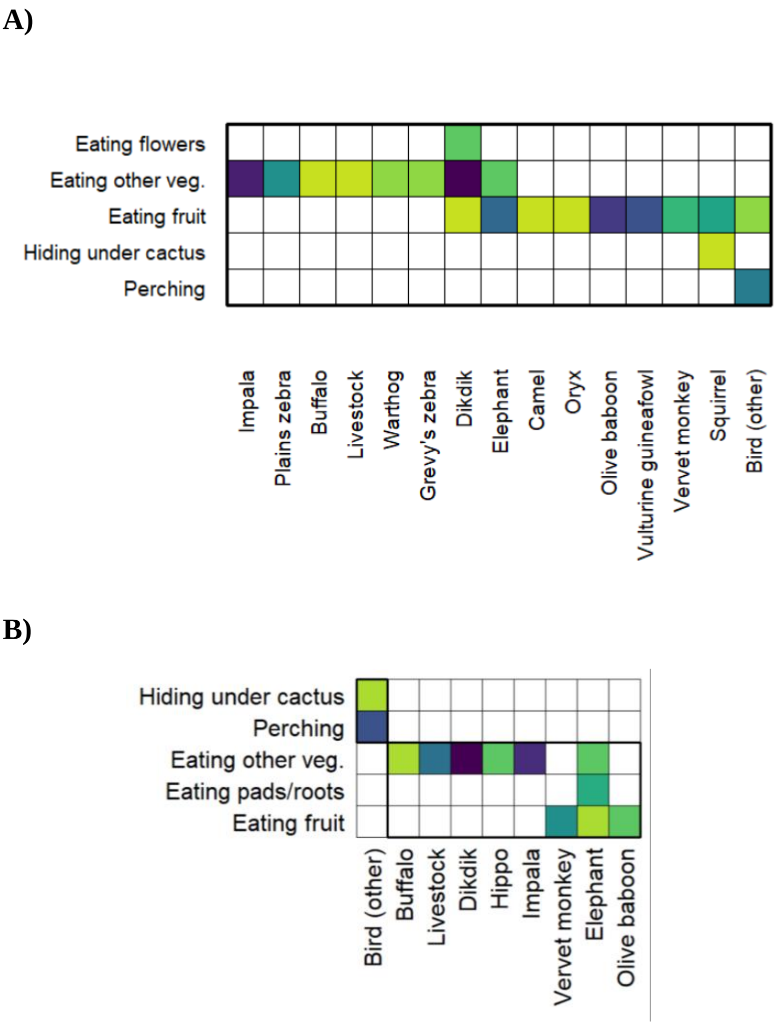


Figure S6. Interaction matrices for **A)** *Opuntia engelmannii* and **B)** *O. stricta*. Rows represent interaction types, while columns represent animal species. Darker colours indicate a greater number of distinct interaction events; white cells indicate no observations. Individual compartments are delineated with a bold black border. For interaction category definitions, see main text table 1.

Appendix D: Software information

Table S1. R packages used in my analyses. I used R version 4.1.2 and RStudio 2022.07.1 build 554 throughout.

Name	Citation	Version	Link
rethinking	McElreath, R. (2021). rethinking: Statistical Rethinking book package.	2.21	https://github.com/rmcelreath/rethinking
cmdstanr	Gabry, J. & Cesnovar, R. (2021). cmdstanr: R Interface to 'CmdStan'.	2.30.1	https://mc-stan.org/cmdstanr
MASS	Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0	NA	https://cran.r-project.org/web/packages/MASS/index.html
dplyr	Wickham, H., François, R., Henry, L., & Müller, K. (2021). dplyr: A Grammar of Data Manipulation.	1.0.7	https://CRAN.R-project.org/package=dplyr
tidyr	Wickham, H. & Girlich, M. (2022). tidyr: Tidy Messy Data.	1.2.0	https://CRAN.R-project.org/package=tidyr
lubridate	Grolemund, G. & Wickham, H. (2011). Dates and Times Made Easy with lubridate. *Journal of Statistical Software*, **40**(3), 1-25.	NA	https://www.jstatsoft.org/v40/i03/
viridis	Garnier, S., Ross, N., Rudis, R., Camargo, A.P., Sciaini, M. & Scherer, C. (2021). Rvision - Colorblind-Friendly Color Maps for R.	0.6.2	https://cran.r-project.org/web/packages/viridis/index.html
activity	Rowcliffe, M. (2022). activity: Animal Activity Statistics.	1.3.2	https://CRAN.R-project.org/package=activity
stringr	Wickham, H. (2022). stringr: simple, consistent wrappers for common string operations.	1.4.1	https://CRAN.R-project.org/package=stringr
forcats	Wickham, H. (2022) forcats: tools for working with categorical variables (factors).	0.5.2	https://CRAN.R-project.org/package=forcats
bipartite	Dormann, C.F., Gruber B. & Fruend, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. R news Vol 8/2, 8 - 11.	2.18	https://cran.r-project.org/web/packages/bipartite/index.html

Chapter 6

Conclusion

Thesis summary

In this thesis, I have explored the impacts of invasive plants on animal behaviour, using the invasion of *Opuntia* cacti in Laikipia County, Kenya, as a specific case study. In the opening chapter, I introduced the topic of biological invasions, addressing essential background material and identifying key knowledge gaps.

In the second chapter (Stewart *et al.* 2021), I focused on the impacts of invasive plants on animal behaviour, an important – yet neglected – topic. I synthesised the disparate literature on invasive plants' behavioural impacts within a novel mechanistic framework, revealing that invasive plants can cause profound behavioural changes in native animals, with ecological consequences at multiple scales. I also found that environmental context played an important role in moderating how an invader's modes of impact translate into behavioural changes in native species, and how these behavioural changes then generate ecological impacts. Finally, I identified priority research questions relating to the behavioural impacts of invasive plants.

Invasive plants' behavioural impacts can manifest as changes to the occurrence patterns of native animals. In Chapter 3 (Stewart *et al.* 2023), I used simulations to explore model selection in occupancy models, which are a powerful tool for studying the patterns and drivers of occurrence. Specifically, I investigated the consequences of collider bias – a type of confounding that can arise when adding explanatory variables to a model – for model selection using the Akaike Information Criterion (AIC) and Schwarz Criterion (or Bayesian Information Criterion, BIC). I found that the effect of collider bias, and consequently the inferential and predictive accuracy of the AIC/BIC-best model, depended on whether the collider bias was present in the occupancy or detection data-generating process. My findings illustrate the importance of distinguishing between inference and prediction in ecological modelling and have more general implications for the use of information criteria in all linear modelling approaches.

In Chapter 4, I applied the mechanistic framework from Chapter 2 and the modelling conclusions from Chapter 3 to the problem of understanding *Opuntia*'s behavioural impacts in Laikipia County. Specifically, I used camera traps to explore the effects of *Opuntia* on occupancy and activity for eight key mammal species. I found that the effects of *Opuntia* varied among mammal species and depended on the spatial scale of the *Opuntia* cover covariate. These findings have important implications for the conservation of endangered mammal

species in the region, the future spread of *Opuntia* through seed dispersal, and interactions between wildlife and local communities.

In Chapter 5, I addressed key knowledge gaps pertaining to *Opuntia*'s biotic interactions with native animals. First, I quantified the relationship between height and fruiting in *O. engelmannii* and *O. stricta*, finding that height was positively related to fruiting for both species, and that the relationship was stronger for *O. engelmannii* than for *O. stricta*. I also found that local habitat variables were related to height and/or fruiting in both *Opuntia* species. Second, I documented the interactions between animals and *Opuntia* using camera traps. In so doing, I confirmed the importance of interactions that were previously thought to be important, while also highlighting interactions which have previously received little attention in the published scientific literature.

Implications for *Opuntia* invasions in Laikipia County, Kenya

Our understanding of the *Opuntia* invasions in Laikipia County has previously been limited by a lack of empirical data. By collecting new camera trap data, alongside measurements of habitat characteristics and individual *Opuntia* stands, I have taken steps towards addressing this challenge. This has important implications for our understanding of the dynamics and impacts of the *Opuntia* invasions. Furthermore, my data can be used in future research on the *Opuntia* invasions in Laikipia County.

I found that *Opuntia* can affect the behaviour of native animals, altering the occupancy and activity of key mammal species in the landscape. As discussed in Chapter 4, this finding raises important conservation concerns. In particular, I found a strong negative relationship between broad-scale *Opuntia* volume and reticulated giraffe (*Giraffa reticulata*) occupancy; in the most heavily invaded areas that I observed, the posterior median giraffe occupancy was just 0.08. This suggests that as *Opuntia* continues to spread, giraffes will be largely extirpated from the landscape. As around a quarter of the world's reticulated giraffes live in Laikipia and the neighbouring Isiolo and Samburu counties (Muneza *et al.* 2018), the continued spread of *O. stricta* from the Doldol area, as well as the potential for *O. engelmannii* to spread from Loisaba Conservancy (which sits close to the Laikipia-Isiolo-Samburu border), poses a serious risk to the giraffe population, and thus the species as a whole.

Although my investigation sheds light on the probable consequences of *Opuntia* invasion for reticulated giraffe occupancy, I was not able to determine the precise mechanisms underlying this result. However, as I briefly discussed in Chapter 4, there are several plausible explanations for the effect of *Opuntia* on giraffe occupancy. One possibility is that *Opuntia* invasion inhibits giraffe foraging by reducing access to food. In the region where I conducted my research, reticulated giraffes predominantly feed on *Vachellia* and *Senegalia* (formerly *Acacia*) species, mainly at a height of 2-3 metres (O'Connor *et al.* 2015). Therefore, it is plausible that tall *O. engelmannii* stands could interfere with giraffes' ability to feed. Furthermore, the diameter of *Opuntia* stands could prevent giraffes – particularly small juveniles – from moving close enough to the base of trees to be able to forage. The conjecture that *Opuntia* affects giraffe occupancy through impeding their foraging is supported by my camera trap data; I did not observe any giraffes feeding on vegetation growing amongst *Opuntia*, nor did giraffes consume the *Opuntia* itself (Chapter 5). However, it should be noted that this observation could be an artefact of the height at which I deployed my camera traps, as my approach was not optimised for observing giraffe foraging behaviour. Furthermore, evidence against a foraging-based explanation is provided by my comparison of occupancy models with and without measures of the native plant community, including shrub cover and the number of trees. I found similar results in both sets of models (Chapter 4), suggesting that the effects of *Opuntia* on occupancy are not mediated by changes to the native plant community. Consequently, other mechanisms – such as a lack of suitable resting sites in heavily invaded areas or changes to the risk of calf predation – may underly the effects of *Opuntia* on giraffe occupancy.

The mechanistic basis of *Opuntia*'s effects on reticulated giraffe occupancy could be explored in future research. If *Opuntia* restricts giraffe foraging, we would predict that in invaded areas, giraffes would preferentially forage on trees growing in the open rather than those growing within *Opuntia* stands. Furthermore, we would expect this preference to be stronger for smaller giraffes, particularly juveniles. These predictions could be tested using behavioural surveys or upward-angled camera traps. These approaches could also be applied to test the resting site explanation for *Opuntia*'s effects on giraffes; if giraffes avoid heavily invaded areas due to a lack of resting sites, then we would expect that giraffes exhibit less recumbency among *Opuntia* stands than in open areas. Given that giraffe recumbency often occurs at night, camera traps would be more suitable than in-person behavioural surveys for testing this prediction. A camera trap-based approach would also have the benefit of minimising disturbance, which could alter the giraffes' natural behaviour patterns. An alternative would be to use GPS collars fitted with accelerometers to follow specific individual giraffes. Hidden Markov models (McClintock *et al.* 2020) could then be employed to decode each giraffe's probable activity state (*i.e.,* whether it is recumbent) at each point in time from the accelerometer data, and to relate this to the level of *Opuntia* in the area where the giraffe is situated at that time. Furthermore, if the characteristics of a suitable resting site (*e.g.,* an open area over a certain size) can be determined, then aerial photography or high-resolution satellite imagery could be used to map the distribution of resting sites in heavily invaded versus less-invaded areas. These data would allow us to test whether there are really fewer suitable resting sites in heavily invaded areas.

Another important concern related to the effects of *Opuntia* on mammalian occupancy and activity patterns is the potential for indirect effects on other ecosystem characteristics. In particular, I observed negative effects of *Opuntia* on the occupancy and activity of one of the region's most abundant herbivores, the impala (*Aepyceros melampus*). As discussed in Chapter 4, these effects are likely due to changes in actual or perceived predation risk caused by *Opuntia* blocking escape routes and sightlines. Research on the avoidance of woody cover by impala, which is also driven by predation risk (Ford *et al.* 2014; Epperly *et al.* 2021), illustrates the possible effects of *Opuntia*-driven changes to impala occupancy and activity for native vegetation. When impala avoid woody areas, plant species with relatively poor physical defences (*e.g., Senegalia brevispica*) are released from herbivory, and thus become more prevalent (Ford *et al.* 2014). Therefore, it is plausible that *Opuntia* invasion will favour native plants with reduced physical defences. This effect may be exacerbated by nurse plant effects, in which *Opuntia* stands physically shield other plant species from herbivory (Oduor *et al.* 2018). There is also the potential for complex interplay between herbivore-mediated effects of *Opuntia* on native plants, and effects which are mediated through other pathways such as changes to soil properties. For example, in other systems, *Opuntia* is known to benefit from fertility islands created by some native trees, while simultaneously creating its own fertility islands that may influence the native plant community (Novoa *et al.* 2021). Consequently, herbivore-mediated effects of *Opuntia* on tree community composition could feed back to influence the growth of *Opuntia* plants in the area. Investigating whether *Opuntia*'s effects on impala habitat use result in indirect effects on native vegetation represents an important topic for future research.

In addition to providing information about the effects of *Opuntia* on mammalian habitat use, I have provided insights into key aspects of the interactions between native animals and the *Opuntia*. For example, my data help us to interpret the results of experimental work by Wells *et al.* (2023), which aimed to establish whether wild herbivores confer biotic resistance to *O. stricta* invasion. The key finding of this work was that *O. stricta* densities are higher in plots where ungulate herbivores are excluded (Wells *et al.* 2023). However, this result is difficult to interpret in isolation because there are multiple possible explanations for the observed pattern; as I discussed in Chapter 1, the difference in *Opuntia* densities between experimental plots could be due to herbivores consuming *Opuntia*, indirect effects due to herbivory on native plants, or other effects of the exclusion plots (*e.g.,* effects on *Opuntia* seed removal). By using my camera trap images to document interactions between native animals and the *Opuntia*, I have provided data to help assess these competing explanations. In preliminary data provided for the Wells *et al*. (2023) paper, I evidenced cases of elephants (*L. africana*) digging up *O. stricta* stands and consuming the cladodes and roots. This provides some support for the argument that elephant herbivory suppresses *O. stricta* densities. However, it is currently unclear whether the net effect of elephant digging events on *O. stricta* is to suppress growth through cladode consumption, or instead to facilitate the *Opuntia* by scattering viable cladodes over the surrounding area, aiding vegetative propagation (Foxcroft & Rejmánek 2007). Measuring *Opuntia* growth in elephant feeding sites relative to nearby control areas could provide insight into the net effect of elephant herbivory on *Opuntia*. Notably, I did not observe any other animals feeding on the cladodes or roots of *O. stricta* (Chapter 5). This suggests that if the net effect of elephant herbivory is found to be neutral or positive, then the likely explanations for the herbivore-exclusion results are: 1) herbivores consuming or trampling *Opuntia* seedlings, which were not well-represented in my camera trap images; 2) indirect effects due to herbivores influencing native plants; 3) effects of the herbivore exclusion plots on *Opuntia* fruit and seed removal. Testing these competing explanations presents a promising avenue for future research.

My camera trap data also provides insights into another key aspect of the interactions between native animals and the *Opuntia* – consumption of *Opuntia* fruits by frugivores. In Chapter 5, I confirmed that elephants (*L. africana*) and olive baboons (*P. anubis*) are among the main consumers of *Opuntia* fruit. I also found that vervet monkeys (*C. pygerythrus*) commonly consumed the fruits of both *O. engelmannnii* and *O. stricta*. As well as verifying the role of these species in *Opuntia* fruit consumption, my behavioural observations support the conjecture that the strong positive relationships between *Opuntia* and the occupancy and activity of these species (Chapter 4) is due to their attraction to *Opuntia* fruit. In addition, I found that a variety of other animals – particularly vulturine guineafowl (*A. vulturinum*) – consume the fruits of *O. engelmannii*. This finding suggests that a wide range of native animals potentially disperse *O. engelmannii* in Laikipia County; as I discussed in Chapter 5, determining whether frugivory translates to *Opuntia* dispersal will require additional information on the viability, germination rate, and transportation distance of ingested seeds.

Once further data on *Opuntia* dispersal by native animals have been obtained, the findings can be incorporated into models with the aim of improving our understanding and management of the *Opuntia* invasion. As mentioned in Chapter 5, these models could also my data on *Opuntia* size and fruiting. One option would be to create a spatially explicit agent-based model; similar models have been successfully applied to other invasive plants, for example to model the spread of *Rhododendron ponticum* under different control scenarios (Travis *et al.* 2011). The agents – individual *Opuntia* stands – could transition between different states (*e.g.*, height, diameter, fruiting), with the rates of these transitions informed by the biological data I have collected. For example, the number of fruits produced by a stand could depend on its height, following the relationships which I estimated in Chapter 5. The transition rate parameters could be further refined when region-specific growth rate data are available. To model the spread of *Opuntia* through vegetative growth, new stands could be generated in areas adjacent to existing stands; the vegetative growth rate could be higher for large stands, which can drop more cladodes. To represent seed dispersal, fruiting stands could randomly disperse their fruit within a buffer zone, with the dispersed fruits then having a probability of germinating to form a new *Opuntia* stand. The relationship between distance from an *Opuntia* stand and the probability of fruit dispersal represents *Opuntia*'s dispersal kernel; until data on the actual dispersal kernel are available, a range of functions could be used to explore the role of seed dispersal in the invasion. Management interventions could be represented in the model by removing stands from defined areas at a cost, with this cost depending on the number and size of *Opuntia* stands removed, and possibly how accessible the area is by road. The model could be further extended to represent imperfect detection of small stands by removal teams, perhaps with the probability of detecting small stands being increased at a cost to represent the allocation of more resources to the search. The spatial and cost-explicit nature of the model would allow for a variety of important management questions to be addressed. For example, how much effort should be allocated to detecting small, non-fruiting stands far from the main invasion source? Should management be focused on the periphery of the invaded region, or is it also necessary to reduce the *Opuntia* density in areas at the invasion's core in order to stop the spread? If multiple removal teams are available, should they allocate their efforts to nearby areas, or areas which are further apart?

The data I collected also provide opportunities for studying ecological impacts of *Opuntia* which lie outwith the scope of my thesis. In particular, my camera trap data could be used to examine *Opuntia*'s effects on the population density of key animal species in Laikipia County, providing a complementary perspective to my results for occupancy and activity.

Estimating effects of *Opuntia* on mammalian population density using camera trap data

A variety of methods are available for estimating population density from camera trap images. For these approaches to be suitable for studying the effects of *Opuntia* using my camera trap data, they must allow for covariate effects to relate *Opuntia* cover to population density, and the model's assumptions and data requirements must be met by my study design. One option is spatial capture-recapture (Efford 2004; Tourani 2022), which can be employed to estimate population density when individual animals can reliably be identified. In Laikipia County, this approach would probably be most suitable for species like reticulated giraffe (*G. reticulata*) and zebra (*E. grevyi* and *E. quagga*), which have well-defined markings. Elephants (*L. africana*) would also be suitable, as individuals can be identified by their ear notches and tusks (Oduor *et al.* 2020). Individual leopards (*Panthera pardus*) can be identified by their rosette patterns, and the species is often studied using spatial capture-recapture (Tourani 2022). However, I suspect that the approach will be unsuitable for leopards in my dataset because the images taken at night often exhibit motion blur, making the rosettes difficult to distinguish. Consequently, leopards – along with the numerous species for which reliable individual identification from images is not possible – will need to be treated using methods designed for density estimation using unmarked data.

For species where individuals cannot be readily distinguished, and thus spatial capture-recapture cannot be used, several modelling options are available which allow for population density estimation using unmarked data (Gilbert *et al.* 2021). Site-structured models, such as Royle-Nichols and N-mixture models (Royle & Nichols 2003; Royle 2004), are one option. These models allow for the estimation of covariate effects (Gilbert *et al.* 2021), meaning they would be suitable for quantifying how *Opuntia* affects mammalian population density. The N-mixture model requires counts of individual animals in each photo; although I obtained counts from the Zooniverse volunteers, it would be sensible to assess volunteer count accuracy using the expert-classified image subset (Chapter 4, Appendix D) and to develop a reliable method for generating consensus counts before employing the N-mixture model. However, two aspects of my study may be problematic for the application of site-structured models. First, several species in the dataset live in groups, which violates the N-mixture model's assumption of individuals being independently detected; this challenge could be dealt with by extending the model as per Martin *et al.* (2011). A second, more challenging, issue is due to the paired design of my camera trap study; cameras in the same pair were situated close enough together that the same individual animals could be detected on neighbouring cameras, violating the key assumption of no overlap in cameras' effective sampling areas (Gilbert *et al.* 2021). This problem could potentially be overcome by pooling data from neighbouring camera traps, which would still allow for estimation of the grid square-level effects of *Opuntia* on density.

Another option for estimating *Opuntia*'s effects on animal population density is to employ distance sampling (Kéry & Royle, 2015; Howe *et al.* 2017). Although the formulation of distance sampling that is usually used for camera trap studies (Howe *et al.* 2017) does not allow for covariates (Gilbert *et al.* 2021), this issue could be overcome by using the hierarchical model of Kéry and Royle (2015). The critical information required for distance sampling is an estimate of the distance from each detected animal to the camera (Gilbert *et al.* 2021). In principle, it is possible to obtain these data for my camera trap images by comparing them with the calibration images that I took in the field (Chapter 4). To use distance sampling, it is also necessary to censor times of day when animals are inactive (Gilbert *et al.* 2021). This could be accomplished by examining each species' activity kernel using the methods I employed in Chapter 4.

The random encounter model (REM; Rowcliffe *et al.* 2008) is a popular approach for density estimation from unmarked animal observations, but the model as originally formulated is not suitable because it does not allow for environmental covariates (Gilbert *et al.* 2021). However, an extension of the REM – the random encounter and staying time (REST) model (Nakashima *et al.* 2018, 2020) – does allow for covariates. An added advantage of the REST model is that the key information required – the mean number of detections by each camera during its survey period, and the mean staying time of individuals within the detection zone – can be derived directly from camera trap images (Nakashima *et al.* 2018). Furthermore, the model can be extended to account for spatial autocorrelation (Nakashima *et al.* 2020), which is necessary due to the short distances between paired sites in my study. However, several of my study's characteristics necessitate that caution is exercised when applying the REST model to my data. First, Nakashima *et al*. (2018) recommend that no cool-down period is used for camera traps when the REST model is going to be applied, but my cameras were set with a five second cool-down. Therefore, it would be prudent to use simulations to ensure that the cool-down period does not result in inaccurate inferences before applying the model. Second, features of animals' daily activity patterns, such as extended periods of inactivity, can result in inaccurate density estimates (Nakashima *et al.* 2018). Consequently, for some species it will be necessary to use activity information derived from the camera trap data and natural history knowledge to correct the estimates (Nakashima *et al.* 2018). Finally, the REST model assumes are detected with certainty within a defined subset of the field of view (Nakashima *et al.* 2018). Consequently, may be necessary to restrict the analysis to animals sighted close to the camera; I suggest restricting the analysis to animals detected within 10 metres, as this was the range up to which I validated the camera's field of view by taking calibration photos.

Several other methods are available for estimating density from camera trap detections without individual recognition (Gilbert *et al.* 2021) but, for various reasons, these are unlikely to be suitable for studying the effects of *Opuntia* using my dataset. Space-to-event and instantaneous sampling models (Moeller *et al.* 2018) are unsuitable because they require the use of time-lapse photos (Gilbert *et al.* 2021), which my cameras were not set to collect. Unmarked spatial capture-recapture models (Chandler & Royle 2013) require the array of camera traps to be spaced so that individual animals are detected at multiple cameras (Gilbert *et al.* 2021); although in my study it is likely that individual animals were detected on both cameras within a site pair, the distances between site pairs were probably too large for individuals to be detected in more than one pair. The time-to-event model (Moeller *et al.* 2018) is also unlikely to be suitable, principally because the model assumes perfect detection (Gilbert *et al.* 2021) and this assumption is extremely unlikely to hold; camera traps often miss animals due to limitations of the passive infrared sensor and the potential for unidentifiable photos (Findlay *et al.* 2020). Furthermore, in my volunteer-classified data the sensitivity of consensus classifications is less than one for most species (Appendix D, Table S1). Another issue is that the time-to-event model assumes that detections are spatially and temporally independent (Gilbert *et al.* 2021); the former assumption is unlikely to hold due to the short distance between camera traps within a pair, while the latter is likely to be violated because the cameras' 5-second cooldown period often resulted in multiple consecutive photos of the same individual animal.

Regardless of whether marked or unmarked methods are used to estimate *Opuntia*'s effects on mammalian population density, the choice of model covariates will be a key consideration – just as it is when modelling occupancy (Chapter 3). Understanding how *Opuntia* affects population density is an inference problem, and although simulations analogous to those I conducted in Chapter 3 have not yet been conducted for population density models, there is no reason to expect that the results will be substantially different. Therefore, I suggest that the guiding principle should be to consider the purpose – inference or prediction – of each sub-model within the main density model. This suggests that predictive tools, such as information criteria, should not be used to guide the choice of covariates for the density variable itself, but may be suitable for tasks such as guiding the choice of detection function for spatial capture-recapture (Efford 2004). For the density covariates, I suggest that a causal inference approach – as detailed in Chapter 3 – could be applied.

Wider implications: mechanism and causal inference in invasion ecology

The topics of mechanism and causal inference are among the main themes of my thesis. In my introductory chapter, I argued that a mechanistic understanding of invasive species' impacts is important for facilitating proactive and effective management. In Chapter 2 (Stewart *et al.* 2021), I aimed to further our mechanistic understanding of invasive plants' impacts on animal behaviour by developing a mechanistic framework that explicitly considered the drivers and ecological consequences of behavioural change, as well as the moderating role of environmental context. In Chapter 3 (Stewart *et al.* 2023), I took a different approach to the understanding of mechanism, applying insights from the field of causal inference to the problem of modelling the patterns and drivers of species occupancy. In Chapter 4, I combined these two approaches by using the framework from Chapter 2 (Stewart *et al.* 2021) to help develop a directed acyclic graph (as per Chapter 3; Stewart *et al*. 2023), which I then used to inform my choice of covariates when modelling the effects of *Opuntia* on mammalian occupancy. I again applied a causal inference-based approach in Chapter 5, modelling the relationship between *Opuntia* height and fruiting. Through these chapters, I have illustrated how causal inference can be applied to help further our mechanistic understanding of the behavioural impacts of invasive species, and the *Opuntia* invasion in particular. In this section, I argue that causal inference has broader implications for the field of invasion ecology.

Causal inference presents an exciting opportunity for invasion ecologists, arming us with a powerful array of quantitative tools. As argued in Chapter 3, causal inference allows us to deal with the problem of model selection and complements existing tools, like the widely used information-theoretic approach (Anderson *et al.* 2000; Burnham & Anderson 2001; Lukacs *et al.* 2007; Burnham *et al.* 2011). The functionality of causal inference is particularly relevant for invasion ecology because field-based studies are often limited in their scope for experimental intervention (*e.g.,* deliberate addition of invasive species is generally unethical, while experimental removal at scale may be prohibitively expensive). Furthermore, invasion ecologists often begin studying the system only after the invasion has already spread, and are left trying to explain the factors underlying an invasion *post hoc*. This point fits well with the counterfactual perspective (Pearl *et al.* 2016, p. 89) of causal inference, as we are often asking whether an invasion would still have occurred had circumstances (*e.g.,* land use, the traits of the invasive species, management efforts) been different. I argue that a specific case where causal inference could provide novel insights is in the study of the factors underlying the global-scale patterns of invasive species occurrence. The most recent work on this topic (*e.g.,* on the effects of land use; Liu *et al.* 2023) is largely reliant on information-theoretic methods, which limits the strength of conclusions that can be drawn. Further advances could be achieved by using directed acyclic graphs to simultaneously consider the direct and indirect drivers of biological invasions, and to examine whether the conclusions are robust to varying the assumptions about how these drivers operate.

The quantitative tools provided by causal inference are not limited to the problem of model selection. A second area where the approach can be applied is to deal with cases where data are missing or measured with error (McElreath 2021, pp. 489-521). These situations are common in invasion ecology. For example, invasive species occurrence data which have been collected by the general public can form a vital part of the effort to monitor, understand, and predict the distributions of invasive species (Roy *et al.* 2015). However, these efforts can be vulnerable to spatial and temporal biases in data collection, as well as selective recording by the volunteers (van Strien *et al.* 2013). The application of causal inference methods may allow us to overcome these biases in cases where other methods (*e.g.,* occupancy models; van Strien *et al.* 2013) are unsuitable, and could also allow for sensitivity analyses to explore whether the results are robust to different types of recording bias.

As well as its uses in observational studies, causal inference also provides methods to examine the transportability of experimental results to observational settings (Pearl & Bareinboim 2014). In particular, selection diagrams – a particular form of directed acyclic graph – can be used to explicitly state assumptions about ways in which the experimental and observational settings are similar or different, and to then determine whether a result from the experimental setting is likely to generalise to the observational setting (Pearl & Bareinboim 2014). Selection diagrams are potentially useful in invasion ecology because the field has a wide array of hypotheses (see Enders *et al.* 2018) which are often tested in experimental settings like bacterial microcosms (*e.g.,* Jiang *et al.* 2010), greenhouses (*e.g.,* Feng *et al.* 2019), and pond mesocosms (*e.g.,* Fey & Herren 2014). Hypotheses which survive experimental testing in these relatively artificial conditions are not guaranteed to play an important role in the dynamics of real biological invasions. Therefore, it is important to understand the conditions under which experimental results are transportable to real biological invasions; causal inference has the potential to play an important role in addressing this research topic.

Causal inference is not only important because it provides a powerful set of tools, but also because it broadens our perspective, illuminating previously unseen possibilities and allowing us to view old problems from new angles. One of the most important ways in which causal inference adds to our perspective is by improving our understanding of included-variable bias. In ecology, the idea that including variables in a model can bias effect estimates has been discussed mostly in the context of multicollinearity (Graham 2003). However, a high correlation between explanatory variables is not a reliable indicator that adding them to the same model will induce bias; it is entirely possible for the inclusion of a highly correlated explanatory variable to improve inferential accuracy, and for the inclusion of a variable to harm accuracy even when its correlation with other explanatory variables is low (Chapter 3). This insight suggests that it is time to rethink how we approach multicollinearity in ecological modelling.

A second important point which causal inference helps to clarify is that included-variable bias can arise not just through covariate choice in a model, but also through aspects of study design or the intrinsic features of the biological system under study. For example, Berkson's (1946) eponymous paradox concerns a spurious association between two diseases in a study of hospital patients. A causal view of this paradox (Pearl & Mackenzie 2018, pp. 197-200) tells us that because both diseases influence the probability of hospitalisation, to study only hospitalised patients is to condition on a collider (*i.e.,* hospitalisation), producing a spurious association between the two diseases. The explanatory power of causal inference is not limited to Berkson's paradox, but also encompasses a diverse array of phenomena including Simpson's and Lord's paradoxes, post-treatment bias, case-control bias, and multicollinearity (Pearl 2014; Pear & Mackenzie 2018, pp. 189-217; McElreath 2021, pp. 163-175; Cinelli *et al.* 2022). By helping us to understand why these phenomena occur, causal inference allows us to avoid common pitfalls in our analyses and study designs.

Finally, the causal inference perspective changes the way we interpret parameters, particularly in the linear models that are ubiquitous in ecology. In so doing, the approach helps us to avoid potential pitfalls during the model interpretation stage. It is tempting to interpret linear model effect sizes as estimates of the direct effect of each covariate on the response variable. However, after adopting a causal perspective we instead see that while some effect sizes can be reasonably interpreted as direct effects, some represent total effects, others are the combination of multiple direct and indirect pathways, and some 'effects' are in fact biologically meaningless (Westreich & Greenland 2013).

Until recently, causal inference approaches were rare in ecological studies (Laubach *et al.* 2021). However, ecologists are increasingly recognising the power of the quantitative tools and novel perspectives offered by causal inference; the last two years have seen an explosion of papers discussing and applying causal inference methods to ecological problems (*e.g.,* Kimmel *et al.* 2021; Addicott *et al.* 2022; Arif & MacNeil 2022, 2023; Dee *et al.* 2023; Hone & Krebs 2023). By exploring model selection in occupancy models from a causal inference perspective (Chapter 3), and applying my findings to the problem of *Opuntia* invasions in Laikipia County (chapters four and five), I aimed to further this paradigm shift. In the coming years, I believe that causal inference will occupy a niche alongside complementary methods, like the information-theoretic approach, as an important part of the analytical toolbox available to invasion ecologists.

Conclusion

In the 65 years since Charles Elton's foundational work (Elton 1958), the scale of the challenge posed by biological invasions has substantially increased. However, invasion ecologists have risen to the challenge; we have seen significant advances in our understanding of the invasion process, the impacts of invasive species, and how we can intervene to mitigate these impacts. Over the coming decades, we are likely to see the number of invasive species continue to rise as new introductions occur, and biological invasions will increasingly interact with other global change processes such as climate change (Pyšek *et al.* 2020; Seebens *et al.* 2021). Therefore, it is vital that our work continues towards developing a mechanistic understanding of biological invasions, so that we are well-situated to tackle the ongoing and emerging problems resulting from invasive species.

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