Drivers, consequences and perceptions of newly arriving range-shifters in the United Kingdom

Submitted by James Cranston to the University of Exeter
as a thesis for the degree of
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: James Cranston

Abstract

CONTEXT:

Species distributions are rapidly altering in the 21st century. Climate change and other anthropogenic effects threaten historic ranges but also open up new regions for expansion. Distributional changes will create novel biotic interactions that may significantly affect ecosystems, and humanity, both positively and negatively. Range-shifters create conservation conundrums, which may require us to balance the conservation value of newly arriving species against their impacts on existing biodiversity. To tackle these conundrums we will have to understand why and how species are moving, be able to make predictions of what potential effects may be felt in the new range and recognise how species are perceived when they arrive there.

APPROACHES:

I explore three aspects of species redistribution: processes, consequences, and perceptions. To better understand the redistribution process, I investigate the importance of climate, habitat, and proximity to source populations in predicting 14 range-shifting birds' distributions in Britain. I explore consequences by estimating effects of a range-shifting damselfly on UK Odonata with dynamic multispecies occupancy (DMSO) models. Finally, I explore perceptions by surveying UK wildlife recorders' attitudes towards range-shifting species and their management.

RESULTS:

I found that climate did not predict most analysed range-shifters' British distributions effectively. Despite being comparatively better, neither habitat nor distance from European breeding sites were good absolute predictors. Counter-intuitively, our DMSO model predicted that 15/17 resident dragonflies were more likely to persist at sites where the range-shifting damselfly established. Survey responses revealed that recorders opposed efforts to either control or support range-shifters, instead favouring non-intervention.

IMPLICATIONS:

The poor predictive power of climate suggests that we should explicitly study the full potential suite of range-shift processes, including biotic interactions and constraints on species movement. The absence of a negative association between the range-shifting damselfly and most Odonata species should be welcomed, but cautiously as other factors (e.g. habitat) may confound the range-

shifters' effect. Recorders' averseness to interventions suggests that ecological research focused on the feasibility of both assisted colonisation and range-shifter threat should also seek to understand social contexts for successful conservation. Integrating these findings, I argue that we should use rapidly growing ecological datasets to not just detect but to test and refine theories of range-shift. Future model refinement alongside fuller understanding of stakeholder perspectives will help enable equitable – and ecologically beneficial – range-shift management.

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Thanks also to Dr Nick Isaac, who has always provided insightful comments on and support for my work. Nick also has introduced me to the wonderful world of Bayesian Statistics. I’d also like to thank Dr Sarah Crowley and Dr Rachel Turner for their help in developing my skills in social science, Dr Jo Judge for helping me to build links with the NBN’s wonderful recording community, and all the recorders who contributed their time completing my surveys. I thank NERC, UKCEH and the NBN for enabling this project and their support through the COVID-19 pandemic, alongside the University of Exeter’s dedicated Doctoral college staff.

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List of Contents

List of Tables and Figures

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

List of Accompanying Materials

APPENDIX A: CHAPTER 2 (SUPPLEMENTARY MATERIALS)

APPENDIX B: CHAPTER 3 (SUPPLEMENTARY MATERIALS)

APPENDIX C: CHAPTER 4 (SUPPLEMENTARY MATERIALS)

APPENDIX D: QUESTIONNAIRE SENT TO WILDLIFE RECORDERS

Author's declaration

I declare that the thesis has been composed by myself and that the work has not been submitted for any other degree or professional qualification. I confirm that the work submitted is my own, except where work which has formed part of jointly authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated below. I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others, in particular Figures 1.1, 1.3, 1.5 & 5.3, which were taken from open-access sources (referenced in captions).

The work presented in Chapter Four has been submitted to People & Nature as “UK wildlife recorders cautiously welcome range-shifting species but incline against intervention to promote or control their establishment” by myself (James Cranston), Sarah L. Crowley and Regan Early. I carried out the conception of the scope and questions in the study, questionnaire design and administration, analysis and manuscript write up, with aid from the other authors.

Chapter 1: General Introduction

1.1 Understanding species redistribution

The greatest challenge for humanity in the 21st century is navigating the two interacting dangers of climate change and ecological collapse. As precipitation patterns change and the world warms, some species are shifting into areas in which they did not previously occur, losing some or all of their historic range, or both (Figure 1.1). These patterns of changing occurrence and abundance are termed “species redistribution” (Bonebrake et al., 2018). The precise processes shaping these shifts are complex, with many details still to be unravelled. I specifically focus on those species that are expanding their distributions into new areas which they did not previously occupy, which often receive less focus than species which are declining in range and abundance (McGeoch and Latombe, 2016). While this knowledge will ultimately need to be synthesized with an understanding of processes at the retracting range edge and within range core, these latter processes are not directly considered further in this thesis.

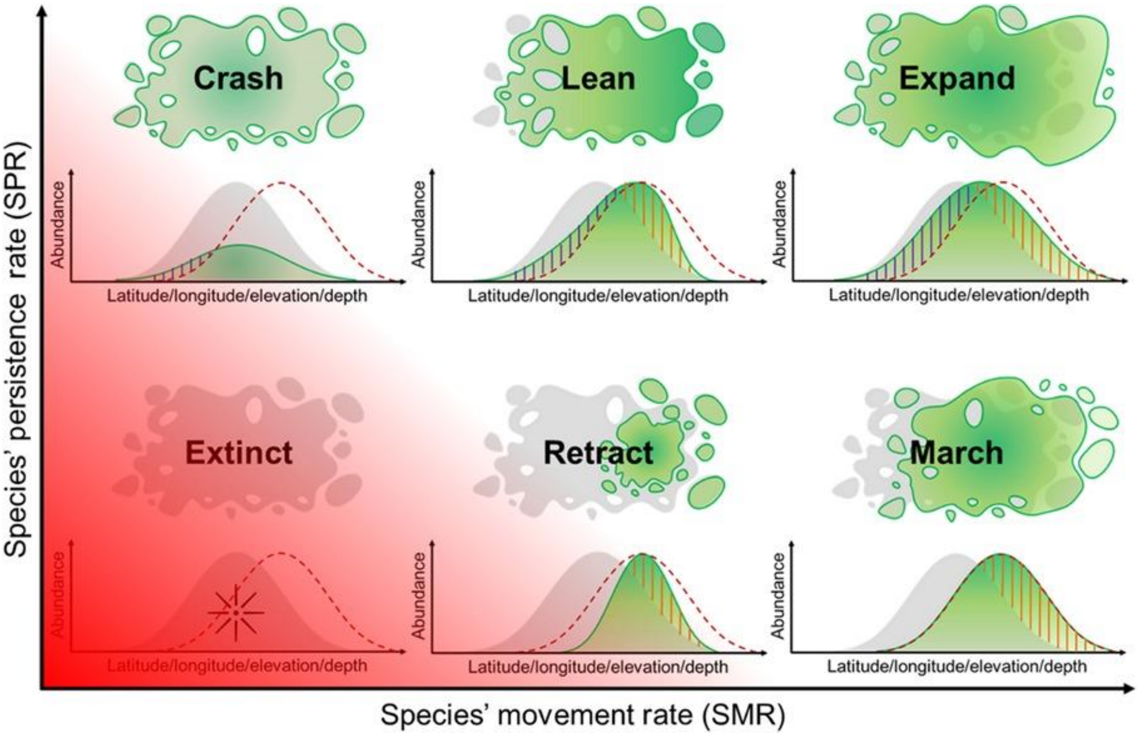


Figure 1.1: Range-shifts arising from different persistence and movement rates, from (Lenoir and Svenning, 2015). The historic abundance-latitude relationship (grey) is contrasted with potential future one (dashed red).The green shaded area shows the realised distribution under different assumptions of species movement and persistence rates. Species in the bottom left are at high risk of extinction, while those in the top right are expanding.

Given the existential threat to many species from anthropogenic pressures, most attention to range-expanding species has focused on predictions of where they may move and how far. However, these predictions have rarely been tested on currently occurring range-shifts. Such testing will be necessary to refine theories of the processes involved in range-shift and make more accurate predictions at more precise spatial resolutions. The aim of these predictions is to understand the risk of extinction faced by range-shifters and design effective conservation strategies to prevent it. But I argue there is also a need to acknowledge and understand the potential impacts of range-shifting species on the new ecosystems in which they arrive. Novel interactions may occur that could both benefit or harm currently resident species, which are themselves likely to be reacting to abiotic pressures. These biotic interactions will have direct and indirect socio-economic impacts, which again may be positive or negative. Human actions and reactions will influence the outcomes of range shift for species as they have done throughout history (Kessler, 2019). Therefore, species redistribution science requires a holistic interdisciplinary approach incorporating both natural and social sciences to better understand range-shift and its implications (Pecl et al., 2017).

A thorough examination of species redistribution would require a library rather than a PhD thesis. Therefore, I restrict my thesis' scope to consider only terrestrial and freshwater animals in the UK, excluding parasites. These animals have the best currently available occurrence data and are often both more visible and engaging to the public than marine species or plants. The UK has a richness of data to investigate species redistribution thanks to intense recording effort. Indeed, the country, has some of the best spatial data coverage in the world, much of which is publicly accessible through organisations such as the UK's National Biodiversity Network.

In the rest of Chapter 1, I begin by outlining how I defined an arriving range-shifter for the purposes of this thesis (Section 1.2). I then introduce the three aspects of species redistribution examined in this thesis's three data chapters. First, I discuss the drivers and processes through which species redistribution occurs (Section 1.3) – the focus of Chapter 2. Second, I look at the consequences for the ecosystems receiving range-shifters (Section 1.4) – the focus of Chapter 3. Third, I consider possible perceptions of range-shift amongst the UK public and their implications for the management and conservation of nature (Section 1.5) –

the focus of Chapter 4. Finally, I conclude the introduction by setting out the structure of the thesis, and its specific research questions (Section 1.6).

1.2 Thesis criteria for defining a range-shifting species

In this section, I will examine the ways that range-shifts are defined and measured as this is challenging both conceptually and in practice (Araújo and Guisan, 2006; Thuiller et al., 2004). I focus on the species level when defining range-shifters because, as discussed above, this is the dominant level at which data are collected. I use two criteria for identifying a range-shifting species.

1.2.1 Criterion A: Range-shifters move through their own dispersive powers

The first criterion is that the species must have shifted its range through its own powers of dispersal, directly originating from an area where they were present without human intervention. This criterion distinguishes range-shifters from introduced species that are dispersed by human activity, rather than through their own innate ability. It is worth noting that for some areas both introduced and range-shifting populations of the same species may exist; a historically present species may have been reintroduced in some locations but in others arrived successfully under its own steam and begun breeding. An example is the Common Crane (Grus grus) in the UK, which (after going extinct in the 1600s) returned naturally to the Norfolk Broads but which was also later reintroduced to Somerset. In many cases, it is challenging to determine the mechanism of arrival (Hoffmann and Courchamp, 2016) – as has been found for the introduction pathways of alien species (Saul et al., 2017). For some species this first criterion may even be slightly subjective (Figure 1.2). Species where the arrival mechanism is unclear are not further addressed in the thesis, though the uncertainty of classification will be important to incorporate into future analyses comparing the effects and arrival rates of introduced species and range-shifters.

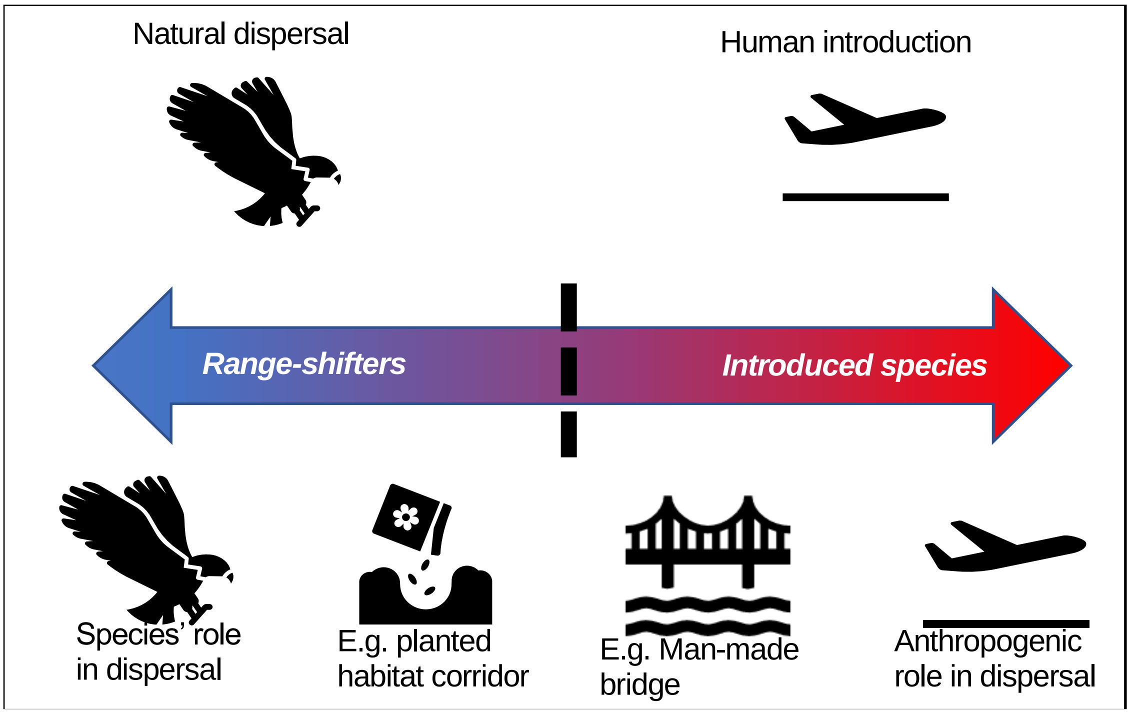


Figure 1.2: Rather than a simple binary of natural (blue) or human-mediated (red) dispersal, the causes of species distributional changes are points on a spectrum. Deliberate species introductions, such as the Cane Toad to Australia, are intuitively artificial. So too, most people would consider a species dispersing to an isolated island via a concrete bridge as an introduction. But a planted habitat corridor in areas of past degradation could be equally considered restoration or intervention, and artificial or natural. The dashed black line bisecting the arrows approximately indicates the division I make between range-shifters and introduced species.

1.2.2 Criterion B: Range-shifters are self-sustaining in their novel region

The second criterion for identifying a range-shifter is that the species should have formed a self-sustaining population in the novel region without dependence on humans. Applying this criterion requires addressing three implicit considerations (addressed in the following sections). First, what evidence is needed to label a population as self-sustaining? Second, how is the novel region delimited in space and time. Finally, what degree of dependence on humans would rule out a species from this definition?

Evidence requirements to label a population as self-sustaining

Species ranges arise and shift as a result of both deterministic and stochastic processes and these can be difficult to disentangle. Consider a Red-eyed Vireo

(*Vireo olivaceus*) blown across the Atlantic in a freak storm to the UK, well outside its normal range (Figure 1.3). Thus, for measuring range-shifts we need to eliminate atypical “vagrants” (Davis and Watson, 2018). My approach was to use breeding success as an indicator of a potentially self-sustaining population. Using the example of the vireo, we could classify it as a vagrant as they routinely die without reproducing or successfully raising young in the UK.

Figure 1.3: Red-eyed Vireo native to the Americas but with over 100 UK records Photo Credit: William Majoros.

Unfortunately, many cases are less clear-cut than this. For example, individuals may occasionally breed successfully but fail most years, implying a spectrum from vagrant (no successful breeding attempts) to range-shifter (sufficient breeding attempt success to be self-sustaining). To compound this problem, available data on breeding success are imperfect. Datasets containing occurrence records with associated notes of breeding success are much rarer than unannotated data, existing primarily for birds. Even annotated datasets are an incomplete subset of true breeding success. Failing to detect a species in a given location does not necessarily imply that the species is absent or not breeding (MacKenzie et al., 2003), particularly if it is elusive (Durso et al., 2011). Disentangling the observed data from the true state requires complex statistical inference. Differing methodologies for addressing this disentanglement may produce different results for the date which a species could be said to be established.

Using new breeding success outside a historic breeding range to define range-shifters is particularly complicated for migratory species, which occupy different parts of their range at distinct times, for example to exploit seasonal resources (Williams et al., 2017). Partial migrancy can also occur where not all individuals migrate from a non-breeding area (Berg et al., 2019; Menz et al., 2019). If, as climate changes, the proportion of individuals staying and breeding in the previously non-breeding area increases (Doswald et al., 2009), this can be interpreted as a range shift by our definition because significant breeding, which sustains the population, is now occurring in a novel part of the range. Breeding areas are clearly crucial for population persistence. However, a potential weakness of a definition of range-shift solely in terms of breeding success is that any ecological effects that range-shifting migrants may have outside their breeding areas might not be accounted for. For example, changes in their non-breeding areas could still affect key ecosystem services such as seasonal pollination (Wotton et al., 2019).

Delimiting the novel range in space and time

The United Kingdom offers a useful spatial extent to delimit the novel range when investigating the range shift process. The UK as an island has a degree of ecological isolation relative to continental systems as many species avoid flying over or swimming across open water. However, unlike very remote islands, e.g. Hawaii, it is still relatively near to potential source populations in continental Europe. In addition, due to its intensity of recording, the UK has a richness of biological data which allows us to be more confident which species occurred here historically and which are newly arrived species, compared to areas with fewer records. This combination of a present but not strong ecological barrier (by moderating the number of arriving species) along with high recording effort helps to identify range-shifters with more confidence. The high recording effort means that when new species arrive it is easier to distinguish whether they may be beginning to establish vs if they are still “vagrant”. As the ecological boundary (the English Channel) aligns with a political boundary (the UK), there is also an alignment between the process of species arrival and detection. Species detection is sometimes only available as reported presence within political boundaries, rather than as point data. Within these geographical bounds e.g. counties, regions, nations, data is often most accessible at the top level of this hierarchy. The alignment in the UK setting made it easier to define clearly what was considered to be an arriving range-shifting species.

To some extent the transition from vagrant to established range-shifter becomes irrelevant when considered at broad timescales. Over long time periods, even seemingly chance events such as island rafting arrivals in Madagascar, can be viewed as a statistical probability (Ali and Huber, 2010). But this timescale is not relevant to any attempts to manage range-shift. In this thesis, I used a baseline of c.1900 to delineate a newly establishing range-shifter. It is worth noting that choices of baseline period can lead to different conclusions on the velocity and magnitude of range-shifts and are intrinsically subjective (Figure 1.4); (Mannocci et al., 2017). But the turn of the 20th century is a useful baseline as it marks the start of the modern industrial era where one of the key drivers of range-shift, climate change, really began to be felt. This choice excludes species that may have been extant in Britain between the first fossil fuel emissions and my chosen baseline but a significant increase in data availability after 1900 justifies this trade-off.

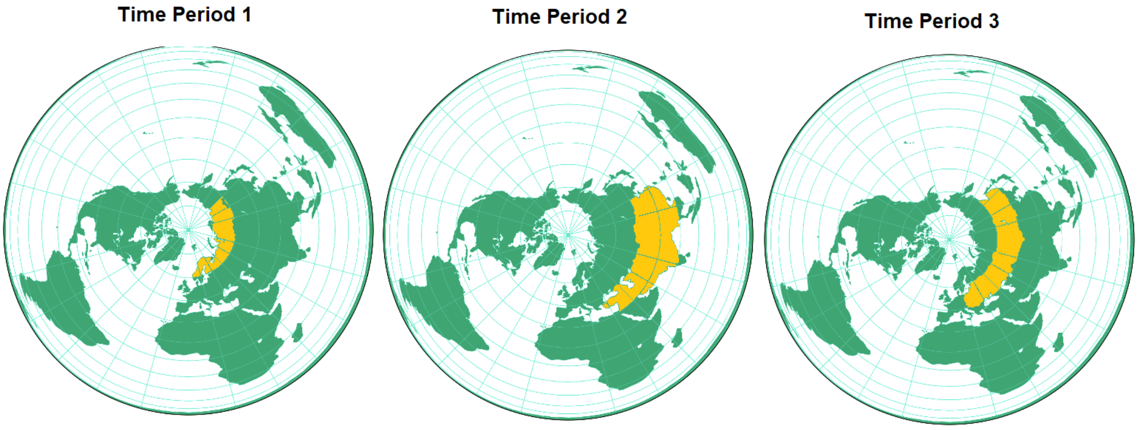


Figure 1.4: Range-shift velocities vary with choices of temporal resolution. If we consider the range of a theoretical species in three time period, we see that in taking a recent perspective from time period 2 to 3, there is a polewards shift, however, using a longer baseline this species has shifted equatorward. The choice of appropriate time scale is important.

Historic data of the number of “vagrant” individuals (i.e. putative immigrants) seen each year numbers are often unavailable or of uncertain quality, with data becoming more uncertain with its age. Historically, there may not have been an awareness particularly for less known insect groups that individuals found in the

UK may have originated elsewhere. This potential bias in historic recording makes it is more difficult to establish whether certain species which appear tenuously established in Britain are very rare natives or are in fact in the process of range-shifting into the UK. Some range-edge populations are dependent on source-sink dynamics for persistence (Lieury et al., 2015). This possibility suggests that in some cases we may be conserving some species that have never been naturally self-sustaining in Britain but had the fortune to be detected and adopted as native before knowledge about species range-shift was widespread.

Appropriate threshold for degree of dependence on humans

This thesis took a broad approach to dependence on humans. Essentially, I did not consider species which were obligately synanthropic to be range-shifters, but did include species whose persistence in the novel range may have been, or still is, indirectly assisted by human activity, e.g. the Black Redstart (*Phoenicurus ochurus*), whose post-WWII spread in Britain is associated with bomb sites (Morgan and Glue, 1981). In this thesis, I would consider species to be obligately synanthropic, if they met either of the two following criteria: could only persist inside artificially heated structures, e.g. greenhouses; relied solely on a human-introduced host plant, e.g. horticultural species and thus would have not chance of population persistence in the absence of continued human intervention.

1.3 Species redistribution drivers and processes

Section 1.3 discusses the current state of knowledge on modelling range-shift processes. I begin by introducing the evidence for range-shifts that are happening, why they are believe to be linked to ongoing anthropogenic climate change. I then now discuss how we might better understand the processes involved in range-shifters' expansion (the focus of Chapter 2), in particular the roles of climate, habitat and dispersal, and the limitations of these factors in predicting range-shift. I use both ad-hoc presence-only and systematically collected presence-absence occurrence datasets in this thesis and therefore will also consider the important role of the data gathering process and recorder effort.

1.3.1 Modelling range-shift processes

Overview

Empirical evidence shows that over recent decades there is a general trend for species ranges to have shifted polewards – on average – as anthropogenic climate change has progressed (Chen et al., 2011; Hickling et al., 2006; Mason et al., 2015; Poloczanska et al., 2016; Sunday et al., 2012). These observations align with the current paradigm that climate is the major determinant of species distributions at global to regional scales (Araújo et al., 2005; Merriam, 1894), for example through thermal optima (Gerick et al., 2014; Rummer et al., 2014), mass mortality in extreme climatic years (Parmesan et al., 2000; Seabrook et al., 2014) and many other mechanisms. However, we rarely see full alignment between the velocities of shifting climates (Loarie et al., 2009) and the velocities of shifting ranges (Fei et al., 2017; Lenoir et al., 2020; VanDerWal et al., 2013). Both directions and magnitudes can diverge. Some species are observed to move equatorward or downslope (Gibson-Reinemer and Rahel, 2015; Hilbish et al., 2010; Seabra et al., 2015). These misalignments indicate that important processes in species redistribution are not explained by climate change alone.

Effects of climate

One of the key ways in which the effects of climate and climate change on ranges are studied is using correlative Species Distribution Models (cSDMs). Predictions from cSDMs have been hugely important in mobilising action on climate change but have rarely been tested on species currently range-shifting, as this thesis attempts. cSDMs can relate species occurrence data to climate through various mathematical functions (Figure 1.5). Popular methods include MaxEnt, GAMs, GBMs, Neural Networks and MARS (Elith et al., 2006). Once a relationship is inferred then it can be used to project where the species may range-shift to in future climatic conditions or anticipate the areas that are currently suitable (Heikkinen et al., 2006).

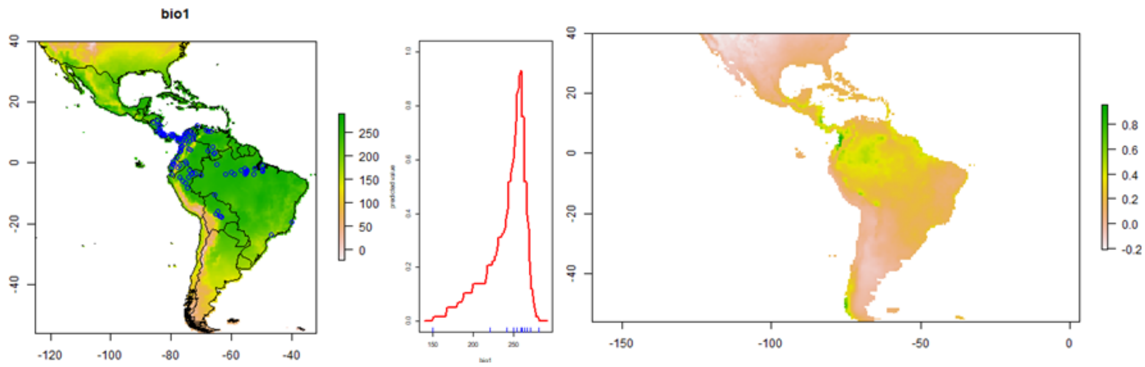


Figure 1.5: A diagram showing the cSDM process, starting with occurrence and climate data (far-left), to derive a climate-occurrence relationship (centre) followed by projected climatic suitabilities (right). Images from Spatial Data Science with R website (Hijmans, Robert J., 2020) used under GPL-3.0 License.

Considerable efforts have been made to develop best practices for linking existing climate and distribution data using cSDMs, particularly to ensure models are interpreted appropriately to their caveats, with clarified processes and standards (Araújo et al., 2019). Models can mitigate the risk of overfitting by limiting the range of climate variables they use (Gardner et al., 2019) or reducing the dimensionality of the climate data (Petitpierre et al., 2017). Use of independent test data and rigorous cross validation (Hijmans, 2012), along with ensemble models (Buisson et al., 2010) may help to assess the uncertainty arising from chosen datasets and modelling techniques respectively. While these practices continue to be widely discussed, here I focus directly on the problems inherent with the available data and why cSDMs may not be able to capture the role of climate (and climate change) in the range-shift process.

Scale-dependency is a one such issue; climate is not uniform over short scales in either time or space, being an average of experienced conditions (Yackulic and Ginsberg, 2016). This matters for understanding range-shifts for two reasons. First, insufficiently fine resolution temporal and spatial data can lead to inaccurate estimates of climatic limitations and therefore the areas to which species can shift or persist. The longer the period over which we measure climate, the greater the risk of differences from the “true” climate at a location at the time of species detection, particularly given the rate of climate change in the 20th century. Relict populations occurring in currently unsuitable areas can spuriously imply a species has broader climatic tolerances than it does (Keppel et al., 2012). A similar problem occurs spatially as the climate experienced by species can be highly localised, for example topography creates diverse microclimates across slopes. If we assume a species is able to persist at the climate average of a location but in fact it can only persist in a cool microclimate, we may infer a false level of thermal tolerance.

Climatic variability is an additional concern; if we average annual climatic variables over time, we may miss climatically extreme events which might limit or permit changes in species ranges more than typical years, e.g. irruptive dispersal (Therrien et al., 2014) and mass mortality (Lynch et al., 2014) events.

The two issues discussed above are technical challenges which could be addressed by better cSDMs or better resolution data (Maclean, 2020). However, results from applying cSDMs to model the naturalised ranges of invasive species highlight some potential for concern in applying these models to range-shift as they frequently find significant disparities in the inferred climatically suitable areas between the native and naturalised areas (Early and Sax, 2014; Pili et al., 2020).

Effects of species dispersal

One reason for potential disparities between climate conditions occupied in the native and naturalised range is that species may not occur in areas of suitable climate as they have not able to disperse to reach it. This could be due to either a) insufficient time and/or b) barriers to dispersal, e.g. mountain ranges (Araújo et al., 2005; Loehle, 2018). In cSDMs for introduced species, it is common to include metrics such as distance from roads or airports or urbanisations which act as a proxy for the ease with which a species may have spread from an incoming propagule to the location of observation (Václavík and Meentemeyer, 2009). By contrast, it is difficult to include barriers in models of range-shift other than through *a priori* assumptions.

In the native range, if species are prevented from occupying areas to which they are in fact climatically suited, absences in those areas are described as contingent absences (Lobo et al., 2010). Such absences are problematic for modelling range-shift with cSDMs as they may lead the model to incorrectly identify a species' climatic limitations. As with the previously described issues of scale and climatic variability, improved models can attempt to account for constrained dispersal, and thus distinguishing contingent absences from areas of unsuitable climate, allowing a more accurate climate-occupancy relationship to be derived.

When modelling range-shifts, incorporating dispersal is common for species where spread processes are likely to be relevant, e.g., introduced species.

However, estimates of species dispersal ability are challenging to obtain, often proxies have to be substituted such as wing size (Estrada et al., 2018). Choice of temporal resolutions can significantly affect measures of range-shift by affecting both the location and frequency of absences in the novel range, simply because of the different time that species have had to reach sites and be detected (Pennino et al., 2019). Therefore, shorter timeframes may have more absences in sites of potentially suitable climate for the range-shifter. This is an analogous issue with the calibration of the cSDM, but effectively for cSDM validation, in that both arise from erroneously assuming a climate-occupancy equilibrium.

Effects of other non-climatic factors

Non-climatic factors might also restrict species' ranges and their ability to disperse. When species are significantly constrained by non-climatic factors, cSDMs focused on correlations with climate will fail to correctly estimate climate limits on current ranges, and to predict the direction and speed of range-shifts. cSDMs have incorporated other data to attempt to control for these processes, for example geological, soil and nitrogen datasets for plants (Buri et al., 2017). However, crucially for modelling range-shift, there is greater uncertainty associated with future projections of non-climatic factors (Alexander et al., 2017; Prestele et al., 2016), a potential cause of a focus on climate in the literature (a "street-light effect").

To make matters worse, over recent millennia habitat and land cover have changed even more rapidly than climate. Human activity has recently (geologically speaking) affected habitat in large parts of the world. Such anthropogenic impacts are likely to be reflected in species ranges (Rodrigues et al., 2019). Agricultural land conversion may have pushed species into less disturbed but more climatically marginal areas (Ceballos et al., 2017; Dirzo et al., 2014). Without the historic data on past landcover and species occurrence, it is difficult to disentangle climate and landcover as constraints on species distributions. Ongoing ecological restoration and protection or simply land abandonment in Europe could be a sufficient explanation for some species range-expansions, as species return to habitat from which they were previously excluded (Drummond and Loveland, 2010). Indeed, in Europe, stricter wildlife protection laws seem to have facilitated the expansion of large carnivores such as bears and wolves into their historic ranges (Boitani and Linnell, 2015).

A further non-climatic limit is biotic interactions, such as facilitation and competition, which are also likely to alter species ranges (Early and Keith, 2019). Some human impacts such as anthropogenic food subsidies could also be conceived of as a biotic interaction assisting spread (Hoffmann et al., 2003; Oro et al., 2013). While I was not able to incorporate biotic interactions directly into my research on species redistribution processes, I discuss the potential implications of this omission further in Chapter 2 and Chapter 5.

Effects of recording effort and species detectability

As well as being absent from potentially suitable sites, a species may not be detected at a site it in fact occupies. Correlative models can then wrongly infer that the site is not suitable (Comte and Grenouillet, 2013). Ideally, models for range-shift should be trained on reliable presence-absence data to distinguish climatically suitable and unsuitable cells. However, this is rarely available: most datasets are presence-only records. To get around this problem, cSDMs often use pseudo-absences. Pseudo-absences are selected cells where the species is assumed (rather than assessed) to be absent. A range of techniques exist for generating pseudo-absences, all of which aim to select potentially suitable areas that are not occupied – solely because of climatic constraints, thus they often implicitly make assumptions about species dispersal. Having decided on a pseudo-absence selection method, the user must then determine how many pseudo-absence points to generate. Using more pseudo-absences increases the risk of mistakenly excluding suitable cells (contingent absences or failed detections). This would result in underestimation of species' climatic tolerances. Thus, when range-shift occurs into locations with climate that matches conditions in cells with contingent absences or failed detections, species appear to expand their climatic niche. The opposite pattern occurs when too few pseudo-absences are chosen, or they are selected over a large spatial extent. Poor knowledge of species dispersal hinders cSDMs' from discriminating contingent absences from climatically unsuitable areas using pseudo-absences (Vanderwal et al., 2009).

Data generation can also be spatially uneven; for example, recording intensity often correlates strongly with population density – as people don't collect records in places they can't get to. But they may go to places such as protected areas which they expect to be species-rich or to areas that are aesthetically pleasing such as mountainous regions. These human processes can confound attempts to model range-shift (Bates et al., 2014; Hassall and Thompson, 2010; Mair and

Ruete, 2016). An issue particular to range-shifters is that they may have strong temporal patterns in their detectability. Detectability may be low when a range-shifter first arrives, since it is unlikely to be in any local field guides and people might not be expecting to see it. Moreover, some recorders might not even view range-shifting species as of the natural fauna, and therefore not include them in their recording, as occurs with naturalised-native plant hybrids (Preston and Pearman, 2015). However, conversely, it is also possible that newly arriving species could be highly sought after as exciting novelties, and thus their detectability could be high immediately after arrival but then tail off. Whichever is the case, these problems in occurrence data have to be accounted for when investigating range-shift processes. This should include social science based efforts to understand recorder motivations better (Chapter 4).

1.3.2 Research gaps: monitoring and predicting the range-shift process

These earlier sections have highlighted the potential limitations of current range-shift models. Such models have primarily focused on climate change as the major driver involved in the species redistribution process and are usually correlative. These models have frequently been used to make predictions of future ranges, but they have more rarely been applied to ongoing range-shifts. I argue that there is a pressing research gap to be filled by testing and refining these models on the natural range-shifts that are currently ongoing, which I attempt in Chapter 2. As more occurrence data becomes available, it is now more possible than ever to investigate range-shifts as they are occurring, and ask how well current cSDMs based on climate predict the locations where range-shifters come to be found. If they do not perform well, this would indicate a need to investigate other factors affecting the range-shift process, such as habitat, movement, recorder behaviour and biotic interactions. As well as the gains for conservation in an era of climate change, this research has the potential to enhance biogeographic theories that explain species distributions a question that has intrigued scientists since Linnaeus.

1.4 Species redistribution consequences

Section 1.4 discusses the consequences of species redistribution on the recipient ecosystems that range-shifters are arriving into, with a focus on ecological impacts. I begin by discussing the different scales at which the effects of species redistribution could be categorised: genetic, species, community and functional levels. I then explore firstly, our current knowledge advancing that we may anticipate the effects of range-shifters being minimal and subsequently the theory and evidence anticipating negative impacts, before synthesizing these together. Section 1.4.2 outlines past approaches to detecting and predicting the impacts of novel species in their recipient communities before introducing the method used in Chapter 3 to detect the impact of a range-shifting damselfly – dynamic multispecies occupancy modelling. I conclude the section by positioning the work conducted in Chapter 3 within the existing knowledge gaps on the effects of range-shifting species on recipient ecosystems.

1.4.1 Evidence for effects on recipient ecosystems

Categorising the effects of species redistribution

We can categorise species redistribution effects on recipient ecosystems at four hierarchical levels. First, within species, we can identify genetic effects, perhaps resulting from selection pressure. Second, we can consider range-shifter effects on individual species, for instance trends in occurrence and abundance. Third, we can look above species at whole communities, where metrics like species richness or diversity may alter (Hiddink and Hofstede, 2008). Finally, at the highest level, we can look for alterations to the dynamics and functions of the ecosystem as a whole (Wardle et al., 2011). While not the focus of this section, it is important to remember that as well as impacts on recipient ecosystems, changes at any of these four levels may also indirectly affect human health, economies and societies. An example of how these effects can in turn impact humans is the reestablishment and expansion of large predators from their historic ranges. As these carnivores range-shift, they are likely to affect ungulate abundance which may impact human hunters through direct competition for prey (though in some parts of the world this could be viewed more positively as control of ungulate over-population (Cromsigt et al., 2013)). The effects of these abundance changes may also lead to functional effects that affect humans more positively, such as increased forest regeneration, boosting carbon and water storage (Ripple and Beschta, 2012).

Theory and evidence for minimal negative or even positive effects from species redistribution

At the species level, we might expect the effects of naturally redistributing species to be less impactful than those of introduced species (Strauss et al., 2006; Urban, 2020), which can cause widespread harm (Manchester and Bullock, 2000). The spatial proximity of range-shifters and recipient ecosystems is often higher (than for invaders). Most range-shifters are moving within the biogeographic regions in which they are native (Olivero et al., 2013) rather than between them (as are most invasive species). This shared biogeographic history may mean that species in host ecosystems had past interactions with the current range-shifters. In comparison, native species may be naïve to species introduced from other biogeographic regions, and thus lack behavioural or physiological adaptations to invaders. Consequently, we might expect native species to have greater genetic adaptation for co-existence with range-shifters than for species introduced from further afield (Blackburn et al., 2004; Salo et al., 2007). Even if native species initially lack phenotypic adaptations that would promote resilience to range-shifters, the more recent shared genetic history might at least speed adaptation to the range-shifter by providing useful genetic variation for selection (Erbilgin, 2019). Finally, if range-shift also proceeds at a generally slower rate than invasive spread, as appears to be the case (Sorte et al., 2010), this would also allow more time for adaptation.

At the community level, range-shifting species may not trigger large changes if they primarily fill niches left vacant by declining species or resident species moving further polewards (Martay et al., 2017). If balanced, immigration and emigration might maintain species richness. In fact, if the increase in energy in the ecosystem were to increase as temperature warms, plant growing seasons may lengthen, and we might expect to see increases in species richness, following the energy-richness hypothesis (Gillman et al., 2015). Linking these community level changes to ecological functions is complex. Linking these community level changes to ecological functions is complex and as discussed in the following section on the potential negative effects of range-shift – species identity also matters. The loss of keystone species can have significant negative impacts on ecosystem functioning. In some cases, increases in diversity and species richness have been linked to stronger ecological resilience (Downing et al., 2014), particularly in the face of environmental change (Elmqvist et al., 2003).

This resilience is vital for maintaining essential provisioning services such as crop pollination. In addition, increased species richness could improve human health and wellbeing (Marselle et al., 2019) and newly arriving species could support ecotourism.

Theory and evidence for negative effects from species redistribution

Despite the arguments laid out above, it is important not to dismiss the potential for negative effects of range-shifting species (Wallingford et al., 2020), which create conservation dilemmas.

At the genetic level, species hybridisation could occur, which might be viewed as biotic homogenisation (Sánchez-Guillén et al., 2013), potentially threatening locally important populations. An example would be the Black-winged Stilt (*Himantopus himantopus)* hybridising with the Pied Stilt (*H. leucocephalus*) in New Zealand (Steeves et al., 2010). Past spatial proximity could mean range-shifters pose a greater risk of hybrid swarm than invasives as they are likely to be more recently diverged from residents. Range-shifters could also exert selection pressures on resident species, as is potentially the case for the range-shifting butterfly *Araschnia levana* on two of its congeners in Sweden (Audusseau et al., 2017). These pressures could be particularly likely for range-shifters if phylogenetic proximity is associated with functional traits that mediate competition. In extreme cases, a range-shifter could cause considerable losses of diversity if they caused native populations to experience a bottleneck.

At the species level, direct impacts such as predation or competition (Caswell et al., 2020; Yackulic et al., 2019), or indirect effects such as mesopredator release (LaPoint et al., 2015) or suppression (Newsome et al., 2017) might impact native species' extent or abundance (Fitt and Lancaster, 2017). More subtly, we might see changes in native species' behaviour, either from plasticity or adaptation to help them adjust to the new arrivals, for example avoidance in time (e.g. shortened or shifted foraging periods) and space (e.g. switching hostplants) (Flaherty and Lawton, 2019). For animals with social learning we might even hypothesise about the potential for cultural transmission between range-shifters and natives (Barrett et al., 2019; Keith and Bull, 2017).

At the community level, species richness might decrease if new range-shifters cause declines in multiple native species. Even if there is no decline in overall species richness from range-shifter arrival, the loss of specific keystone species or specialists can have significant effects on ecosystem functioning, with risks such as functional homogenisation (Clavel et al., 2011) and the loss of key functions. For example, predator identity rather than species richness has been shown to mediate the pest suppression of the green peach aphid an economically significant agricultural pest (Straub and Snyder, 2006). Our understanding of ecological communities suggests that they can exist in multiple stable states (Beisner et al., 2003). If thresholds exist in recipient ecosystems, it may be very difficult to reverse or ameliorate range-shifters' effects once they have occurred. In the invasion literature, there are frequent examples of impacts of species having unanticipated impacts (Branch and Steffani, 2004) or being overlooked for considerable periods of time. For example, it took more than 50 years to discover the African Snail (*Achatina fulica)* predated native Hawaiian molluscs (Meyer et al., 2008). Thus, an irreversible switch in ecosystem state could be well underway by when a range-shifter's impact is realised. This possibility would suggest using the precautionary principle no matter the perceived likelihood (Jarić et al., 2019).

Even if range-shifters do not have strong negative effects, we might still observe biotic homogenisation of native communities if only a small number of species are able to successfully range-shift. For example, if only generalist species were able to shift effectively through the landscape, the different habitats of the novel range might contain only generalists rather than the array of specialists that might have exploited them in the historic range (Estrada et al., 2016; Tayleur (née Davey) et al., 2011). Functional changes from range-shift can also have negative consequences for humans, e.g. reduced carbon sequestration from range-shifting beavers' effects on Alaskan permafrost (Tape et al., 2018).

Evaluating the evidence for positive and negative effects

The previous section's catalogue of potential risks and impacts should be tempered by remembering that these examples represent only a subset of available evidence. No systematic literature reviews on range-shifters' impacts have yet been conducted. It could be the case that publications focus on the range-shifters of most impact and in particular on negative impacts (Hulme et al., 2013; Warren et al., 2017). While acknowledging that these harmful range-shifters may be of greatest concern to managers (Kuebbing and Nuñez, 2018), we should not draw generalisations based solely upon them.

While evidence syntheses will be a big step forward it is important to consider that literature reviews and meta-analyses can also suffer from results bias themselves (Drucker et al., 2016; Saunders et al., 2020). Historical context may channel patterns of research. For example, EICAT (Bacher et al., 2018; Blackburn et al., 2014; Hawkins et al., 2015): a framework for assessing introduced species' impacts, only considers negative effects. EICAT arose from an intention to facilitate risk assessment and prioritise resources to the most harmful invaders. However, when considering categorising the effects of range-shifters, we may also wish to consider their potential positive effects (Schlaepfer et al., 2011) and be cautious of coercing range-shift into past frameworks, even if range-shifters in some cases behave "invasively". Invasion impact frameworks have been critiqued for ignoring positive effects (García-Llorente et al., 2008; Rodriguez, 2006; Shackleton et al., 2020; Wootton et al., 2005) – sometimes for quite marginalised groups in society – a mistake that should not be repeated. For example, in South Africa, some rural villagers sell and barter the fruit of introduced prickly pear (*Opuntia ficus-indica*) to meet subsistence needs (Shackleton et al., 2007). Finally, while empirical evidence assessing range-shift impacts has a particular value for policy-making, not all important effects of range-shift can be metricised or even compared, as I explore in Section 1.5.1.

1.4.2 Detecting and predicting range-shifters' ecological effects

Ex Situ and experimental approaches to predict and verify effects

Initial predictions about the various effects (e.g. competition, predation, parasite spillover) that range-shifters might have on resident species could be garnered from experimental approaches before the species come to co-occur in natural systems. For example, focusing on single-species study systems, comparisons of functional trait data such as feeding, metabolic or reproductive rates could inform assessments of the relative competitive ability of range-shifters and resident species (Alexander et al., 2014). However more realistic assessment of potential impacts will require pairwise species or community experiments. We might use direct competition experiments between range-shifters and natives, e.g. larval damselfly perch competition (Kessel et al., 2011). Mesocosm competition experiments may also be useful as they can incorporate many environmental treatments (including future climatic conditions) and density-dependent effects (Stewart et al., 2013). Finally, field experiments, such as range-shifter exclusion or supplementation, might offer greater realism albeit sacrificing ability to control conditions (Alexander et al., 2016).

Using occurrence data to detect range-shifters effects

Both time and resources are limited for experiments, so observational approaches may be a low-hanging fruit. The arrival of miniaturised sensors and personal electronic devices have democratised biological recording and led to the development of many citizen science projects such as eBird (Newman et al., 2012). Our ability to convert these remotely sensed sounds and images into useful occurrence data continues to grow as machine learning automates identification and verification (August et al., 2020). These revolutions have rapidly increased the availability of big data in ecology (Snaddon et al., 2013), supported by the infrastructure of data aggregators such as the National Biodiversity Network (in the UK) and GBIF (globally). Tapping these resources has allowed trends to be assessed for a broad range of taxa (Outhwaite et al., 2019).

Unfortunately, despite the vast number of occurrence records, they are often perceived as a poor-quality resource (Hyder et al., 2015) and are not straightforward to analyse robustly (Isaac and Pocock, 2015). As explored in section 1.3.1, detection is imperfect, meaning that there may be false absences in datasets. Not all observations are equally informative. Some records can be misleading, e.g. misidentified species or those with inaccurate spatial or date information (Bayraktarov et al., 2019). Records may have diminishing returns after a certain threshold number are achieved for a site (Hsing et al., 2018). Observational studies based on occurrence data are more limited than experiments at suggesting causal patterns (Figure 1.6), as controls are not usually possible to rule out confounding effects and there is no direct control of temporal sequencing (Antonakis et al., 2010; Rohrer, 2018). Inference of genuine biotic interactions from co-occurrence data alone is hazardous (Dormann et al., 2018) but can serve as a starting point for further research and to detect overarching trends. Despite these challenges, increasing volumes of data and advances in computing power and modelling techniques, are enabling progress in harnessing occurrence datasets for detecting signals of biotic interactions.

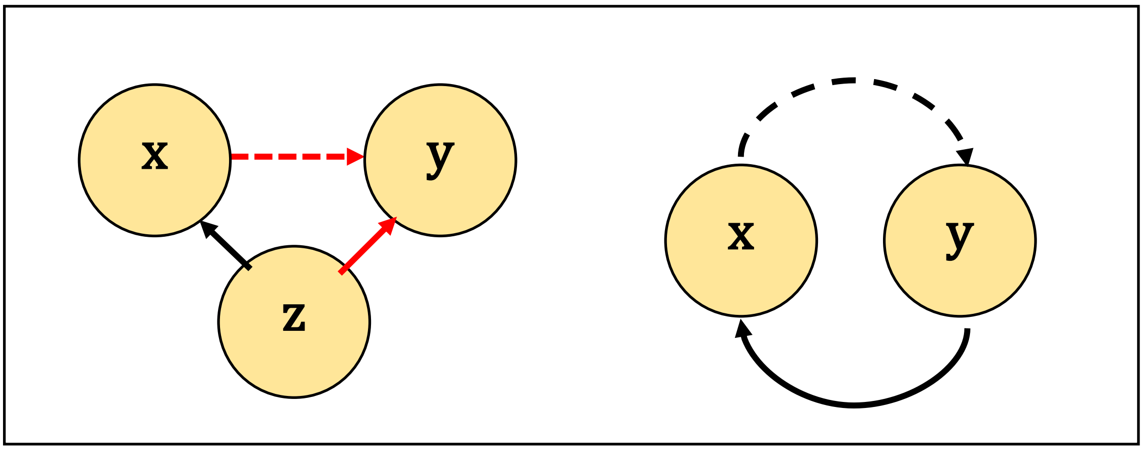


Figure 1.6: Two common pitfalls of correlational models. A third variable related to two observed variables controls both effects (left), e.g. climate change (z) could both increase the probability of a range-shifter being present (x) and of a decrease the probability of a native species being present (y). The direction of causation could be mistaken (right). Solid lines show true causal effects. Dashed lines show associations which could wrongly be inferred to be causal. Black shows positive effects, red shows negative ones.

Dynamic Multispecies Occupancy Models (DMSOs) are a novel method to potentially apply to range-shifter effects (Peron et al., 2016; Ruiz-Gutiérrez et al., 2010). To apply this approach, the occupancy of natives could be modelled as a function of range-shifter arrival and from this function a range-shifter's potential impact on native persistence could be detected, as has been done with models of invasive impacts (Kass et al., 2020; Rowe et al., 2019). One priority for future models is the effective incorporation of uncertainty. When DMSOs are Bayesian (as is common), they excel in this aspect. Firstly, they can handle some assumptions very explicitly, for example estimates of dispersal ability from the literature could be incorporated as a prior. Using such priors can help to estimate other unknown model parameters. The sensitivity of the analysis to the prior assumption can be assessed simply by varying the prior. As DMSOs hierarchically distinguish detection and occupancy processes, they can also address uncertainty associated with occurrence data gathering, e.g. recorder effort (Kery and Royle, 2008). A second priority is flexibility; an advantage of a multispecies approach is that it allows inference across taxonomic groups for those species with less data (Govindan and Swihart, 2015). DMSOs can also exploit heterogeneous occurrence data, helping to tackle gaps in data coverage. This might be a particular advantage in areas where occurrence datasets are still sparse, which includes much of the developing world. A final priority is that the information gained by macroecological modelling should be amenable to rapid reporting and updating (Rapacciuolo, 2019). The DMSO in a Bayesian framework focuses on the posterior distributions of parameters rather than p-values, thus avoiding the false dichotomy (significant vs non-significant) embedded in null hypothesis significance testing (Stephens et al., 2007). DMSOs also raise the possibility of examining range-shifters' effects in near real-time, as more data becomes available to estimate parameters in the same model.

1.4.3 Research gaps: modelling range-shifters' ecological impacts

There are currently limited data available to understand both the current and potential impacts of range-shifting species. Increasing numbers of studies have followed *ex situ* and experimental approaches described in the first part of Section 1.4.2. However, while these are potentially useful for predicting impacts, they have some shortcomings. These experiments are rarely field based so do not account for the complexity of the real-world. They are also not very scalable to the number of range-shifters anticipated this century.

To tackle this shortfall, I suggest the need for methods to detect range-shifters effects at larger spatial scales. Estimates of effects will be important for determining a generic management strategy for assessing range-shift threat (i.e. how appropriate is the precautionary principle). In addition, such estimates will help focus limited resources for further work on interactions of the greatest potential concern. I suggest that an evaluation of the ability of DMSO models to detect these effects would be a particularly useful next step in addressing the research gap. DMSOs are increasingly being used in conservation to identify impacts e.g. poaching (Marescot et al., 2020), and their use, if effective, for estimating range-shifters' potential impacts could be a vital conservation tool.

1.5 Perceptions of species redistribution

Section 1.5 discusses how species redistribution is currently perceived amongst different publics. As an emerging topic, this discussion draws strongly from related theory. I begin by outlining past frameworks on the values of nature and the human nature relationship in section 1.5.1 and their implications for how wildlife should be managed. In section 1.5.2, I use this outline as a framework to explore three potential future scenarios which could describe the future management of range-shifters: resisting their spread, supporting their spread and a laissez-faire approach. I round off this section by identifying existing research gaps in the perceptions of species redistribution and linking them to the questions I explore on the attitudes of wildlife recorders to range-shifting species in the UK in Chapter 4.

1.5.1 Attitudes to natural management

Thus far, I have scrutinised impacts through the lens of ecological science, which epistemologically foregrounds the scientific method and empiricism. However, the consequences of range shift will also be felt and modified by human societies. Some of these consequences, may be measurable in economic frameworks, others may be less tangible and be best described by anthropologists or even humanities and the arts. Understanding human attitudes to range-shift is vital. Attitudes are likely to influence management of range-shift processes, for example decisions about whether and how to increase habitat connectivity. Management actions will feed back into the range-shift process, e.g. a decision to cull range-shifters to ameliorate impacts on vulnerable natives might be expected to reduce the range-shifters' rate of spread.

Instrumental, intrinsic and relational values of range-shifters and residents

Asking how nature should be managed is a question which will inevitably generate a wide variety of (often conflicting) responses (Mace, 2014; Soulé, 1985). However, most people would agree that the goal of management is to increase the values of nature (Ducarme and Couvet, 2020). Natural values have often been divided into intrinsic (the values nature has itself in its own right) and instrumental values (the values nature provides to humans); (Justus et al., 2009).

Both these contrasting value systems fit under the umbrella framework of ecosystem services (Rieb et al., 2017) and natural capital (Schaefer et al., 2015). Instrumental values, e.g. carbon sequestration, often have an associated economic value (though its measurement can be difficult). In most cases, these metrics are blind to the specific aspects of biodiversity that produce the service, a range-shifting tree may store just as much carbon as a native one. From this stance, some regions could even stand to gain net benefit from anthropogenic change, if e.g. metrics such as species richness (Virkkala and Lehikoinen, 2017) or fishery productivity increase (Maltby et al., 2020). It is less straightforward to measure the intrinsic values of natives and range-shifters than to measure their instrumental values. Intrinsic values are by their nature intangible and different groups may offer very different valuations (Kendal et al., 2015) to the extent that their legitimacy as a basis for conservation is disputed (Justus et al., 2009). This perspective sees intrinsic values as essentially veiled instrumental values (just those of conservationists).

A critique of the values framework described above is that focusing solely on instrumental and intrinsic values misses the importance of relational values: the values arising from our relationships with nature, e.g. the role of nature in constructing community identity or a perceived moral responsibility for nature (Chan et al., 2016). Relational values are useful because they inherently force consideration of who is receiving the value, so the impacts of any changes can be disaggregated between different stakeholders (Dawson and Martin, 2015).

Implications of different modes of human-nature relationship for range-shifters

Two conflicting relational value systems between humans and nature are of particular interest for range-shift. These are described as “mastery” (asserting the human right to exploit nature for benefit) and “stewardship” (emphasising the responsibility to preserve) (Kessler, 2019). Management in the former system would emphasise human needs from range-shift, e.g. maintained crop productivity or increased aesthetic value. In the stewardship system, management would emphasise protecting or restoring past natural states and processes. These two perspectives are important to understand as they represent the dominant current approaches to managing nature (and thus range-shift): traditional conservation (“stewardship”) and natural capital (more inclusive of “mastery” perspectives). Of course, many other relational systems exist: a desire to work with nature as a “partner” is one which is increasing, associated with a growing rewilding movement.

A problem for stewards aiming to restore nature is humanity’s long history of environmental management. We have long altered the world’s biomes and habitats to “anthromes” (Martin et al., 2014); from indigenous practices of fire-cultivation in the Amazon (Maezumi et al., 2018) to Victorian land drainage (Lamers et al., 2015), from the near-eradication of bison (Moloney and Chambliss, 2014) to the modern conservation movement (Biermann and Mansfield, 2014). As such, any attempt to find an empirically rooted baseline at which to restore both natural states and fluxes is challenging if not impossible (Campbell et al., 2009). A growing paradigm of dynamic nature challenges a more established stewardship tradition aimed at retaining a “balance of nature” (Ladle and Gillson, 2008; Zimmerer, 2000). This may require conservationists to address more explicitly the relational values implicit in their stewardship managerial preferences. If no natural pristine state to return to can be identified, then reconciling different stakeholders’ diverse relational values is thrust centre-stage for range-shift management.

Mastery and stewardship relational value systems may generate different future scenarios for managing range-shift. I examine three themes of particular interest for range-shift on which people’s attitudes may draw: existential risk, moral responsibility and nativeness. Existential risk to humanity from biodiversity collapse is relevant as range-shifters are a) a particularly visible aspect of rapid ecosystem change and b) may be required for future climate adaptation. Moral responsibility and nativeness are interesting for stewardship due to the potential conflict between native species and range-shifters that must be navigated. From a mastery perspective, it will also be interesting to see how they value “nativeness” compared to less intangible values of residents and range shifters.

My first theme, the existential threat posed by the collapse of ecological systems, is a risk to humanity equal to that of climate change (Ceballos et al., 2017; Dirzo et al., 2014). Both mastery and stewardship value systems would aim to avoid this catastrophic scenario and seek to manage species redistribution within planetary boundaries (Rockström et al., 2009). However, only stewardship would be likely to seek to preserve all aspects of current biodiversity. A mastery perspective might only focus on those parts of biodiversity *considered* of value to humans, and not invest resources in protecting range-shifters of little aesthetic or economic value.

My second theme, moral responsibility, may particularly motivate a stewardship perspective, given that climate change is anthropogenic in origin, caused mostly by European and North American states. Arguably this places a greater moral responsibility to ameliorate effects on range-shifting species and prevent their extinction than if biodiversity changes had a natural origin (Albrecht et al., 2013; Singer, 2010). Thus, moral responsibility might encourage a stewardship perspective to adopt more active forms of management to protect species affected by climate change than in the past (Hagerman and Satterfield, 2014), e.g. assisted translocations.

My final theme, nativeness, is of interest as a traditional stewardship perspective would often distinguish between native (important to protect) and alien species (not valued or important to remove). Range-shifters blur this boundary. Essl et al. (2019) argue that range-shifters should be considered “neonatives” and treated similarly to current natives, an argument replicated by (Gilroy et al., 2017; Pereyra, 2020). Separate evidence suggests that the public and professionals reason similarly to one another about invasive species judging them mostly by their impacts rather than their origins (Fischer et al., 2014; Van Der Wal et al., 2015). However, little is known about how the public view range-shifters. Range-shifters have the potential to split the stewardship mode into functionalists (preserve current ecosystem functions) and compositionalist (preserve current species assemblages) camps. The mastery perspective may not particularly care about this distinction, focusing on the impacts and values of the range-shifting species alone. These mastery and stewardship perspectives along with myriad others will both respond to developing range-shift consequences and also cause feedbacks into range-shift processes. Dependent on these interactions, we could expect three broad potential management scenarios to develop: resistance, laissez-faire or support.

1.5.2 Approaches to management: three future scenarios

Resisting the spread of range-shifters

Given the potential negative consequences of range-shifters explored in section 1.4.1, it is possible management may wish to take efforts to hinder or stop the establishment and spread of certain range-shifters. A good example would be insect vectors for malarial diseases (Baylis, 2017) or crop pests such as fall army-worm (*Spodoptera frugiperda*) (Early et al., 2018). A mastery-aligned perspective would be less likely to tolerate such species than a less anthropocentric stewardship one. However, this pattern might be reversed for range-shifters with more ecological than economic impacts. Management is likely to vary between taxa, the preceding examples are both invertebrates and efforts to control or eradicate these species have typically caused less public controversy than for charismatic vertebrates like mink and hedgehogs (Mill et al., 2020). However, invertebrate species may be logistically harder to control, as they are harder to both locate and eradicate (Kennedy et al., 2018). Furthermore, there is often greater collateral damage associated with insect control, which may involve fumigation or generalist insecticides (Tobin et al., 2014), than for mammalian invasives where, for example, greater effort is usually made to avoid trap bycatch (Buckmaster et al., 2014). The rate of incoming arrivals (i.e. propagule pressure) is also likely to determine the feasibility and cost-effectiveness of control efforts (Lambin et al., 2020).

Support

Rather than resisting the spread of range-shifters, the moral responsibility and stewardship perspective explored in section 1.5.1 suggests that we should endeavour to help them. Support could vary in its directness and intensity. Increasing landscape connectivity is an identified need to conserve both range-shifters and historically resident species (Beger et al., 2010; Littlefield et al., 2019). While increasing connectivity may risk further spreading pests and pathogens this policy is mostly uncontroversial (Phillips et al., 2020). Indeed, many would frame it as ecological restoration rather than management intervention (DellaSala et al., 2003; Magilligan et al., 2016). However, other more active forms of support attract greater controversy. Assisted translocation is one such approach where predicted range-shifters are introduced beyond their current distributions to areas of predicted future suitability (Richardson et al., 2009; Willis et al., 2009). Variants on this theme, include transporting locally adapted populations with a species range or restocking individuals to maintain population viability over short-terms and reintroductions (Seddon, 2010).

Another way range-shifting species could be supported is effective integration into legislative (Trouwborst et al., 2015) and management frameworks. For example, range-shifters might be given protection under international directives (Somsen and Trouwborst, 2020) rather than rejected as alien species or left in a legal limbo. At more local levels they could be the subject of biodiversity action plans and thus be incorporated into management with (funding a possible consequence) rather than ignored (Robillard et al., 2015).

Laissez-faire

A laissez-faire approach veers away from a habitual instinct to front-load conservation action (Iacona et al., 2017). It is hard to stand by in the face of extinction, and funders often want impacts to be quantified and delivered quickly (Goldstein et al., 2008). However, in practice current management of range-shifters seems to sit between a “wait and see” approach and “benign neglect”

(Young and Duchicela, 2020). Non-intervention has the advantage of being cheap, at least in the short-term, particularly appealing to a “mastery” perspective. Non-intervention may also have less ecological risk to native species than supporting range-shifters (though it may increase the risk of range-shifter extinction) (Albrecht et al., 2013). It may have less political risk of public opposition or ecological damage than resisting the range-shift (Caceres-Escobar et al., 2019). As our current knowledge base on range-shift is relatively small, there could still be a net gain for conservation outcomes by investing in further research rather than potentially ineffective or even harmful actions (Cook et al., 2013; Grantham et al., 2009). An important caveat to this is the risk that the window to act or form policy may be limited (Rose et al., 2020). The accepted precautionary principle in invasion biology warns that the costs of harmful species are much greater the later intervention occurs and may include irreversible damage. A laissez-faire approach has some support from rewilding advocates (whose relational values unlike those of mastery or stewardship, see humans as partners with nature and value allowing natural processes to take their own course rather than intervening to promote certain outcomes), who argue conservation management needs to step back from intensive approaches (Cooper, 2000; Pettorelli et al., 2018), i.e. that governing range-shift should involve working with nature not managing of it (Jepson et al., 2018).

1.5.3 Research gaps: understanding attitudes to range-shift

Section 1.3.2 has shown that people’s attitudes towards range-shifters are likely to affect not just perspectives on and beliefs about range-shifters’ potential ecological consequences but also judgements about their management. Therefore, understanding public attitudes towards range-shifters is another key research gap. Without this understanding it will be difficult to navigate a path away from the future scenarios of stakeholder conflicts in range-shift management that are imagined in Box 1.1. The scenarios illustrated demonstrate that without understanding the potential social dimensions of range-shift, the impact of ecological evidence may be reduced. For example in Box 1.1, the Torreya Guardians are aware of the danger of disease spread but they choose to prioritise reacting to a different threat – climate change. As well as this pragmatic perspective, the legitimacy of wildlife management is based on the consent (or at least involvement in the case of conflicts) of the people it effects. Therefore, this research is important from a normative standpoint.

A second research gap is identifying the knowledge needs of wildlife managers and stakeholders for managing range-shift (Game et al., 2013). Conservation resources are limited, so research must be prioritised. A known deficiency with applying conservation research is the science-policy gap (Bradshaw and Borchers, 2000), which can be successfully narrowed by better engagement between scientists and practitioners (Dubois et al., 2020).

Support

USA: Florida Torreya (*Torreya taxifolia*)

Synopsis: The Florida Torreya is an endangered (previously abundant) conifer, threatened by fungal pathogens & climate change. It is federally protected by the US Fish and Wildlife Service (2020). A local group, the Torreya Guardians has been involved in transplanting the species beyond its current range (Barlow and Martin, 2004) & lobbying to ease restrictions on assisted translocation (Barlow, 2020). This is despite concern from scientists about the potential to spread disease to other endangered plants (Schwartz, 2005). The preferred government management strategy is to use GM to increase fungal resistance.

Imagined future scenario: *T. taxifolia* overlaps with endangered natives after supported movement from local conservation groups, e.g. the Torreya Guardians. However, they spread disease to native hemlocks. Conservation managers aim to prevent assisted translocation but can't convince local groups to cease their support. Local groups dispute the evidence of disease spread as unproven and strongly oppose GM as more unnatural.

Laissez-faire

UK: Little Egret (Egretta garzetta)

Synopsis: Little Egrets first arrived in the UK in 1999 (Musgrove, 2002). It has been received quite positively: "No Regrets about ... Egrets" in the Oxford mail (2016). There is no evidence of significant ecological impact (Wood and Stillman, 2014) and it has been assimilated into UK conservation (Eaton and Noble, 2020.; Stroud et al., 2001) but has not been given particular attention.

Imagined future scenario: Public attitudes to Little Egrets harden over time, as their novelty wears off and negative effects occur or are perceived to increase, e.g. predating on fishponds, and the bird's abundance grows. However, evidence suggests that egret predation of fish in natural habitats stabilises trends in declining dragonflies. Conservationists resist public demands for little egret management wanting to maintain a compromise laissez-faire policy and dismiss perceived societal impacts.

Resistance

USA: Barred Owl (*Strix varia*)

Synopsis: Barred Owls spread West across the American Prairie, possibly associated with conifer plantations (Monahan and Hijmans, 2007), arriving on the west coast, they appear to outcompete a native & threatened owl species (Strix occidentalis) (Buchanan et al., 2007) & have been subject to lethal control to protect *S. occidentalis* (Diller et al., 2014; Livezey, 2010).

Imagined future scenario: Efforts to control *S. varia* intensify as *S. occidentalis* declines steeply. Local groups are already resentful of the opportunity costs they experience (a mastery perspective) due to attempts to conserve the native owl. These groups oppose controls of the range-shifter arguing that ecological evidence predicts probable extinction for the native species even if the range-shifter is controlled. Conservationists are unable to adopt a laissez-faire approach due to the USA's Endangered Species Act.

Box 1.1: Case studies of the three management approaches: resistance, support, laissez-faire with a synopsis and an imagined conflict. All conflicts show ecological evidence is needed: Torreya disease risk, Egret nuisance and Barred Owl demographic impacts respectively. But, they also show how understanding public perceptions is needed to resolve conflicts: why do the Guardians ignore translocations' risk, why are Brits suspicious of egrets, & why do foresters oppose control of range-shifting owls? The social environment alters the evaluation of ecological evidence.

1.6 Thesis Structure

I present three data chapters in this thesis, followed by a discussion and synthesis in the closing chapter. Throughout this thesis, I deliberately avoid two historical terms used to describe newly arriving range-shifters: ‘colonists’ from biogeography (MacArthur and Wilson, 1967) and ‘immigrants’ from population ecology. While these terms have a valid and limited meaning in a scientific context, they have undesirable associations in a social context particularly for marginalised communities, e.g. stigmatisation of immigrants and colonial oppression (Peretti, 1998), so I adopt a more inclusive terminology.

In Chapter 2, I examine species redistribution processes, looking at how well we can predict the ranges of 14 bird species which have established in the UK. I train cSDMs on their European ranges and use the r-INLA package to compare the effectiveness of climatic suitability, habitat suitability, and proximity to their nearest European breeding cell in predicting their European distribution (Section 1.3.1). Disentangling these factors will help evaluate our current ability to understand range-shifters’ distributions and the range-shift process.

In Chapter 3, I examine some consequences of species redistribution (Section 1.3.2). Specifically, I investigate whether we can detect effects from a recently arrived damselfly on the UK’s native Odonata. I construct dynamic multi-species occupancy (DMSO) models with data from the British Dragonfly Society to infer effects of Small, Red-eyed Damselfly (*Erythromma viridulum*) on natives’ site persistence probability while accounting for climatic variation. Exploring this model allows me to test its usefulness as a potential method for investigating the impacts of range-shifters (Section 1.4.3) and to suggest future refinements.

In Chapter 4, I investigate species redistribution management by examining wildlife recorder attitudes towards range-shifters through an online survey. Recorders are a useful group to focus on as it includes both the nature-engaged public and wildlife managers. Section 1.5.3 identified that engaging both groups is needed to fill current research gaps. While controlling for different perspectives on human-nature relationships (Section 1.5.1), I explore the importance of a range of factors in predicting their attitudes towards range-shifting species and their management using mixed methods analysis. These attitudes offer a reference for comparison with other stakeholders. The results may also be useful for conservation policy as we sound out reactions to three broad approaches: support, resistance and laissez-faire (Section 1.5.2).

Chapter 2: Climatic and habitat suitability only weakly predict range-shifting birds’ new distributions in Britain

2.1 Abstract

I. Globally, species are rapidly shifting their ranges in response to sudden environmental changes, with important implications for recipient ecosystems and humanity. Understanding what factors shape novel distributions (e.g. habitat, climate, etc.), and whether range shifts can be predicted is critical for 21st century conservation planning.

II. We investigate fourteen range-shifting birds that established in Britain over the last century. We used climate suitability projections from species distribution models trained in Europe, habitat suitability from UK landcover data and distance from European breeding sites as predictors of the species British ranges.

III. We find that for most birds climatic and habitat suitability predicted their novel British distributions poorly. For most species, a simple model using just distance had greater support though it still had a weak absolute predictive performance.

IV. We suggest that there is an urgent need to improve upon simple correlative models in planning for species redistribution. Dispersal constraints may partially explain climate’s weak performance, as much of Britain was forecast as climatically suitable for most species. However, distance was still only a weak predictor of novel distributions. This indicates the need for future modelling of fine scale range-shift mechanisms, particularly movement and establishment processes, to better predict range-shifters’ distributions.

2.2 Introduction

Across the globe, species’ ranges are moving polewards with estimates ranging from a mean of 16.9 km/decade (Chen et al., 2011) to 18-23.2 km/decade (Mason et al., 2015). However, this general pattern masks considerable variation in the directions and magnitude of range shift (Fei et al., 2017; Fredston-Hermann et al., 2020; Gillings et al., 2015). Climate change is a major recognised driver of range-shift, but other anthropogenic changes may also have important effects (Betzholtz et al., 2013; Grytnes et al., 2014). Conservation science has historically focused on how species’ ranges shrink rather than how they expand or move (McGeoch and Latombe, 2016). However, in an era of range-shift, the attention of conservationists will now have to include the latter. Biodiversity planners’ preparations will be helped by projections of the areas to which range-shifting species will move and an understanding of the drivers carrying them there.

In the past, climate suitability has been most commonly used when attempting to predict the future ranges of species undergoing range shifts, often through correlative species distribution models (cSDMs);(Elith et al., 2010; Thuiller et al., 2009). Climate data are widely available across the globe. Therefore, if climate can yield useful predictions, this would allow a large number of range-shifters to be modelled. However, climatic cSDMs are underpinned by several assumptions. cSDMs assume species are at equilibrium with climate in their range and that inferred climate-occurrence relationships are consistent across time and space (Araújo et al., 2019). Using these assumptions, models can project species distributions into new geographic areas (or time periods), and if these projections are accurate the model is said to be transferable. This assumption of transferability has been regularly challenged and often fails, but continues to be widely used (Fitzpatrick et al., 2007). For instance, naturalised plants often expand their naturalised ranges beyond the climatic limitations observed in their native range (Early and Sax, 2014). cSDMs outputs can err in two ways. The models for these naturalised plants had low sensitivity in their novel range, i.e. they underpredicted distributions by projecting species absences where they were in fact able to establish. On the other hand, models can also have low specificity, where they overpredict future ranges by failing to discriminate between suitable and unsuitable sites. All cSDMs seek to optimise both sensitivity and specificity. However, it may be more important to prioritise one of these, depending on a model's purpose. For risk assessment we might prioritise sensitivity, e.g. to find all potential areas that a harmful range-shifter might affect. On the other hand, we might prioritise specificity instead, e.g. to find areas to protect for range-shifter conservation.

Habitat suitability, reflecting the realised landcover and land-use rather than climate per se, is a second constraint on species’ distributions. The availability of appropriate habitat may constrain the expansion of range-shifting species, even if the climate is suitable (Guo et al., 2018). This is especially likely to be the case in highly modified landscapes, such as western Europe. Land-use changes can hinder or promote the spread of range-shifting species. For example, the development of coniferous plantations has been shown to promote the southerly spread of several moth species in Britain (Conrad et al., 2004). Wetland habitat restoration and protection is also linked to the expansion of many European bird species (Ausden et al., 2014). Given the potential importance of habitat, it is surprising that it has been excluded from most models of species range shift. Thus far, no assessment has been made of the relative importance of habitat and climate for species range-shifting across major geographic barriers.

Species distributions could also be limited by their movement processes, particularly in the face of geographic barriers (Paul et al., 2009; Pinkert et al., 2018). The possibility of contingent absences should be considered as a null model when evaluating the potential effect of changing climate and habitat on range-shifting species occurrence. Distance from a species' historic range offers the simplest measure of the likelihood of an area being unoccupied due to dispersal constraints (more distant areas are less likely). If a species expands for non-climatically related reasons and was channelled to move polewards, for example by barriers like seas or mountain ranges, then movement could be misattributed to changes in climate. However, it is tricky *a priori* if dispersal is limiting range-shifts. In anthropogenically impacted areas the ability to navigate diverse human influenced habitats may be just as important (Barbet-Massin et al., 2012), which may be evidenced by the comparative range-shift success of habitat generalists over specialists (Estrada et al., 2016). Habitat permeability is an important constraint on species ability to track climate change (Oliver et al., 2017).

Disentangling the factors that determine which sites are first occupied by range-shifters is important for effective conservation. Management must be targeted to specific factors in order to work effectively (Oliver and Morecroft, 2014), as species could be subject to multiple factors at different scales (Jørgensen et al., 2016). For example, if range-shifters are constrained by habitat then interventions to create or restore suitable habitat are likely to be effective. Such efforts would be less effective if climate is the primary constraint. In the climate case, a more suitable strategy could be to identify “stepping stones” (areas of equatorward microclimate) to conserve where range-shifters may be able to establish more readily (Hannah et al., 2014). If neither habitat, nor climate constrain range-shifts, wasted management effort can be prevented and further research incentivised.

In this paper, we explore how well three key elements in the range-shift process – climate suitability, habitat suitability and distance from European source population (as a proxy for dispersal constraint) – explain the current distributions of 14 bird species which have established in the United Kingdom over the last century. The islands of Great Britain (hereafter Britain) are an ideal study system to approach the question of how well we can currently predict how species' ranges shift. Britain has extremely rich data on species distributions and as an island has clearly delineated political boundaries that also moderates species arrival, i.e. a sea crossing. Despite this, and demonstrating the richness of recording effort, over 100 species have range-shifted into Britain since 1900 and the rate of arriving range-shifters appears to be increasing (Gurney, 2015). Much of the biodiversity in Britain persists in highly managed protected areas and range-shifters will need to be considered by policy makers as part of this localised conservation strategy. Thus, our analysis seeking to disentangle current predictors of range-shifters current distributions is particularly timely.

Our aim to better understand species redistribution processes is advanced by this chapter through exploring a number or related questions. We ask whether climatic suitability is an effective predictor of the range of arriving UK range-shifters, hypothesizing that it will be of limited utility, due to violations of an assumption of climate-occupancy equilibrium in both the native and naturalised range. Using novel modelling methods to account for spatial structure in the colonisation process (INLA, se section 2.3.3), we evaluate the extent to which climatic suitability can describe current patterns of range-shift informing the need to refine further models to predict evolving patterns of species redistribution in the future, for example the role of habitat.

2.3 Methods

2.3.1 Overview

We collated occurrence data on 14 bird species that have established in Britain from mainland Europe, all of which met the following criteria: they 1) had arrived through their own powers of dispersal, 2) arrived from an area in which they were present without human intervention, and 3) formed a self-sustaining population without dependence on humans.

For each species we created maps at a 10km x 10km cell resolution of climatic and habitat suitability as well as distance to the nearest European breeding population. We then assessed how well these three explanatory variables predicted the observed British distribution. We also compared the British and European climate envelopes of each species for changes in climatic preferences. All data processing and analysis was conducted using R version 3.4.4 (R Core Team, 2020).

2.3.2 Data

Range-shifter Occurrence

We considered for analysis all birds that had newly established in Britain after 1900. This includes species which had been found in Britain prior to 1900 and had gone extinct but then re-established in the study period. We included the 17 birds listed in (Gurney, 2015), and extended this to 32 species using information from the Rare Breeding Birds Panel and an extensive literature review (Supp. Table A.1). We then restricted our analysis to species included in the EBCC European Breeding Bird Atlas (Hagemeijer and Blair, 1997) to ensure we had accurate presence-absence data to determine the species’ climate niche in Europe. We also excluded birds found in less than ten 10km grid cells in Britain (Balmer et al., 2014). This avoided the possibility of ambiguous results for species whose British ranges are potentially poorly characterised and ensured the safety of extremely rare birds. This left 14 range-shifters for our analysis. As well as the number of cells (as a proxy for British range size), the best estimate of year of first breeding for all birds was taken from (Gurney, 2015) and other literature sources to contextualise our results (Supp. Table A.1).

Defining Climatic Suitability

We constructed ensemble cSDMs to model the climatic niche for our 14 focal species, using the R biomod2 package (Thuiller et al., 2014). We used data from the historic range in mainland Europe excluding Britain to construct our model (full extent shown in Supp. Fig. A.1). Through focusing on the nearest areas of Northwestern Europe to Britain, we hoped to train the cSDMs on the most likely source populations for the British range-shifters. The study area still represented a sufficient area of climate space to fairly represent the potential climates available to the range-shifters in Britain, whilst not including cells of very different climates. The input climate variables were the first two principal component axes

(PCA) (Supp. Fig. A.2). obtained from the first nineteen Worldclim bioclimatic variables at 10-minute spatial resolution (approx. 20 km grid cells, climate averaged over 1960-1990) (Hijmans et al., 2005). The PCA approach has been found to produce transferable predictions in space (Petitpierre et al., 2017), i.e. the niche inferred by the model was found to be robust when tested on independent data in a distinct geographic area.

Presence-absence data for each species were taken from the European Breeding Bird Atlas (50 km grid cells, data collected 1972-1995). No data were included from the UK or Ireland. This presence-absence data was linked to the scale of the climate data through interpolation of the centroid points of each 50km cells onto the 10-minute grid using the R package gstat. To construct cSDMs in biomod2, we used the same techniques as (Morrison et al., 2018): Classification Tree Analysis, Surface Range Envelope, Flexible Discriminant Analysis, Artificial Neural Networks, Generalised Linear Models, Generalised Additive Models, and Generalised Boosting Regression Models. We used ten-fold cross-validation, which splits the data 10 times, each time using 70% of the distribution data for training and the remaining 30% for evaluation (Naimi and Araújo, 2016). We evaluated our models using True Skill Statistic (a TSS score of 0 = a random model, 1 = perfect prediction, <0 = more wrong predictions than expected by chance); (Allouche et al., 2006).

We then constructed a single ensemble model for each species. The ensemble could potentially draw on 70 models for each species (7 methods x 10 70% validation subsets) but only initial models with a TSS > 0.6 were included (which avoids the inclusion of poorly fitted models); (Araújo et al., 2011). The TSS score, is calculated by discretising the continuous climatic suitability predictions into binary predicted presences and absences. This requires identifying a threshold value of climatic suitability at which to split, hereafter the TSS threshold. Ensemble models were constructed using a weighted mean probability using proportional decay, an approach which produces significantly more robust predictions than other consensus methods (Marmion et al., 2009), and evaluated on the whole of the original dataset. Next, the ensemble models were used to project occupancy probability for Britain at 10-minute resolution. Finally, this projection was interpolated onto the British Breeding Bird Atlas 10 km grid using inverse distance weighting with a power of 1 using only the closest point.

Defining Habitat Suitability

We generated British habitat suitability maps using the Landcover2015 dataset (Rowland, 2017), following a similar approach to (Fordham et al., 2018). For each species we classified the LCM2015 21 target classes as suitable or unsuitable breeding habitat using information from the Birdlife International Datazone, validated by expert opinion (Supp. Fig. A.7 and Supp. Table A.4). We then calculated the percentage cover including saltwater areas for every bird's suitable target classes within each British 10km cell. The output was therefore a 10km resolution raster of habitat suitability ranging continuously between 0 (no suitable breeding habitat in the cell) and 100 (all habitat suitable for breeding).

Defining Species' Distance To Nearest European Breeding Populations

For each species we calculated the distance (rounded to the nearest 10km) from each 10km cell in Britain to the nearest European Breeding Bird Atlas location where the relevant species was established, i.e. listed as confirmed, probably or possibly breeding in the atlas. The distance were measured from cell centroids, taking into account the curvature of the earth using the R raster package.

2.3.3 Assessing the importance of climate, habitat, and distance for range-shift locations

Model Creation

We asked whether the geographic locations of each bird species' presence or absence in Britain was associated with climate suitability, habitat suitability, or distance from its mainland Europe population. For every species, the correlation coefficients between all potential explanatory variables (Climatic Suitability, Habitat Suitability and Distance) were below 0.7. Therefore, we compared models using every combination of the three explanatory variables for each species, so eight models in total per species (one of which was the intercept-only model). Interaction effects were not considered, in order to a) minimise the risk of model over-fitting and aid interpretation of the coefficient outputs and b) difficulties in getting the full model with all interactions to converge.

We constructed models using a Bayesian approach which models occurrence as an approximated Gaussian random field. This approach is implemented in the R package INLA (Martins et al., 2013; Rue et al., 2009). In order to minimise the effects of unknown spatial autocorrelation in these models we also included a

Matern spatial covariance function. This reduces but does not eliminate the risk of falsely attributing explanatory power to one of our variables arising from spatial structure not in fact driven by that variable. Further details of the input parameters given to INLA to construct the model from the explanatory variables and response can be found in Supp. Method A.1.

Model Evaluation

To calculate the comparative goodness-of-fit of the 8 possible models for each species, we ranked the models using Watanabe-Akaike Information criteria (WAIC). The best model for each species is the model with the lowest WAIC. For each model we also calculated its WAIC weight from the differences between the models' WAICs (∆WAIC): $\left(WAICw = \frac{e^{-0.5*\Delta WAICi}}{\sum_{r=1}^{R} e^{-0.5\Delta WAICr}}\right)$. The WAIC$_W$ is the relative likelihood of each considered model given the data, this information shows the relative likelihood of the best model compared to alternative model formulations, similar WAIC$_W$ have similar likelihoods. It is not a measure of absolute performance. We also calculated WAIC$_W$ for all variables, which is the summed weight of all models that include the variable.

We examined the models' absolute predictive performance using Tjur's r^2 (Tjur, 2009). Tjur's r^2 is the difference between the mean predicted probabilities of the two categories of the dependent variable, in this case species presence and species absence. We first calculated Tjur's r^2 for the model based on the fitted values (i.e. linear predictors + spatial effect, i.e. the Matern covariance) and just the linear predictor (i.e. without a spatial effect, i.e. the Matern covariance)

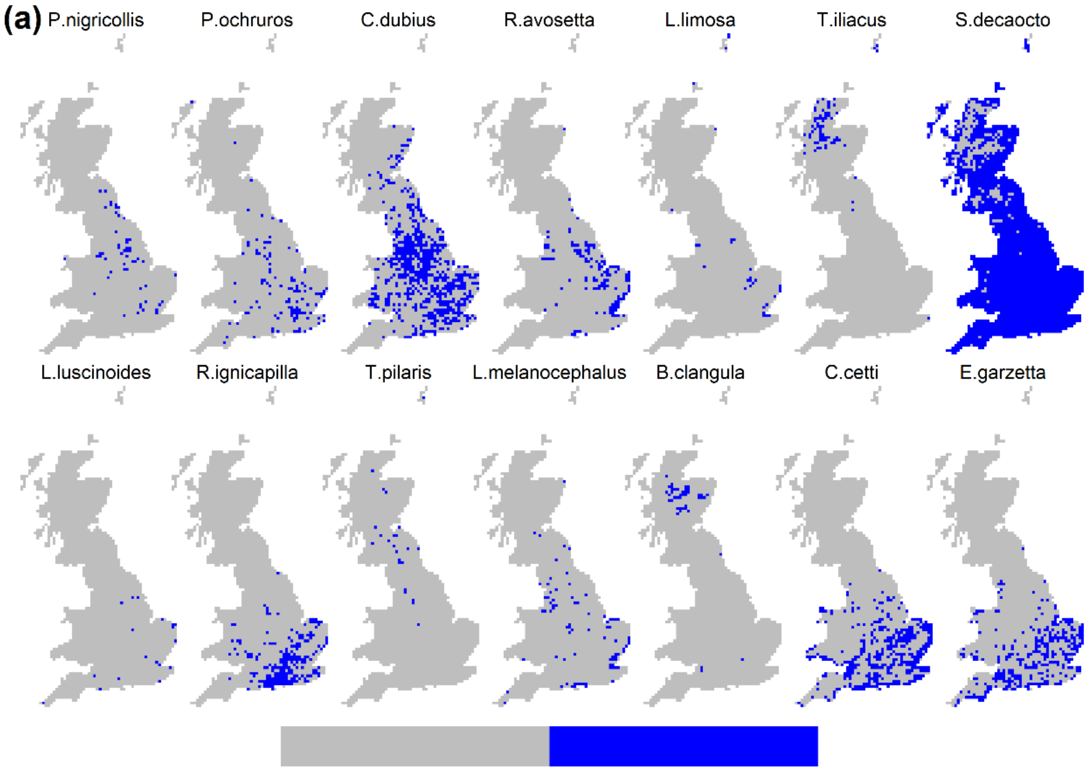
Finally, we also tested the predictive ability of each explanatory variable separately. To do this for climatic suitability, we converted the modelled climatic suitabilities to predicted presences, used the same thresholds which maximised the species' TSS scores in the European range. We then calculated the sensitivity, specificity and TSS of these British predictions. However, for habitat suitability and distance, we used the threshold that maximised the TSS for the British range, as there was no equivalent European data.

2.3.4 Assessing Niche Shift

We examined whether species had shifted the climate niche that they occupy between their native ranges (using the geographic extent in Supp. Fig. A.1) and Britain by comparing the climatic envelope of the European and British range. We calculated smoothed maps of occurrence density for all range-shifters in environmental PCA space (resolution = 100 x 100 cells) split into historically resident and newly resident areas. We then calculated the global overlap and the number of cells showing niche expansion. Tests for niche divergence were conducted by comparing the observed overlap value of the occupied European and British range in environmental space with 1000 simulated overlaps where the novel range is randomly shifted within the available environmental space of the British range and the European range is held constant. This analysis was conducted using the R package ecospat (Di Cola *et al.* 2017), following methods from Broennimann *et al.* (2012).

2.4 Results

We found considerable variation in distributions amongst the species in the study (Figure 2.1a). Several species are concentrated in the Southeast of Britain (Figure 2.1c) but three are distinctly northerly distributed: the Goldeneye (*Bucephala clangula*), Redwing (*Turdus iliacus*) and Fieldfare (*Turdus pilaris*). Most show slightly patchy or scattered distributions but some species such as the Collared Dove (*Streptopelia decaocto*) occupy most of the available cells within their apparent climatic range limits. The number of occupied 10km cells does not appear to relate strongly to a species’ year of arrival (Spearman's ρ =0.05) (Figure 2.1b).



(b)

Latin Name	Common Name	Number of Hectads	Year of Arrival
P.nigricollis	Black-necked Grebe	53	1904
P.ochruros	Black Redstart	131	1923
C.dubius	Little Ringed Plover	597	1938
R.avosetta	Avocet	141	1941
L.limosa	Blacktailed Godwit	39	1952
T.iliacus	Redwing	75	1953
S.decaocto	Collared Dove	2384	1955
L.luscinioides	Savi's Warbler	19	1960
R.ignicapilla	Firecrest	212	1962
T.pilaris	Fieldfare	23	1967
L.melanocephalus	Mediterranean Gull	90	1968
B.clangula	Golden-eye	44	1970
C.cetti	Cetti's Warbler	417	1973
E.garzetta	Little Egret	327	1996

(c)

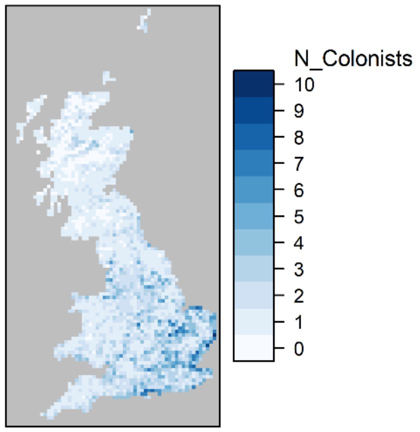
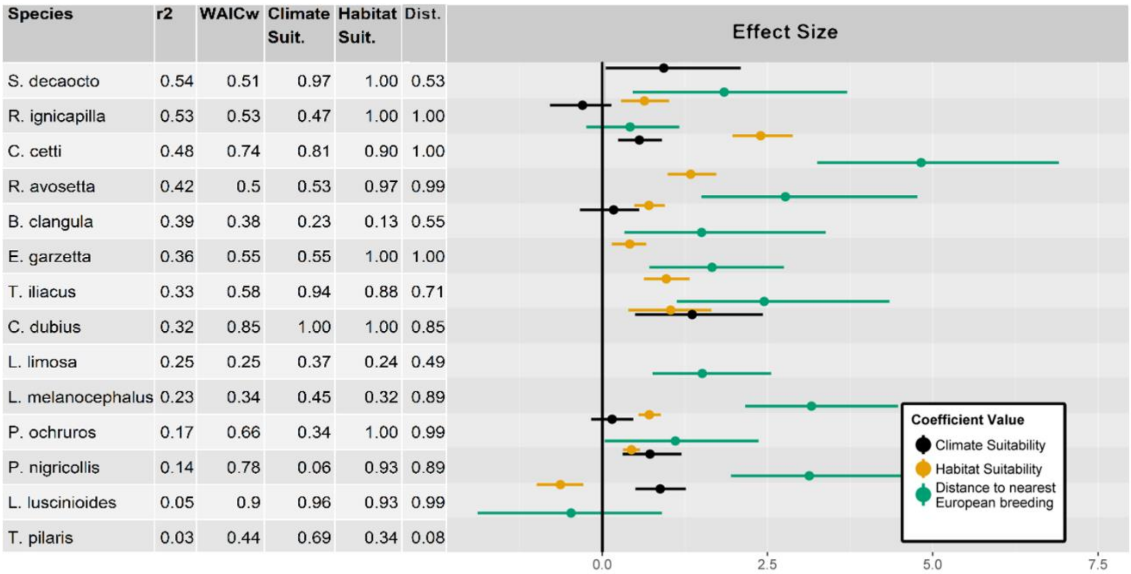


Figure 2.1(a): The breeding distribution of each range-shifter in Britain ordered by year of arrival from left to right, top to bottom (P =Presence, A = Absence), (b): The number of breeding 10km raster cells and year of arrival for each species (c): Total number of range-shifting species breeding in each British 10km cell.

When all variables were considered together with a spatial covariance function using INLA, distance to the nearest European breeding populations was the most frequently retained variable in the best model (i.e.lowest WAIC) of current range-shifter distribution, being retained for 12 out of the 14 species. Distance had the highest mean variable importance (WAIC$_W$) of 0.783 ± 0.0742 SE. Habitat suitability was kept for 10 of the 14 species and had a similar mean variable importance to distance (0.76 ± 0.0896 SE). Climate suitability was only retained for 8 birds and had the lowest mean variable importance 0.598 ± 0.0809 SE (Figure 2.2).



Species	r2	WAICw	Climate Suit.	Habitat Suit.	Dist.
S. decaocto	0.54	0.51	0.97	1.00	0.53
R. ignicapilla	0.53	0.53	0.47	1.00	1.00
C. cetti	0.48	0.74	0.81	0.90	1.00
R. avosetta	0.42	0.5	0.53	0.97	0.99
B. clangula	0.39	0.38	0.23	0.13	0.55
E. garzetta	0.36	0.55	0.55	1.00	1.00
T. iliacus	0.33	0.58	0.94	0.88	0.71
C. dubius	0.32	0.85	1.00	1.00	0.85
L. limosa	0.25	0.25	0.37	0.24	0.49
L. melanocephalus	0.23	0.34	0.45	0.32	0.89
P. ochruros	0.17	0.66	0.34	1.00	0.99
P. nigricollis	0.14	0.78	0.06	0.93	0.89
L. luscinioides	0.05	0.9	0.96	0.93	0.99
T. pilaris	0.03	0.44	0.69	0.34	0.08

Figure 2.2: Predictors median estimated coefficients (points) and 95% CIs (lines) from the best model, inclusive of spatial effect, (chosen by WAIC) for each species(right), the facets are ordered top to bottom by Tjur's r^2. The variable importance scores (WAICw) of Climate, Habitat Suitability and Distance variables averaged across all models for each species (left).

The predictive performance of the INLA models varied widely (Figure 2.3). When models included a spatial covariance function, (i.e. fitted values), r^2 was >0.25 for nine species and r^2 <0.1 for only two species. However, when the model predicted without the spatial function (i.e. just the linear predictor) r^2 exceeded 0.25 for only four species, for two species r^2 fell between 0.25 and 0.1 and for the remaining species r^2 was less than 0.1. The spatial effect only accounts for spatial structure in the data used for each species and therefore does not in itself offer any predictive power for modelling future changes in the species distributions or for the distributions of future range-shifters.

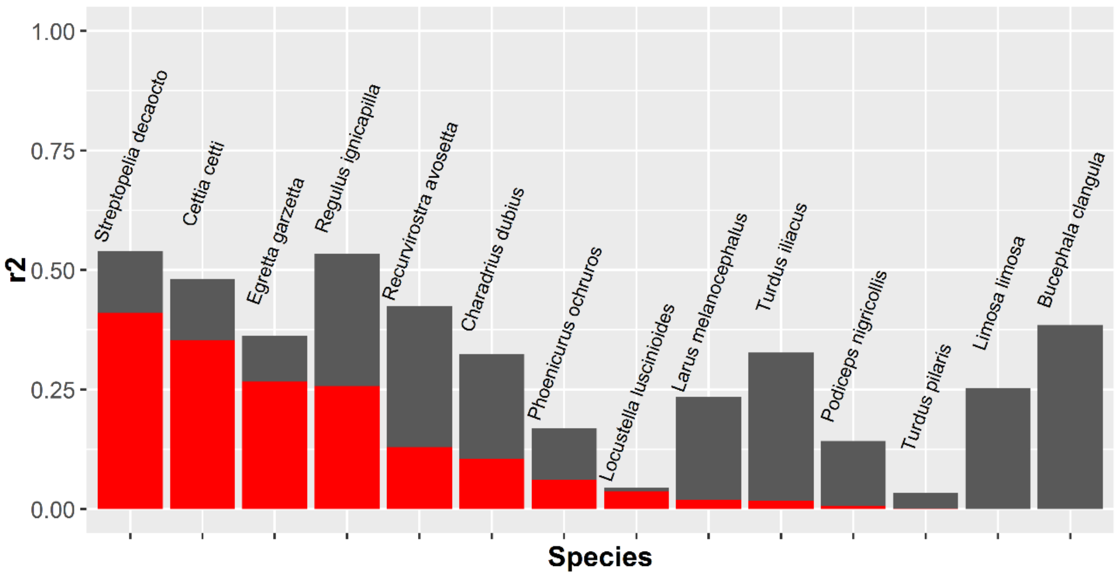


Figure 2.3: Tjur's r^2 of the best model for each species, the dark bar shows the full model, the red bar shows the portion of r^2 which is attributable to the predictors once the spatial random effect has been removed. The bars are ordered left to right by the part of r^2 explained by the non-random effects (red bar).

When we considered the explanatory variables separately, we found our climate cSDMs (Supp. Fig. A.4) which had a mean TSS = 0.77 ± 0.03 in Europe (Supp. Fig. A.3, Supp. Table A.2) when evaluated on the British distribution only had a mean TSS score of 0.19 ± 0.04 (Figure 2.4). For all species, climate predictions generally had high sensitivity in Britain with the exception of *B. clangula* and *T. iliacus* which had high specificity, i.e. they predicted the sites where the species occurred as occupied (Supp. Fig. A.8, Supp. Table A.7). Climate and habitat had similar TSS scores when used in isolation (mean 0.22 ± 0.07 SE), but climate had lower sensitivity (Supp. Table A.7). The TSS score was highest when calculated using distance (mean TSS 0.36 ± 0.04 SE, Supp. Fig. A.8).

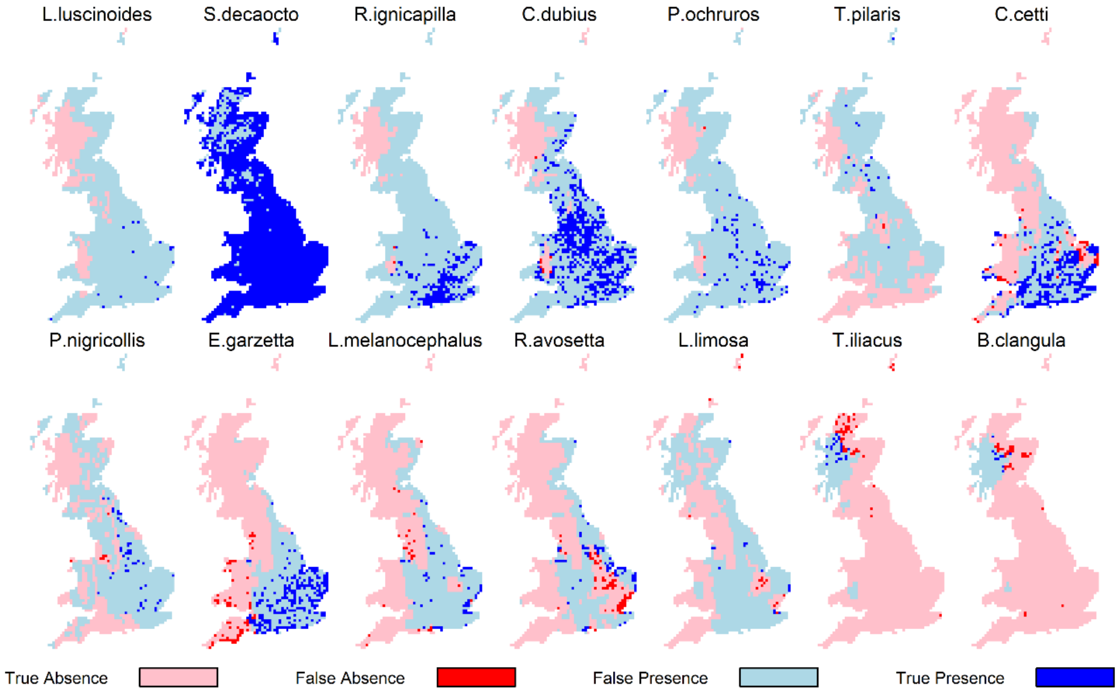


Figure 2.4: The predictive performance of climatic suitability models in Britain at the species's optimal TSS threshold used in the European range, ordered by sensitivity. True absences in pink, false absences in red, false presences in light blue and true presences in dark blue.

Three species, Goldeneye, Redwing and Black-tailed Godwit *(Limosa limosa),* showed greater than 10% niche expansion (a widely used arbitrary threshold to identify niche expanders; Supp. Figs. A.6 & A.9, Supp. Table A.3); (Strubbe et al., 2013).

2.5 Discussion

We found that climatic suitability, habitat suitability, and distance to historic breeding range all had consistently low predictive power for most birds' British distributions, suggesting that the range-shifters' current distributions are not strongly linked to these factors at 10km resolution. cSDMs forecast that large areas of Britain were climatically suitable for the range-shifting birds. However, birds did not occupy these areas (i.e. specificity was low). Neither did birds' occurrence appear to match predicted habitat suitability. The importance of the distance explanatory variable supports a potential role for dispersal constraints, suggesting it is possible that species may yet spread further. However, it is not possible to rule out other interpretations of the failure of these predictors, principally non-climatic constraints.

One interpretation of climate suitability's low specificity is that there are other important constraints on species distributions in Britain not captured by our cSDMs. We note that the same climate variables did predict the European distributions of most range-shifters effectively (i.e. TSS scores were all above 0.6), suggesting that climate is a strong constraint on historic distributions, (albeit that these scores were not derived from an independent data set). The high sensitivity scores for our cSDMs in Britain suggests that low TSS scores were not due to model over-fitting, i.e. that our cSDMs were not including excess climate parameters to describe the European niche (Figure 2.4 and Supp. Fig. A.6). Without mechanistic data it is difficult to evaluate the extent to which the climate-occurrence relationships we obtained were causal.

One non-climatic constraint in Britain is that the range-shifters may have not yet spread out to fill their full potential extent in Britain. The literature on introduced species demonstrates many cases of long lag times before rapid spread and in some cases becoming invasive (Coutts et al., 2018). However, in our case, the absence of a strong relationship between the length of time since arrival (a value which is hard to estimate) and either the $WAIC_w$ or TSS score of climate suitability suggests it does not seem simply a matter of time until the 14 bird species studied fill their entire potential British distribution. Many other factors beyond time since arrival may control how far a species is able to spread. These include traits as diverse as group size, generalism and generation time (Estrada et al., 2016) as well as landscape variables such as habitat connectivity or conservation practices (Briscoe et al., 2019). Uncertainty in arrival date might also be a factor, especially for the species that arrived long ago.

The limited predictive power of climate cSDMs for the species' British distributions could reflect other constraints on their expansion through Britain which are not related to dispersal. Biotic interactions are a potential explanation, both facilitative and competitive. Many wetland birds, including some of our study species, exhibit strong mutualistic interactions in feeding and predator avoidance (Sridhar et al., 2009) and nest protection (Swift et al., 2018). Larger birds such as the Common Crane (*Grus grus*), which is establishing in Britain, have been shown to reduce nest predation of smaller birds (Fraixedas et al., 2020). The absence of facilitative interactions could halt the range-shifters further spread until mutualistic partners arrive. It is perhaps relatively less likely that competitive interactions limit range-shifters due to the paucity of British species compared to

Europe, though the presence of specific strong competitors could still be significant. However, a potential limiting factor could be high relative abundance of mesopredators, such as red foxes (*Vulpes vulpes*) which have been shown to impact shore birds (Roos et al., 2018). More systematic effort to record and aggregate information on biotic interactions will help build our understanding of biotic interactions' biogeography and its implications for range-shifting species (Carrasco et al., 2018; Early and Keith, 2019).

Our climate suitability models for northerly distributed Goldeneye and Redwing had poor sensitivity and their PCA niche analyses showed expansion into climate not occupied in the historic range, unlike most of the other birds in this study. We suggest that non-climatic factors may be partially responsible for this shift. Conservation actions such as the provision of nest boxes for Goldeneye, may have a role (Dennis and Dow, 1984) as may garden feeding for Redwing. These actions may artificially boost demographic parameters allowing persistence. Alternatively, the niche shift could be due to physiological changes in climatic tolerance arising from evolution, but the short timescale and weak isolation from historic/source populations makes this unlikely (Petitpierre et al., 2012). More plausibly, a phenotypic shift could have occurred which allowed these populations to persist, perhaps by exploiting novel food resources or other adaptive behaviour. A final possibility is that human influences have constrained the European distribution of these two species. Although there is no evidence of artificial constraints for these birds, this is an important consideration for future models of range-shift as it could lead to underprediction of the suitable areas for range-shifters previously forced to occupy climatically suboptimal areas (Scheele et al., 2017) or only a subset of their suitable range.

The poor specificity of climate suitability for British ranges may initially seem counterintuitive as European models did indicate species had climatic limitations. Intriguingly, the large areas of Britain forecast as suitable but unoccupied and the smoothness of the climate suitability gradient could suggest that some of these areas were amenable for range-shifters before recent anthropogenic climate change. If climate change is not the smoking gun, then what other potential triggers might have started these shifts? We suggest that historical ecology offers important context for our understanding of species currently establishing in Britain (Engelhard et al., 2016) particularly considering past species distributions (Evans et al., 2012) or land-use changes (Dolman et al., 2017; Mensing et al., 2018).

Merchant records suggest that Little Egrets and perhaps Spoonbills were previously established in the medieval or even more recent periods before disappearing and re-establishing more recently (Bourne, 2003). Species which may have gone locally extinct in Britain, may have done so due to climate, e.g. little ice age or due to stochastic catastrophes which always threaten small range edge populations. However, these extinctions could also arise largely or in part due to historic human activity such as land drainage, habitat conversion or unsustainable harvesting. These past disturbances are also well-documented in Europe, e.g. egret harvesting for millinery in Southern Europe (Ławicki, 2014). Recent improvements in certain habitats may have helped some species return to Britain, e.g. RSPB reed-bed management for Bitterns (Brown et al., 2012). Historic context will help prevent misattribution of range-shifts to climate change.

Habitat suitability appeared marginally more informative than climate suitability in determining range-shifters' current distributions. In Finland, land-use has been shown to increase in importance for species' ranges relative to climate at finer spatial scales, becoming most important at the same 10km resolution as our study (Luoto et al., 2007). However, habitat suitability performed very poorly for some species. One explanation is that habitat suitability was assigned incorrectly for these species, or that the habitat categories used were too broad. Remotely sensed land cover describes habitat indirectly and therefore masks considerable variation at the spatial resolution relevant to the species. A satellite may correctly identify unimproved grassland for example but not capture sward height or grazing regime which are both crucial for Black-tailed Godwits' reproductive success (Schekkerman and Beintema, 2007). Furthermore, land use changes from modified management (or cessation of management), perhaps in evolving farming and forestry practices, will change the suitability of sites for range-shifters (Kleijn and Sutherland, 2003; Tscharntke et al., 2005), assisting or hampering establishment. Within human-modified landscapes, anthropogenic food sources such as landfill and fisheries discard may also support species establishment but are not easily monitored (Oro et al., 2013). Finally, habitat may also change the climate actually experienced by organisms, by creating local microclimate effects, such as shade or increased water retention. These microclimate effects mediated by habitat weaken the power of comparatively coarse 10km cSDM predictions we used (Bütikofer et al., 2020; Massimino et al., 2020).

Distance had the strongest predictive link to the range-shifters' current distributions, being the most consistently retained variable, but did not achieve strong TSS scores for all species. Indeed, for one species the mean estimate of the distance coefficient was negative, though it's credible intervals overlapped 0 (i.e. species were more prevalent at further distances from the historic population), showing its usefulness as a predictor is not universal. In addition, most species had fragmented distributions with uneven edges. Our attempt to consider dispersal in our models as a null expectation was quite simplistic, generating a smooth field from the European locations. This did not visually match the fragmented pattern that we see in our data. The lack of close matching, despite being the best predictor, could arise from the metric's simplicity. In reality different habitats are differently permeable to species. Prevalent wind and weather patterns may also modify dispersal (Keith et al., 2011; Walls et al., 2005), which may vary in timing between species. Finally, different breeding populations are likely to exert different propagule pressure based on their size and population trend (Clobert et al., 2009; Leung et al., 2004). Current measures of dispersal distance have not been effective predictors of range-shift (Estrada et al., 2016) or range-filling (Estrada et al., 2018). Thus, it is important to consider the diversity and complexity of movement processes in models of range- shift (Evans et al., 2016).

Our ability to predict range-shifting species' British occurrences improved considerably when our models included a spatial covariance function. This finding is consistent with the species expanding from a single or small number of points once they manage to reach Britain rather than as a front from their European populations. However, Europe was not included in the area over which we constructed our gaussian random field (due to different data sources). As such, southern populations could appear to be spreading from a single location while actually being part of an expanding European range front.

Alternatively, a confounding variable (or variables) could be captured by the spatial covariance function unrelated to dispersal (Beguin et al., 2012; Dormann, 2007a). Anthropogenic effects such as human conservation efforts, which may be regionally focused and thus spatially autocorrelated, urban heat island effects and anthropogenic food subsidies might also fit this pattern. Scale-dependency might also cause effects to be captured by the covariance function rather than explicitly by our predictors (Brambilla and Saporetti, 2014). For example, our metric of habitat suitability only described the potential suitability of the cell itself in isolation. As such, it did not include aspects such as habitat fragmentation (Scharf et al., 2018). If breeding requires areas of contiguous habitat which are infrequent and aggregated despite the habitat being nationally common, then this could lead to the occurrence being related to a spatial effect rather than habitat. It is also possible that geographic proximity may contain a signal due to habitat, for example, the Goldeneye, which shows a strong spatial random effect, requires both high quality fresh water and coniferous woodland to breed. The co-location of these two habitats is more localised than that of either of these two habitats independently. Scotland, where the random effect is concentrated, has both fast-flowing rivers and abundant forest unlike southern coniferous plantations (Rowland, 2017).

Finally, the spatial covariance function could also indicate biased detection rather than explanation by our predictors. This could occur where observations are spatially autocorrelated due to high recording effort, perhaps due to past sightings or scenic landscapes. However, due to the quality of the datasets used, we believe the impact of recording effort is unlikely to affect our overall inferences. The British breeding bird atlas has high spatial coverage and used well-planned and documented protocols for data collection (Balmer et al., 2014). But if a recording effort effect exists, it should be strongest for northern upland species as these are harder to survey (Calladine et al., 2009) and this may be reflected in Figure 2.3, as these species have larger differences between results when the covariance function is removed. An improved understanding of recorder behaviour and effort to address non-detection will continue to be an important consideration for modelling novel species which may be under-recorded compared to native species.

Drawing this together, our findings show strong limitations in our present ability to explain the new ranges of range-shifting species and to project their future range-shifts from historically suitable climates. Habitat preferences are similarly weak predictors, possibly due to the available spatial resolution of available data and our ability to discriminate subtle variation between finely distinguished classes. While we found distance to breeding sites performed relatively better than climate or habitat, it still did not achieve a high absolute predictive performance, suggesting more complex processes may need to be brought into account to adequately describe movement. Our ability to conserve both range-shifters and recipient ecosystems will be greatly assisted by efforts to improve our knowledge of the current constraints on species distributions and the processes by which they are expanding.

Chapter 3: Is the spread of a range-shifting damselfly (*Erythromma viridulum*) associated with declines in the UK's native Odonata?

3.1 Abstract

I. Range-shifting species are a conservation dilemma. A loss of climatically suitable space may threaten range-shifters in their historic range. However, some range-shifters may also harm aspects of biodiversity in their new ecosystems, for example by predation or competitive displacement. Therefore, we need to understand which range-shifters may be negatively affecting native species and those which may not.

II. Our research aimed to evaluate effects of the range-shifting small red-eyed damselfly (*Erythromma viridulum*) on the UK's currently resident damselflies and dragonflies (Odonata). Odonata are intraguild predators, a mechanism by which potentially faster growing equatorial species may impact residents. We harnessed the British Dragonfly Society's dataset, using records from 49,788 site visits to construct dynamic species occupancy models for 17 native UK Odonata. We estimated the potential effect of *E. viridulum,* presence on the probability that each species would persist at a given site, while controlling for potential effects of climate and recording effort.

III. Contrary to our expectations, we found that the dragonflies (Anisoptera) persisted more frequently, on average, at sites where *E. viridulum* had established, whilst damselflies (Zygoptera) showed no change in persistence on average. Nevertheless, two native damselflies, including the E. viridulum's congener, did persist less frequently when the range-shifter established.

IV. These results suggest that *E. viridulum* may pose a minimal risk to UK native odonata. However, further integrating potential confounding factors into dynamic multispecies occupancy models is needed to reliably screen range-shifters for negative impacts. The possibility that *E. viridulum* preferentially establishes in sites of high habitat quality and the lack of stasis in residents' distributions are two important mechanisms that could affect methods to estimate range-shifters' impacts.

3.2 Introduction

Novel species interactions are occurring around the world as anthropogenic environmental change causes species distributions to shift (Bonebrake et al., 2018). These interactions may lead to a range of both positive and negative effects depending on the local environmental and social context in which they develop (Pecl et al., 2017). Some effects may be considered beneficial, such as increased pollination, while others may be problematic, such as competition with endangered species (Pettorelli et al., 2019). Despite this potential risk to recipient ecosystems, species that are losing historic range will be at increased risk of extinction if they cannot establish in new areas (Araújo et al., 2011; Thomas et al., 2004). Therefore, we may sometimes see a conservation dilemma between protecting the new arrivals and protecting native species.

Range-shifters, i.e. species immigrating to novel communities without human assistance, are usually considered to have minimal effects on recipient ecosystems (Wilson et al., 2016; Wallingford et al., 2020; Urban, 2020). Nevertheless, some studies have found negative impacts such as: out-competing natives (Fitt and Lancaster, 2017; Yackulic et al., 2019), disease spill over (Dobson, 2009), direct predation, and hybridization (Sánchez-Guillén et al., 2013; Steeves et al., 2010). Horizon scanning (Roy et al., 2014), risk assessment (Hawkins et al., 2015) and proactive monitoring (Kennedy et al., 2018) are often used to identify threats from introduced invasive species. However, these legal or management frameworks focus on species that have been directly or accidentally introduced by humans – not range-shifting species moving under their own powers of dispersal (Trouwborst et al., 2015). It therefore seems prudent also to monitor range-shifters for any undesirable effects as their arrival rate continues to increase (Gurney, 2015; Mason et al., 2015).

Monitoring and quantifying the in-situ impacts of range-shifters on residents is important for two reasons. First, in the short-term, quantification allows limited conservation resources to be spent on the species of greatest impact (Carrasco et al., 2010; Kumschick et al., 2012). Second, in the longer-term, the resultant knowledge base could be used to compare the impacts of range-shifting species at regional and global levels relative to other risks to biodiversity (Turbelin et al., 2017). However, detecting impact is challenging. There is little systematic data on range-shifters' distributions in recently occupied parts of their ranges and even less on their abundance. Most available data are opportunistically collected rather than using standard protocols (Amorim et al., 2014). Unfortunately opportunistic data can suffer from several biases which can lead to flawed inferences over species trends (Isaac and Pocock, 2015). Furthermore, it can be challenging to separate the effects of the arriving species from other environmental changes. If an uncontrolled environmental driver increases both the establishment probability of the new species and the probability of native species extinction, this could lead to a correlation between new species arrival and native species decline (Parmesan et al., 2011). Climate change is a quintessential example. It allows new thermophilic species to establish but by exceeding current residents' thermal limits causes their probability of persistence to decrease. Correlational models should be cautious when inferring biotic interactions without a putative mechanism for interaction as, spurious effects can arise from sampling biases and indirect associations (Blanchet et al., 2020; Dormann et al., 2018). However, occupancy models can act as useful starting points for generating hypotheses and general patterns so long as consideration is paid to the risk of assigning causal links if strong species-specific inferences are identified.

Dynamic multispecies occupancy models (DMSOs) have been used successfully to link environmental change to biodiversity impacts using occurrence records (Woodcock et al., 2016). DMSOs can use datasets that contain data collected using different protocols, which is useful where total available data is limited. Being able to integrate a larger quantity of occurrence records makes it possible to infer trends for more species over wider geographic areas than experimental studies that are often limited to a few species or small areas. Moreover, it is also easier to replicate and adapt these analyses, for example by incorporating different environmental covariates or different model formulations which can be statistically compared, than rerun field or laboratory experiments. Including environmental covariates could help to rule out possible confounding factors such as climate or habitat. In addition, including ecological processes such as dispersal in sub-models could also help to build more biologically realistic models. Our understanding of range-shifters effects can also be updated as more data becomes available to estimate parameters, allowing near real-time inputs into conservation strategy (Mancini et al., 2019).

Here, we apply DMSOs to examine a range-shifting species – the small red-eyed damselfly (*Erythromma viridulum*). The species first arrived in the United Kingdom in 1999 and has continued to establish over the last two decades.

Originally a Mediterranean species, the damselfly has spread gradually northwards, arriving in the UK via multiple irruptive waves from 1999 and becoming established by 2002, at times appearing abundant at certain sites (Watts et al., 2010). The damselfly is at the current poleward edge of its distribution in the UK (GBIF Secretariat, 2019) and thus breeds less frequently there, either annually or biennially, than in the warmer core of its range. It favours static pools or slow-flowing rivers for egg-laying as they have requisite macrophytes, particularly Hornwort and Water Milfoil. It flies principally between May and September (Brooks and Cham, 2014).

E. viridulum in the UK provides a good case-study for investigating measures of impact. First, *E. viridulum* is a representative and timely study species since several new Odonata are expected to establish in upcoming years (Parr, 2010). Second, Odonata are known for their strong inter-specific interactions in both their adult and larval stages, including predation, which constitutes a biologically plausible mechanism for impact (Cerini et al., 2019; Wissinger and McGrady, 1993). Interactions in the larval stage are hard to observe directly and therefore inferring through modelling could be particularly useful. Third, *E. viridulum* also has a congener in the UK (*E. najas)* with whom it overlaps in habitat preference and flight season (Powney et al., 2014). This could mean *E. najas* could be negatively impacted by *E. viridulum*. Previous studies have shown that *E. viridulum* individuals are often larger than their conspecifics in the core range (Hassall et al., 2014). This size advantage could mediate a higher per capita impact. Finally, *E. viridulum* can be readily identified in the field reducing the risk of misidentification or omission compared to cryptic species groups, and its distribution is recorded along with other Odonata in a national monitoring scheme. Thus, DMSO techniques may be readily and accurately applied.

There are reasons to think *E. viridulum* both may and may not affect UK Odonata. The UK Odonata is relatively species-poor compared to similar latitudes in mainland Europe (Kalkman et al., 2018).This is concerning as low biodiversity has been shown to decrease resistance to invasion at site level (Kennedy et al., 2002), which may suggest that some UK sites may be at risk. Impacts may also be amplified since several UK Odonata species are already locally threatened (Daguet et al., 2008). On the other hand, low Odonata species richness may mean that there are vacant niches to exploit (Gauzere et al., 2020), which may not harm residents.

In this study, we investigated whether we could detect and quantify impacts of the range-shifting *E. viridulum* on the UK's resident Odonata. Specifically, we tested for a net effect across both dragonflies (Anisoptera) and damselflies (Zygoptera) on their persistence probability at sites where *E. viridulum* had arrived. We also examined effects on individual species. Our study incorporated data from 2,609 1km^2 sites and recorded effects for 10 native dragonfly species and 7 native damselfly species, compensating for differential recorder effort through a detectability sub-model. While testing for an effect of *E. viridulum*, we controlled for potential climate effects on persistence and colonisation probabilities of individual sites/cells, in an attempt to avoid potential confounding effects. The detection of widespread impacts across a range of species would support the characterization of *E. viridulum* as having negative impacts on UK biota. This would highlight the need for increased monitoring of the impact of range-shifting species in an analogous way to that for prospectively invasive introduced species.

Our aim of better understanding the consequences of range-shift for those recipient ecosystems is advanced by the approach taken in this chapter in the following ways. I hypothesise that an effect of small red-eyed damselfly on native UK odonata can be detected through signals in occurrence data using dynamic multispecies occupancy models. I anticipate that this effect if it exists is likely to be a negative effect on site persistence probability through negative biotic interactions such as intraguild larval competition and predation. Testing this approach on the UK, contributes to knowledge of this methods application to the broader research aim as well as the impact of range-shifting species more widely.

3.3 Methods

3.3.1 Occurrence Data

We used all available species records which had a spatial resolution sufficient to place them at 1km^2 resolution on the British National Grid (EPSG:27700) and a recorded date between 2000 and 2015 from the British Dragonfly Society (BDS) database. We obtained 509,723 records across the UK with records from 39,719 sites in total. For every grid-cell, following (H. E. Roy et al., 2012; Woodcock et al., 2016), we assumed records on the same day could be treated as recorded on the same visit and we excluded grid-cells that were only visited in a single year.

In order to reduce confounding effects, we compared cells where E. viridulum has established against cells without E. viridulum but which have similar potential native species' compositions, habitat, and climate by further restricting the dataset in two ways. First, we included only 1km^2 grid-cells within 100km cells of the British National Grid (e.g. TF) containing at least 50 records of E. viridulum. Second, we included only sites with a confirmed record of either E. viridulum or its congener red-eyed damselfly (Erythromma najas). We only modelled associations with native dragonfly and damselfly species that had a habitat overlap with E. viridulum, following Powney et al (2014) (Supp. Table B.1). Thus, we removed species that are unlikely to interact with *E. viridulum* as they don't occur in the same habitats. Finally, we removed native species with < 2000 records in the dataset as these species would be likely to have few co-occurrences with *E. viridulum* and thus would not add information to the model.

After filtering, our dataset covered 17 native species, 7 damselflies and 10 dragonflies, not including *E. viridulum*. Across 2,609 sites, there were in total 49,788 visits by recorders. *E. viridulum* was reported at 1190 of those sites at least once and was in total reported in 3350 distinct visits. We used these data to model resident species distributions in 1km^2 grid-cells as independent sites, assuming a closure period of 1 year, i.e. that if a species was detected in a site at least once in a year, our model assumes it was present that whole year, regardless of any subsequent failure to redetect it by surveys in that year (MacKenzie et al., 2003). For each of these sites, we used 1km^2 resolution annual climate data from the Met Office (Hollis et al., 2019) to find the mean spatial climate anomaly for the site between 2000 and 2015. For each site, we then calculated the yearly difference in its mean annual temperature from the mean annual temperature across all sites in that year. Finally, we took the mean of those differences to find if the site was typically warmer or cooler than other sites included in the analysis ('climate anomaly').

We could not be certain of the true extent of *E. viridulum* occurrence in each year because not all sites were visited annually. In addition, it is possible that some records, especially in early years, represent ephemeral appearances rather than established populations. Therefore, we constructed occupancy models using two final datasets, based on two different assumptions about the true presence of *E. viridulum*. In the first dataset, *E. viridulum* was considered present in a site when it has been recorded at a site in that year ($EV_{AsReported}$);(Roy et al., 2012). In the second dataset, we instead assumed that once *E. viridulum* was established at a site it did not subsequently go extinct and therefore was present in all subsequent years ($\mathrm{EV}_{\mathrm{NoExtinction}}$). All analyses below were repeated for each dataset.

3.3.2 Model description

In order to estimate the effect of *E. viridulum* on the persistence of UK native Odonata we used Dynamic Multi-Species Occupancy (DMSO) models derived from (Woodcock et al., 2016). The parameter of interest – occupancy – cannot be directly observed (i.e. it is a latent state). We can only infer it from separate detections of species' presences on a particular visit (*k*) at a site (*j*). Therefore, the model describes two sub processes: occupancy and detection. We fitted our models using a Bayesian approach, which permits full propagation of uncertainty. This approach synthesises information from assumptions about the likelihood of different parameter values (priors) with information from the observed data (Y) to find the most likely parameter values given the data (posteriors).

To control for the potential effects of climate on species persistence we parameterised two similar models differing only in whether a parameter for a climate effect was included. For both models, the probability of occupancy E[($z_{i,j,t}$)] for each native species (*i*), at site (*j*) in year (*t*) is modelled as either a persistence probability ($\phi_{i,j,t}$) or a species colonisation probability (γ_i) – depending on if the modelled occupancy state of the site in the previous year ($z_{i,j,t-1}$) was present or not (Eq. 1) respectively.

$$E[z_{i,j,t}] = z_{i,j,t-1} * \phi_{i,j,t} + (1 - z_{i,j,t-1}) * \gamma_i \qquad \text{Eq. 1}$$

In the model without climate ($\mathrm{Clim}_{\mathrm{Exc}}$, Eq. 2), we modelled persistence probability ($\phi_{i,j,t}$) as a linear function, converted to the probability scale with a logit link. Our model had two parameters: a species-specific intercept β_{0i} (the probability that a population of a native species will persist from one year to the next in the absence of *E. viridulum*) and β_{1i} (the difference in persistence associated with *E. viridulum* being present at the site (j) in the previous year ($EV[j, t-1]$)). In the climate model ($\mathrm{Clim}_{\mathrm{Inc}}$, Eq. 3), we also included an effect (β_{2i}) of the previous year's climate anomaly ($SpatAnol[j, t-1]$).

$\mathrm{Clim}_{\mathrm{Exc}}$ $$logit(\phi_{i,j,t)} = \beta_{0i} + \beta_{1i} * EV[j, t-1] \qquad \text{Eq. 2}$$

$\mathrm{Clim}_{\mathrm{Inc}}$ $$logit(\phi_{i,j,t)} = \beta_{0i} + \beta_{1i} * EV[j, t-1] + \beta_{2i} * SpatAnol[j, t-1] \qquad \text{Eq. 3}$$

To test the hypothesis that dragonflies (Anisoptera) and damselflies (Zygoptera) differ in their response to *E. viridulum*, we estimated their β terms as being drawn from two different distributions, allowing the suborders to diverge:

$$\beta_{1i} = Aniso_i(\beta_{Aniso} + \varepsilon_{Aniso}) + Zygo_i(\beta_{Zygo} + \varepsilon_{Zygo}) \qquad \text{Eq. 4}$$

$$\varepsilon_{Zygo} \sim N(0, \sigma_{Zygo})$$

$$\varepsilon_{Aniso} \sim N(0, \sigma_{Aniso})$$

These occupancy states were linked to the observed data – a logical matrix of which species were detected on each visit ($Y_{i,k}$) – through a detection sub-model. The probability of detecting a species on a visit ($P_{i,k}$) is modelled as a logit linked linear function of the number of species recorded on that visit, which provides a measure of sampling effort (Szabo et al., 2010). This function included three binary variables, indicating whether two ($LL2_k$), three ($LL3_k$), or four or more ($LL4_k$), species were recorded on the visit (Eq. 5).

$$logit(P_{i,k}) = \beta_{3i} + \beta_{4i} * LL2_k + \beta_{5i} * LL3_k + \beta_{6i} * LL4_k \qquad \text{Eq. 5}$$

Thus, the logit probability that a visit list recording only one species is a record of focal species *i* is β_{3i}. The other three parameters ($\beta_{4i}, \beta_{5i}, \beta_{6i}$) then capture how the logit probability of detection varies with increasing recorder effort, i.e. if two species were recorded on that visit ($LL2_k = 1$) then the probability of detecting the focal species is $\beta_{3i} + \beta_{4i}$. Informing the model about the visit list length allowed it to estimate a possible impact of list length on detectability: our conception in this parameterization is that longer list lengths imply higher search effort and thus detection probability on that visit (Outhwaite et al., 2019). However, the model formulation does not constrain this to be the case, i.e. ($\beta_{4i}, \beta_{5i}, \beta_{6i}$) can be negative. This might be the case if a species was particularly distinctive, leading inexperienced recorders to include just that species on their list as it was the only one they could identify. We did not estimate parameters for higher list lengths due to the smaller numbers of visits with lists of >5 species, which would make it hard to estimate the parameters. The observations on each visit inform the state sub-model via Eq. 6, e.g. if $Y_{i,k} = 1$ then $z_{i,j,t}$ must = 1.

$$Y_{i,k} = dbern(z_{i,j,t} * P_{i,k}) \qquad \text{Eq. 6}$$

The priors used to fit this model were selected to be as weakly informative as possible and are shown in the JAGS model code (Supp. Method B.1).

3.3.3 Model fitting

In total, we therefore ran four models. For both $EV_{AsReported}$ and $EV_{NoExtinction}$ datasets we fitted the two models $Clim_{Exc}$ and $Clim_{Inc}$. These models were run to convergence using JAGS V4.3.0 (Plummer, 2003) and each model was run with three chains. We allowed our chains to run for 20,000 iterations, after adaptation (the sampling phase, determining how far the model moves in parameter space at each iteration). We discarded the first 10,000 iterations as burn-in and then thinned our chains by a factor of 20 to retain 500 samples of the posterior distribution per chain. Convergence was assessed by visual inspection and ensuring that for all parameters $\widehat{R} < 1.05$, indicating that all Monte-Carlo Markov chains had run to a point where they were sampling from the same area of parameter space (Brooks and Gelman, 1998). We checked for correlations between the sampled posteriors of the model parameters to assess model identifiability. Finally, we ensured that all parameters had an effective sample size of at least 1,000. We describe the posterior distributions of our models' parameters using the mean and width of the 95% credible intervals. We report the Probability of Direction (PD), for our estimates of the effect of E. viridulum which is the proportion of samples which have the same sign as the mean. PD is a metric of confidence in the direction of an effect if it exists.

3.4 Results

E. viridulum was first recorded in the East and South of the UK, with high densities on the East Anglian Coast and the Isle of Wight (Figure 3.1). Sites were otherwise quite well distributed across the study area but with fewer in the North and West. The number of visits made to a site did not strongly relate to the year that E. viridulum was first detected which suggests that *E. viridulum* was not detected in certain regions first simply due to recording effort. (Supp. Fig. B.1)

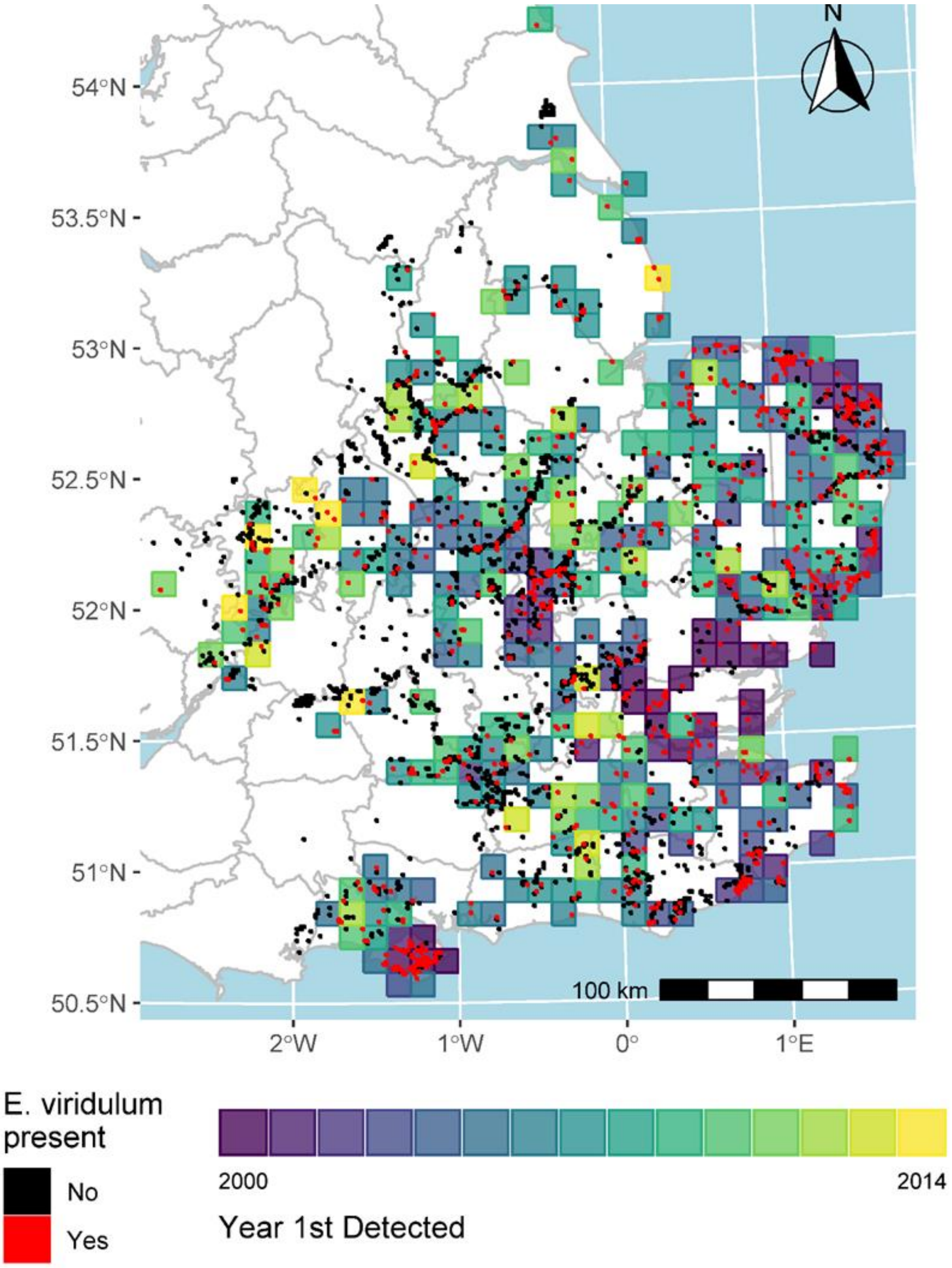


Figure 3.1: Distribution of E. viridulum in the UK in cells from the filtered dataset. Colour scale (blue to yellow) shows the first year E. viridulum was reported in that 10km cells. 1km cells included in the study are shown in red, if E. viridulum was recorded at the site or black if absent.

We found that for all four model-data combinations there was no net negative association between *E. viridulum* and UK damselfly (β_{Zygo}) and dragonfly (β_{Aniso}) site persistence (Figure 3.2). Posterior distributions for model parameters were qualitatively similar regardless of the input data or whether we included an effect of climate. We found that β_{Aniso} was more positive than β_{Zygo}, suggesting that *E. viridulum* had a different effect on damselflies as a suborder than dragonflies as a suborder. All 4 model-data combinations had over 90% of samples from the posteriors (probability of direction - pD) with the same sign as the mean for this difference in *E. viridulum*'s effects between sub-orders (Table 3.1).

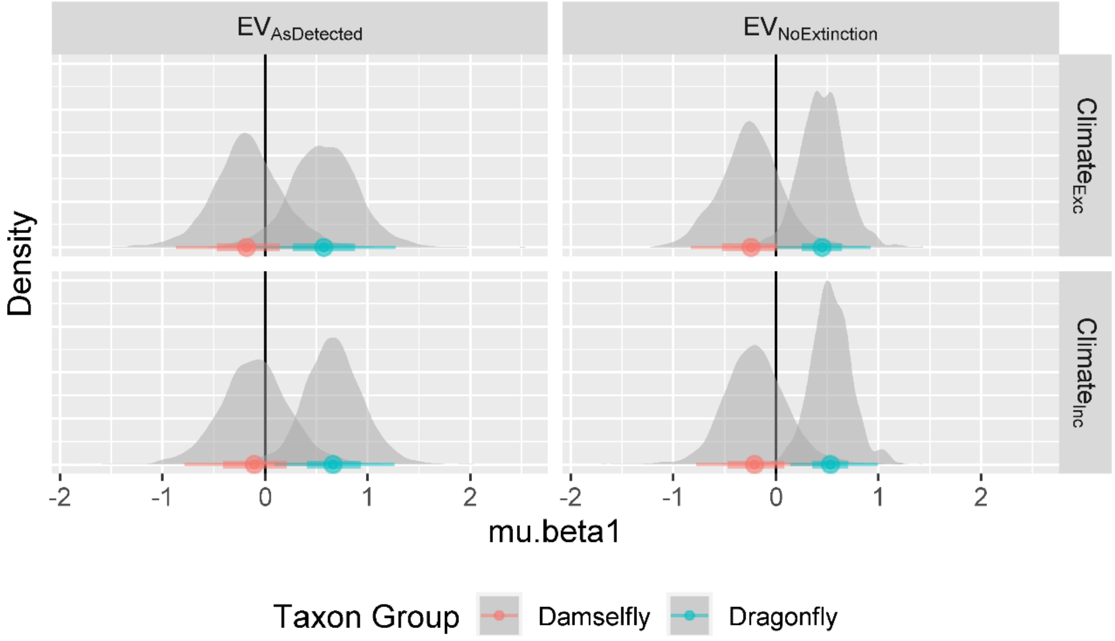


Figure 3.2: The posterior distributions for Dragonflies (blue) and Damselflies (red) from which E. viridulum ($\beta 1$) species effects were drawn, credible intervals are shown for each model-data combination (point = mean, thick band = 66% CI, thin band = 95% CI).The central point represents the model's estimate for the effect of E. viridulum on an "average" damselfly's or dragonfly's probability of persistence at a site.

The species level parameters for the effect of *E. viridulum* (β_{1i}) for the model where we included the effect of climate anomaly and used the unmanipulated *E. viridulum* occurrence dataset are shown in Figure 3.3.The species level results for the other three models are shown in Supp. Fig. B.2 and are qualitatively similar. For damselflies, estimates of *E. viridulum*'s association with native species (β_{1i}) fall either side of 0, with a slight skew towards a negative effect on persistence of native species. The posterior means (μ) of the E. viridulum presence parameters (β_{1i}s) suggested that *E. viridulum* establishment was associated with declines in the persistence of White-legged damselfly (*Platycnemis pennipes*) (pD = 1, µ = -1.1) and *E. najas* (pD = 1, µ = -0.82). The persistence of most dragonfly species was positively associated with *E. viridulum* establishment, with the exception of the brown hawker *A. grandis*. For only three dragonfly species was there less than 80% confidence in the direction of the effect (pD <= 0.8).

Table 3.1: Differences between E. viridulum effects on damselflies and dragonflies site persistence probability, shown by posterior mean (µ) and the proportion of samples matching the same sign as the mean (probability of direction - pD) of the two distributions from which effects of E. viridulum were drawn. The pD for the difference in mean effect was calculated by comparing the two parameters in individual samples, to derive a posterior distribution for the difference.

Model	***E. viridulum* mean effect (damselflies)**	***E. viridulum* mean effect (dragonflies)**	**Difference**
$EV_{AsReported}$ $Clim_{Inc}$	µ = -0.10, PD = 0.62	µ = 0.67, PD = 0.99	µ = 0.77, PD = 0.96
$EV_{AsReported}$ $Clim_{Exc}$	µ = -0.17, PD = 0.71	µ = 0.58, PD = 0.96	µ = 0.75, PD = 0.93
$EV_{NoExtinction}$ $Clim_{Inc}$	µ = -0.20, PD = 0.76	µ = 0.54, PD = 0.99	µ = 0.73, PD = 0.97
$EV_{NoExtinction}$ $Clim_{Exc}$	µ = -0.25, PD = 0.81	µ = 0.45, PD = 0.98	µ = 0.70, PD = 0.96

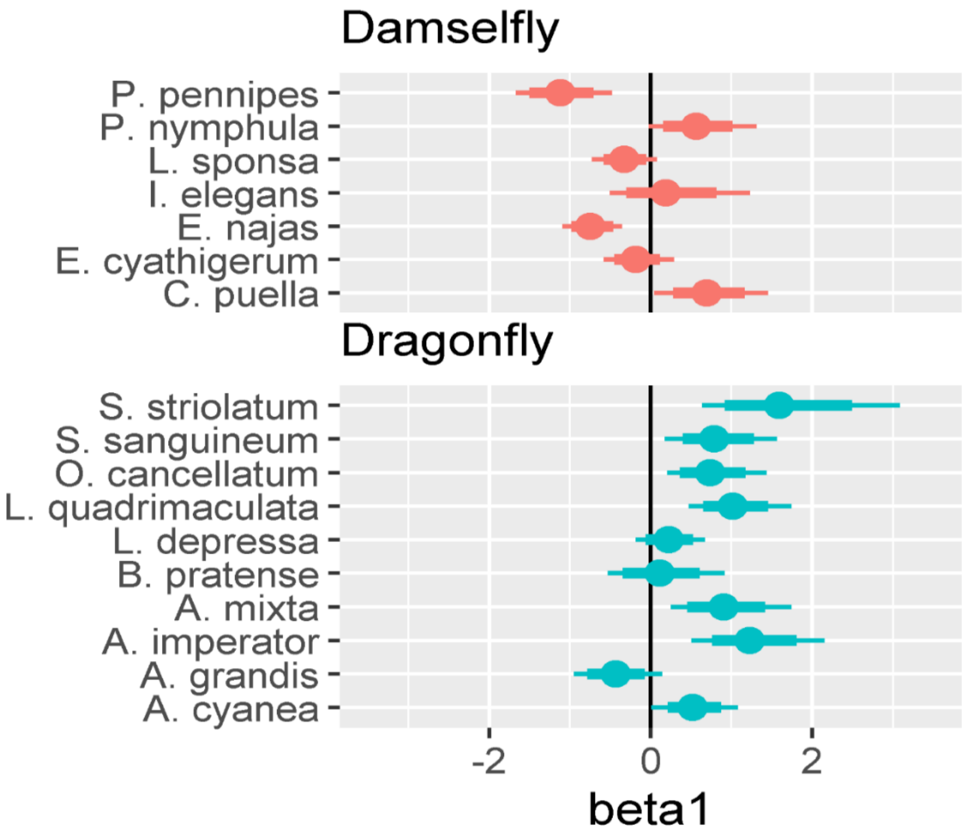


Figure 3.3: E. viridulum's effect ($\beta1$) on persistence probability by species with credible intervals (point = median, thick band = 80% CI, thin band = 95% CI). Estimates shown are from the model where E. viridulum data was as detected and a climate effect was included ($EV_{AsReported\ ClimInc}$). A positive coefficient indicates the species had a higher probability of persisting into the subsequent year, than if it was not present, and a negative coefficient a lower probability.

3.5 Discussion

All four data-model combinations showed no clear negative association, on average, between *E. viridulum* presence and the persistence of either native dragonflies or native damselflies (which showed only a slight negative tendency). In fact, the mean association with native dragonfly species was predicted as a positive effect. If this effect truly reflects the interactions of the species on the ground, then this range-shifting species is not particularly harmful, at least considering Odonata as a whole. However, it is worth noting that species-specific results suggest a negative effect of *E. viridulum* presence on two native damselfly species, including on its congener, *E. najas*.

A possible explanation for this average positive association could be facilitative interactions (Rodriguez, 2006). However, it is hard to identify what these could be in practice. Positive indirect effects such as suppressing existing predators seem unlikely to affect such a broad range of species (Golubski and

Abrams, 2011; Wissinger and McGrady, 1993). *E. viridulum* is a generalist rather than specialist predator so is unlikely to bring new energy flows into the food web. It is also not known to have any ecological engineering behaviour (Thomsen et al., 2010). We therefore suggest that this apparent positive association could be due to a confounding effect masking the true relationship between *E. viridulum* presence and native species persistence probability. If *E. viridulum* preferentially established in sites of high quality for native species (Balzan, 2012; Gibbons et al., 2002), it could lead to a false positive association between *E. viridulum* presence and the site persistence probability of natives. Alternatively, if *E. viridulum* did not establish in sites where native species were declining, then the same correlation would result.

If the interpretation that habitat quality is behind positive associations between *E. viridulum* and native species is correct, then the effects shown in Figure 3.2 would represent the mean effect of habitat quality for dragonflies and damselflies, combined with the effect of *E. viridulum*. The variation in the effect of *E. viridulum* presence found at the species level could then reflect two possibilities. First it could reflect the relative importance of habitat quality for species persistence. Alternatively, if we assume that the effect of habitat quality is approximately constant across species it could reflect the effects of the species interactions with *E. viridulum*. If this were the case, then it would suggest that more species were negatively affected than our results initially suggest. Unfortunately, we cannot yet use our results to distinguish interspecific variation in response to habitat from variation due to interactions with *E. viridulum*. Experimental studies could help resolve these ambiguities in the short-term but disentangling interactions from habitat or other confounding effects in macroecological models needs careful attention. Whilst we tried to control for habitat type by restricting to only those sites with *E. viridulum* or *E. najas* reported, variation in habitat quality could still exist. It would have been desirable to have explicitly included habitat in our models. However, the distribution and quality of habitats for the study species are poorly recorded. In the UK, while datasets of river water quality are available at high resolution, we lack similar high-resolution data for more ephemeral water bodies, such as small ponds and lakes *E. viridulum*'s primary habitat. Moreover, data availability meant we considered co-occurrence in 1km^2 cells to indicate that species encounter one another, i.e. share habitat or otherwise genuinely interact. However, the home range required by damselflies is much smaller, so aggregating habitat data to this level may also be problematic (Dormann et al., 2018; Montesinos-Navarro et al., 2018). Two potential issues are: first, we might not detect small areas of suitable habitat nested in larger cells and second, different species might not co-occur in the same areas of larger cells. Our ability to address habitat quality as a confounding effect would be enhanced if records can be collected and analysed at finer spatial resolution with accompanying habitat data. While high-resolution habitat information is increasingly available from remote sensing (Boyle et al., 2014), the metadata available with which to understand the spatial accuracy of biological records is often poor (Maldonado et al., 2015). Ideally, observations should be explicitly tied to a specific site, but there is variation in how well recorders note record locations. Consequently, our ability to use fine-scale records is constrained. Finally, it would be useful to describe the habitat requirements of both range-shifters and residents more fully. An approach could be to encourage recorders to report interactions that might reveal finer habitat constraints, for example egg-laying behaviour on particular macrophytes (which might then be used as indicators of potential habitat).

One detail we did not explicitly consider in our models is that several UK Odonata species are expanding their ranges (Mason et al., 2015) at the same time as *E. viridulum* is establishing. Therefore, range-expansion could create specious patterns in our data. For example, if *E. viridulum* were to expand slower than natives it would be more likely to be found in natives' core ranges, rather than at their range-fronts. This discrepancy could affect our parameter estimates as core range populations may have more stable demographic rates than those at the range edge (where populations were more stochastic and had a greater potential to be population sinks) (Guo et al., 2005). Therefore, we might misattribute a positive effect of *E. viridulum* on persistence independent of any effects of biotic interactions. A final limitation of our model is that the effect of E. viridulum presence on native species was limited to two levels (i.e. present or absent). It could be that more complex functions, for example, a monotonic or logistic function parameterised with time since arrival could help capture effects dependent on E. viridulum population density (Sofaer et al., 2018). A monotonic or logisitic function would help to describe the delay in impact we might expect from when E. viridulum first arrives, till the time when it has had sufficient time to reach its carrying capacity at the site when we might expect its impact to peak (Parker et al. 1999).

Multi-pronged efforts to address our limited knowledge of both residents' and range-shifters' distributions will be required in the future as they move. We suggest investment in both occurrence and experimental data. Gathering a greater quantity of occurrence data could allow models to include more parameters without compromising accuracy. This data must be of sufficient quality (Raebel et al., 2010) and resolution for questions on biotic interactions. It is also important to note that the timeliness and accessibility of occurrence data is just as important as its volume. Therefore, it is also important to improve both local recording capacity (e.g. resourcing local environmental records centres to provide training and equipment) and national data infrastructure (e.g. development of the National Biodiversity Network Atlas). Experimental data on *E. viridulum*'s rates of dispersal could also assist our ability to model occurrence (Jaeschke et al., 2013). Improved empirical data could inform choices of priors in Bayesian models and potentially reduce the required number of assumptions, increasing their realism. Ideally experimental data could work together with occurrence data, for example to target recording effort and calibrate models of rates of spread.

The detection sub-model of the DMSO also has scope for refinement (Boakes et al., 2016). Recorders are a diverse group and different sub-cultures within it can produce data of different information content, for example those who keep complete lists vs single observations. It is currently challenging to incorporate these behavioural aspects into our models. We use the total list length on the visit as a proxy for recording effort. However, metrics such as recorder experience or even site knowledge could be more relevant. Another unknown aspect is to what extent new species like range-shifters attract different recording effort compared with resident species. Range-shifters could be both under-detected due to rarity or not being included in reference materials or be more likely to be reported through the excitement of novelty. In our study, we did not see a meaningful change in our results dependent on our two assumptions about recording effort, (i.e. whether we assumed *E. viridulum* was present as reported or whether a single report indicated unobserved persistence thereafter). However, for other species this distinction could be more impactful and efforts to understand how we can better model occurrences are the backbone for improving the outputs of DMSOs. In our study, it is probable, that the true state of *E. viridulum* occupancy lay between these two bounds, as the risk of identifying *E. viridulum* at unsuitable site is low and as a new species to the UK, there is a higher risk of the species not being reported relative to a native species, for example due to omission in less recent field guides.

We interpret the negative association between *E. viridulum* and persistence probability of *P. pennipes* and *E. najas* cautiously, given the possibility of confounding effects previously discussed. However, our findings suggest these species as priorities for future autecological studies into negative effects. This prioritisation is particularly useful given the limited available resources for most non-pest entomological research. The negative association between *E. viridulum* and its congener species may suggest competitive displacement as functional traits such as flight period and habitat overlap. A more negative association between *E. viridulum* and other damselflies than on dragonflies also matches the competitiveness-relatedness hypothesis (Cahill et al., 2008) and suggests that intra-suborder interactions may be a greater risk to native species than inter-suborder interactions. However, this literature is still contested (Naughton et al., 2015). A final additional future risk to native species may not be easily quantified, but could be highly impactful: the spread of novel diseases or parasites such as *Arrenurus* mites (Forbes et al., 2004).

Including spatial climate information resulted in minimal changes to our estimated effects of *E. viridulum* presence. This could be for several reasons: it is possible that at the spatial extent considered the effect of variation in climate is much smaller than the effects of other environmental variation; the spatial resolution of the data may be insufficient to reflect the microclimates actually experienced by the Odonata (Suggitt et al., 2015); or more species-specific climate metrics may be necessary. Mean annual temperature has been shown to be important for many species' distributions (Termaat et al., 2019). However, for Odonata, temperature in species specific flying seasons or in the key periods of larval growth could be more important (Collins and McIntyre, 2015).

Our results feed into a mixed literature on the effects of *E. viridulum*. Diet sampling of *E. viridulum* revealed no direct predation of other damselflies (Cox, 2013). However, Cox's study was conducted late in the larval growth period and may not have fully captured the potential complexity of changing intraguild predation (Frances and McCauley, 2018). Furthermore, Odonata larvae are known to predate voraciously on a range of non-Odonata taxa including, diptera and cladocerans, so *E. viridulum* could impact species from these taxa as well as other Odonata. New approaches such as meta-barcoding and stable isotope analysis may be able to clarify the trophic impacts of range-shifters (Do and Choi, 2019). Future DMSOs could complement these laboratory-based techniques by broadening to consider taxa outside the order Odonata (Kaunisto et al., 2020).

In conclusion, we suggest that DMSOs' strength for assessing range-shifters' potential impacts lies in their flexibility through allowing a broad scan of potential impacts taxonomically and in different types of habitats to be investigated at the same time. However, our findings show the current difficulty in interpreting potential biotic interactions inferred by these models due to the possibility of confounding factors such as habitat quality. We argue *E. viridulum* is unlikely to be genuinely facilitating natives as suggested by our model. This highlights that future approaches to identify the effects of range-shifting species should make use of the increasing availability of high-resolution habitat and climate data to minimise confounding effects as the number or range-shifters continues to increase. Field or laboratory competition experiments will remain the gold standard for proving causal impacts but are prohibitively costly to perform for all species. Therefore, we can productively use DMSOs to prioritise species at potential risk, such as the red-eyed damselfly (*E. viridulum*'s congener), for further investigation by more sensitive methods.

Chapter 4: UK wildlife recorders cautiously welcome range-shifting species but incline against intervention to promote or control their establishment

4.1 Abstract

I. The global redistribution of species due to climate change and other anthropogenic causes is driving novel human-wildlife interactions with complex consequences. On the one hand, range shifting species could disrupt recipient ecosystems. On the other hand, these species may be victims of environmental change, with contracting distributions in their historic range. They could also have positive effects on recipient ecosystems. Thus, public opinion on these species may be divided and they may present a unique challenge to wildlife management.

II. We surveyed the opinion of wildlife recorders about the establishment and management of eight birds and eight insects whose ranges have recently shifted into the United Kingdom, and the roles of climate change and species identity in shaping this opinion. We then assessed whether we could explain the respondents’ attitudes using characteristics of the species presented, characteristics of the respondents, and whether or not climate change was emphasised as a cause of range shift. We also conducted thematic analysis of recorders’ written responses from the survey to contextualise our results.

III. Attitudes to range-shifting species were mostly positive but were more ambivalent for less familiar taxa and for insects compared with birds. Respondents were strongly opposed to eradicating or controlling new range-shifters, and to management aimed to increase their numbers. Whether climate change was presented as the cause of range-shifts did not affect attitudes, likely because respondents assumed climate change was the driver regardless.

IV. These findings suggest that it will be difficult to generate public support for active management to support or hinder species’ redistribution, particularly for invertebrate or overlooked species. However, the positive attitudes suggest that on the whole range shifting species are viewed sympathetically. This may represent an opportunity to garner support for conservation actions which will

benefit both currently native and arriving species, such as improvements to habitat quality and connectivity.

4.2 Introduction

Anthropogenic drivers, including climate change, are causing species distributions to move rapidly (Pecl et al., 2017). The societal and ecological implications of these range-shifts will vary between different ecosystems, societies and stakeholders (Tebboth et al., 2020). The need for wildlife management to explicitly consider range shifting species is now pressing because the number of species moving is increasing rapidly (Elith, et al. 2010). In order to make effective management decisions, stakeholders will need to understand both the ecological and social effects of each range-shifter. Our understanding of the ecological consequences of range-shifting is still in its infancy but is growing. However, almost nothing is known about people's reactions to range-shifting species. Species perceived as harmful may face persecution, while those viewed as threatened may gain protection. Climate change's role in shaping these perceptions is unknown, as it is simultaneously a common driver of range-shift, an existential threat to humanity (Kim et al, 2014), and harmful to biodiversity (Newbold, 2018). This association could tarnish newly arriving species as dangerous "climate opportunists". On the other hand, climate change is anthropogenic in origin, therefore people could feel a moral responsibility to protect these 'ecological refugees' from the consequences of human actions.

The importance of public attitudes in shaping ecological outcomes has been demonstrated by research into biological invasions (Andreu et al., 2009), species reintroductions (Klich et al., 2018) and human-wildlife interactions (Baruch-Mordo et al., 2009). The Scottish government's campaign to lethally eradicate non-native hedgehogs from South Uist, subsequently provoking a coalition of opposed NGOs ("Uist Hedgehog Rescue"), provides a compelling example of how a failure to consider local attitudes can sabotage conservation objectives (Crowley et al., 2017). A better understanding of what shapes people's attitudes to species may help inform conservation strategies. For example, species that are viewed as charismatic could act as flagship species (Ma et al., 2016), leveraging public support for conservation of associated range-shifting species. Alternatively, species that are viewed negatively which may be more challenging to conserve, for example wasps (Sumner, Law, & Cini, 2018). Other species may pass beneath the public’s notice altogether, which could avoid concern, but could also make it more difficult to enact measures that promote or restrict their establishment. Of course, attitudes can vary greatly between human communities, and shift rapidly (Jones, et al. 2020). Therefore, establishing baselines in the attitudes and awareness of different stake-holder groups may help to inform future management strategies. For example, knowledge of negative attitudes could suggest initial education programs (Bath, 1989). And evidence of hardening attitudes might suggest a backlash against a particular management strategy and a possible need for review.

Investigating attitudes to range-shifters is timely (Naujokaitis-Lewis et al., 2018). The rate of climate change continues to accelerate, and it is uncertain how many species will be able to shift quickly enough to track their climatic niche across increasingly human-dominated landscapes (Schloss et al., 2012). This has led some scientists to advocate new and bold approaches, such as assisted translocation (Lunt et al., 2013). For species which require large-scale interventions, public attitudes are likely to be important, particularly in densely populated areas or where there is potential conflict (O’Rourke, 2014). In either scenario, the evidence strongly suggests that management is more effective when stakeholders are successfully engaged (Crowley et al., 2017; Redpath et al., 2013). Apart from the evidence for its efficacy, stakeholder engagement is a normative concern. Democratic governance relies on accountability to citizens and public opinion therefore forms an important input into legitimising decisions (Berry et al., 2019; Kiss, 2014).

Wildlife recorders are a key group with whom to engage when considering range-shifting species. We defined wildlife recorders as volunteers contributing to datasets of the times and locations of species occurrences, often as part of a local or national scheme. Recorders are often the first to both identify and report invasive species and also note the arrival of range-shifters (Brown et al., 2018). In addition, they provide much of the raw data underpinning conservation decisions in the UK (Pocock, Roy, Preston, & Roy, 2015). As such, wildlife recorders are a group likely to have greater awareness of range-shifts than the wider population, meaning that their attitudes may be more developed and better informed. Furthermore, recorders are interesting in their own right, as their attitudes could indicate their willingness to adapt their recording to better inform decision making on range-shift management. The UK provides a useful case-study, as it has a well-documented fauna and a very active volunteer recording community. There have also been a considerable number of arriving range-shifters over recent years (Gurney, 2015).

Many factors, aside from climate change, might influence wildlife recorders' attitudes to range-shifters. There is considerable evidence that taxonomic group has a strong effect on public attitudes, with most vertebrates being perceived more positively than most invertebrates, and there is a growing body of theory covering possible mechanisms (Troudet et al., 2017). Furthermore, recorders are a heterogeneous group (Dawson and Martin, 2015). Individuals' attitudes might also differ based on their personal attributes, including level of knowledge about range-shift or their views on the relationship between humans and nature (Sharp et al., 2011).

Our study explores how range-shifting species are viewed by wildlife recorders in the UK through an online survey. Specifically, we sought to learn how aware recorders were of different range-shifting species and whether they viewed range-shifters predominantly positively or negatively. We asked the extent to which the identity of the range-shifting species, and the attributes of respondents, affect attitudes. Finally, we asked what attitudes recorders expressed towards potential management of range-shifters / new arrivals, including both positive management aimed to help them establish and spread, and negative management to control or prevent arrival. This was coupled with additional thematic analysis of respondents' written answers that explained their attitudes to the species and their management as well as how they perceived climate change as affecting those attitudes. If attitudes are positive, then future management may be drawn towards assisting range-shifting species and it may be harder to protect recipient ecosystems from any that are harmful. On the other hand, negative attitudes could drive management to make it harder for threatened species to shift their ranges.

Our aim of better understanding the public perceptions of range-shift is advanced by this survey by addressing several research questions. We ask what attitudes wildlife recorders hold towards arriving range-shifters, hypothesizing that attitudes are likely to be positive, but that in the event of negative attitudes that our collected qualitative data will reveal negative attitudes to be motivated by concern for native wildlife. We further anticipate different attitudes depending on the species, moderated by the groups that respondents record, with familiar groups being viewed more positively. Through an improved understanding of this public's attitudes, and the drivers behind it to both range-shifters and their management we increase scientific knowledge on how range-shifters may be viewed as they spread across the globe and discuss the implications of these views for their management.

4.3 Methods

4.3.1 Survey participant selection

UK wildlife recorders' perspectives on range-shifting species were collected using the online survey software LimeSurvey (http://www.limesurvey.org). A targeted sampling strategy was used to maximise the response rate from our population of interest. A link to the survey was distributed to recorders using selected Facebook groups. These groups were identified using two methods. Initially, all schemes from the Biological Records Centre and British Trust for Ornithology affiliated bird clubs which had a detectable presence on Facebook were contacted. Secondly, Facebook groups were searched for using the following terms: "Field", "Natural History", "Naturalist" and "Record*". A link to the survey was also posted on the National Biodiversity Network website and in the National Forum for Biological Recorders newsletter. The survey design and administration for this study was approved by the College of Life and Environmental Sciences' Ethics Committee (Penryn) at the University of Exeter, reference eCORN000039. We ensured that respondent's informed consent was obtained before they participated. A full copy of the questionnaire is available in Appendix D, including the welcome page where respondents were provided with contact details for the lead researcher, the purpose of the study and a check box to indicate their consent to participate (Supp. Method D.1).

4.3.2 Survey design

Recording behaviour, level of knowledge and relationship with nature

Three questions were asked to characterise respondents' recording behaviour. First, respondents were asked which taxonomic groups they recorded from a checklist. Two questions then assessed the respondents' level of engagement: respondents were asked how long they had been sharing or submitting wildlife sightings or records, then respondents identified which recording activities they performed. This was treated as an ordered factor with four options: only sharing sightings informally (least engaged), submitting formal biological records, verifying records, and organising a recording scheme (most engaged). The maximum engagement level of each respondent was recorded.

Level of knowledge was analysed similarly to Verbrugge et al (2013): respondents were asked whether they had heard of any species establishing in the UK having arrived under their own powers of dispersal. It was clarified that this did not include human-introduced species. If confident, respondents were asked to name a naturally establishing species. Three response levels were recorded: no (0); yes, but couldn't name a correct example (1); yes, and named a correct example (2).

We characterised the respondent's relationship with nature using a shortened survey from (Verbrugge et al., 2013). This consisted of twelve Likert-type questions, with three testing each of four theoretical modes of relationship: master (humans stand above nature and can exploit if for their needs), steward (humans stand above nature but have a responsibility to preserve it), partner (humans and nature are separate entities which should work equally together to develop), and participant (humans are both biologically and spiritually part of nature, no dualistic ontology) outlined in (de Groot et al., 2011; de Groot and van den Born, 2003). We recorded the participant's mean score for each set of three questions testing the four modes of human-nature relationship. We interpreted the mode with the highest score as indicating the strongest alignment.

Respondents' age, gender, level of education and postcode were collected to contextualise the results and to help control sources of potential unknown variation. Employment in the wildlife sector was also included as it has been demonstrated to affect attitudes to species management in the literature on invasive and pest species (Bremner and Park, 2007).

Climate change experimental approach

In our experimental approach we either presented an image of a road sign against a neutral background displaying the term 'climate change' or a control image identical but displaying the word 'information' (Appendix D). Each image was accompanied with a brief explanation that new species were establishing in the UK, either referencing climate change (experimental treatment) or not (control). Respondents were then asked to write down the first word(s) or phrases which came to mind with climate change (experimental treatment) or species range-shift (control) (Appendix D). Later in the survey we asked respondents whether they thought that the arrival of species due to climate change had distinct management implications, compared to other drivers of range-shift.

Attitudes to species and their management

Each respondent was shown four species vignettes: two vertebrate and two invertebrate range-shifters selected at random from a pool of 16 animals (Supp. Table C.1). Vignettes were presented in a random order to avoid order effects (Auspurg and Jäckle, 2017). The vignette consisted of a header repeating the information shown previously in the climate change experimental treatment or control as appropriate, followed by an image of the species obtained from Flickr. We attempted to choose neutral images, where the subjects were at rest, in centre frame against natural backgrounds, similarly to Borgi and Cirulli (2015). We also presented the common and scientific species names, a written description of its appearance, its habitat preference and average body length in centimetres.

For each species, we asked respondents whether they had seen the species in the UK. They were then asked how they felt about the species establishing in the UK on a response scale of very negative (1) to very positive (7). Respondents were then presented with five different management actions for each species (Table 4.1), about which they rated their feelings along the same scale. Respondents could also write personal responses to the attitude and management questions, which we used for qualitative analysis.

Table 4.1: Management options for species presented to respondents.The common name in the vignette was used instead of the "Species X" placeholder.

Management Options
Remove: management should actively try to reduce "Species X" populations and if feasible remove them.
Mitigate: management should try to decrease "Species X" populations where possible and control them if not.
Non-Intervention: management of "Species X" should be avoided where possible and minimal where not.
Adapt: management should try to increase "Species X" populations where possible and conserve them if not.
Support: management should actively try to increase "Species X" populations and if feasible introduce them.

4.3.3 Statistical methods

We constructed a multinomial logit model in R (R Core Team, 2020) to describe respondent attitudes to arriving range-shifters and infer which factors affected those attitudes. Attitudes were collapsed into three categories: positive (original response = 5, 6 or 7), negative (original response = 1, 2 or 3), or neutral (original response = 4). We modelled these three categorical responses using a Bayesian multinomial model using the R package BRMS (Bürkner, 2018). We investigated the fixed effects of respondent gender, education, age, years recording, level of knowledge, employment in the wildlife sector, engagement with recording, the climate change experimental treatment and whether they had seen the species or if it was part of a group they recorded. We also included species and respondent as random effects.

To help regularise the model, all fixed effects were estimated using a horseshoe prior, this causes coefficients for parameters which predict the data least effectively to tend closer to 0, allowing the most informative parameter to be estimated more precisely. Following (Piironen and Vehtari, 2017) we determined the global scale parameter from an *a priori* assumption of the expected ratio of zero to non-zero coefficients. We chose 0.33, to balance model complexity against over-smoothing. The prior for the standard deviation of both random effects was weakly informative (Student's t, df = 3, mean = 0, scale = 2.5). Model convergence was assessed using visual examination of trace plots and the Gelman-Rubin diagnostics (Brooks and Gelman, 1998), which for all parameters was under 1.05. Bulk and tail estimated sample sizes were >1000 for all parameters. We followed the same process to model respondents' attitudes to the five different management options as a multivariate model, but we also included attitude to the species as a fixed effect. We report the posterior mean and lower (LCI) and upper (UCI) 95% credible intervals for all model parameters stated in the results.

4.3.4 Assessing the rationale underlying attitudes through thematic coding

We explored the written answers accompanying each quantitative question on attitudes in order to identify 'themes' in the underlying rationales which might explain respondents' attitudinal responses to range-shifters. Coding was carried out in NVivo 12 (QSR International, 1999) using an inductive approach to create a novel framework to describe the responses. In order to tie themes to attitudes, we had to adopt two approaches. For the question on attitudes to species we simply calculated, by theme or subtheme, the proportion of references (i.e. a given response to a question on a particular species) coded that came from a respondent with a positive, neutral, or negative attitude to that species. However, for the question on attitudes to species management, we had to classify respondents' attitudes into clusters due to the multidimensional nature of the question (5 management aspects), using Multiple Correspondence Analysis (MCA) (Rouanet and Le Roux, 2010). We then plotted the proportion of references coded that came from a respondent with a given attitude (1st question) or assigned cluster (2nd question) for each theme or sub-theme.

4.4 Results

4.4.1 Respondent characteristics

In total, 506 respondents clicked on the survey link and 315 continued to survey completion (median time to complete 21 mins). The respondents had a median age of 56 (Q1 = 44; Q3 = 63), older than the UK median (39), were significantly male biased compared to the 2011 UK population Census (63.5% male, Supp. Fig. C.1), and had attained higher levels of educational qualification than expected relative to the 2011 census (Supp. Fig. C.2). We found 98% of our respondents were aware of range-shifting species before taking the survey (Supp. Fig. C.3) and represented a spectrum of involvement with UK recording (Median years recording = 10, Q1 = 5, Q3 = 25, Supp. Fig. C.4). 40.6% of respondents self-identified as working in the wildlife sector. Respondents most strongly aligned with a ‘stewardship’ vision of nature (Stewardship = 241, Participant = 9, Partner = 3, Master = 1, Tied scores = 61). Respondents were distributed across the whole of the UK (Supp. Fig. C.5).

4.4.2 Wildlife recorders attitudes to range-shifting species

Respondents held positive attitudes to range-shifting species, with 60.2% being ‘a bit positive’ or more, 35.6% neutral, and only 4.2% ‘a bit negative’ or more (Figure 4.1). Results broken down by species and taxonomic groups showed that bird species were viewed most positively, followed by dragonflies; the shield bugs and the wasp (*D. saxonica*) were viewed least positively. However, even for *D. saxonica* the majority of people held a neutral rather than negative attitude (Supp. Fig. C.6).

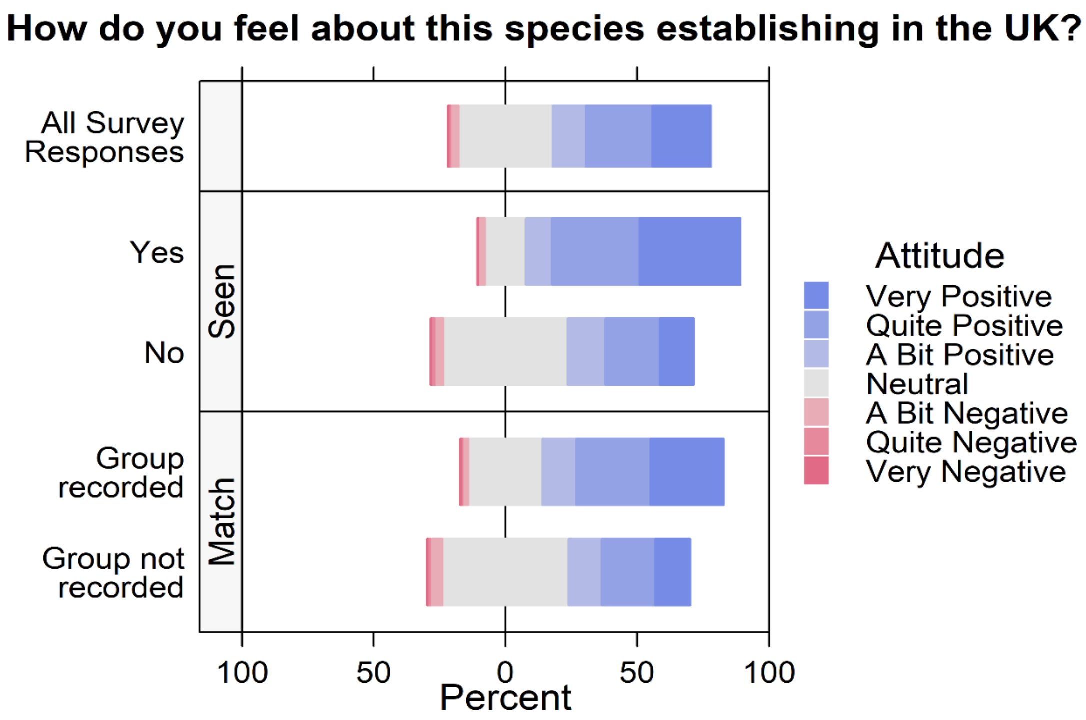


Figure 4.1: Respondent attitudes towards the establishment of new range-shifters in the UK. Positive attitudes are shown in blue, neutral in grey and negative in red. All responses are summarised at the top, responses below are split by those who had seen the range-shifter or not and those who did or did not habitually record that species' taxonomic group.

4.4.3 Factors and themes important to attitudes on range-shifting species

Only two factors were effective predictors of attitudes to range-shifting species. We found that when respondents had seen the species that they were being asked about (mean = 1.76, LCI = 0.34, UCI = 2.51) or when it was part of a group they were involved in recording (mean = 1.45, LCI = 0.87, UCI = 2.06) they were more likely to have a positive attitude towards it (Figure 4.2a). All other fixed effects (see Section 4.3.3 – Statistical Methods) in the converged model were small (95% credible intervals overlapped 0). However, the effect of respondent (Std. Dev. log-odds $_{\textit{positive vs negative response}}$ mean = 2.52, LCI =1.95, UCI = 3.15) and species (Std. Dev. log-odds $_{\textit{positive vs negative response}}$ mean = 1.53, LCI = 0.96, UCI = 2.40) were large relative to the effect of whether the species was in a recorded group or whether it had been seen,

Figure 4.2(b). All of our species groups were recorded by at least a third of recorders in our sample (Supp. Fig. C.7).

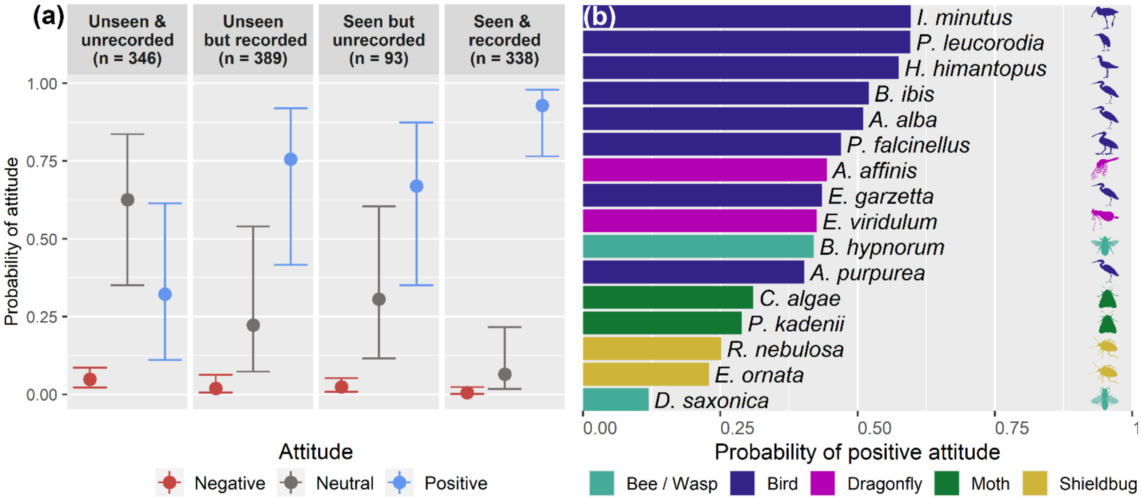


Figure 4.2(a): Predicted probability of a respondent's attitude to a species being a positive (blue), neutral (grey) or negative (red), depending on whether they had seen the species and whether it was in a taxonomic group they recorded. The point shows median posterior probability and errorbars 95% credible intervals. (b): Model estimates predicting probability of a respondent having a positive attitude for a species (coloured by taxonomic group) whilst controlling for other parameters.

4.4.4 Attitudes to management intervention either to promote or restrict range-shifting species

Wildlife recorders most favoured a non-interventionist approach, which was the only option with more positive attitudes (56.2%) than negative (8.6%) (Figure 4.3 and Supp. Fig. C.8). Adapting existing ecosystems to cope with range-shifters (P(Pro), mean = 0.26 LCI = 0.24, UCI= 0.29) was viewed more favourably than supporting range-shifters (P(Pro), mean = 0.13, LCI = 0.11, UCI= 0.15). There was less opposition to supporting range-shifters (P(Anti), LCI = 0.48, UCI = 0.53) than there was to controlling (P(Anti), mean = 0.71, LCI = 0.69, UCI= 0.74) or removing them (P(Anti), mean = 0.74, LCI = 0.72, UCI= 0.76). There was no difference in approval between mitigation and removal. Attitudes to management options for any given species were strongly related to the attitudes respondents held to the species themselves (Supp. Fig. C.9).

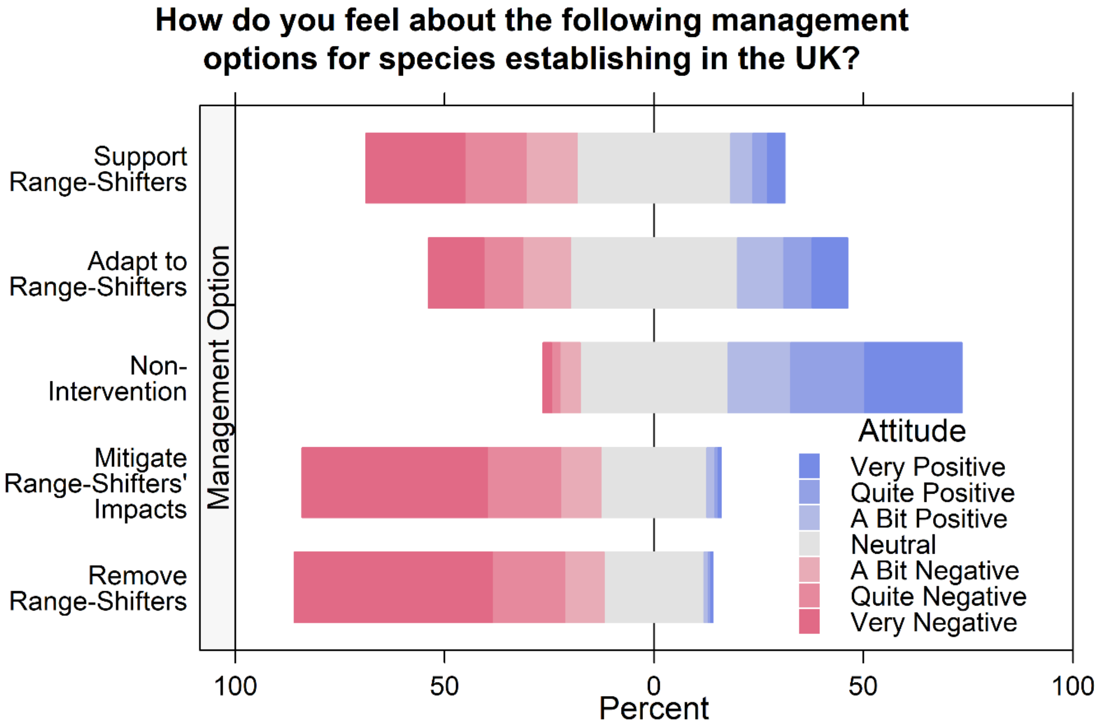

How do you feel about the following management options for species establishing in the UK?

Figure 4.3: Respondent attitudes to the five management options presented in full in Table 1, Attitudes are colour coded from very negative (dark pink) through neutral (grey) to very positive (dark blue).

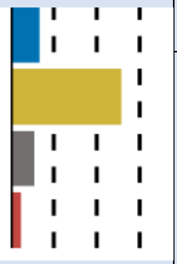
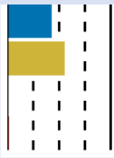
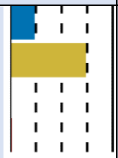
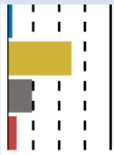
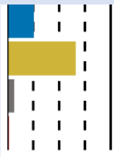
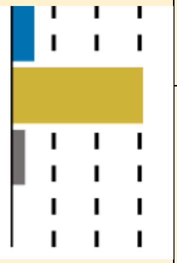
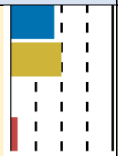
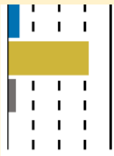
Multiple correspondence analysis allowed us to identify four clusters in the quantitative responses to questions about range-shifters management, and we interpret them as loosely representing four putative attitudes: range-shifter supporting, non-intervention, neutrality, and range-shifter wariness (Supp. Fig. C.10).

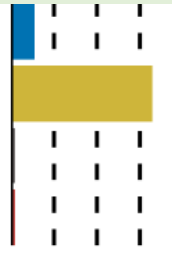
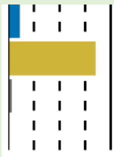
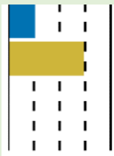
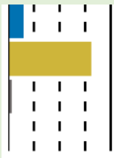
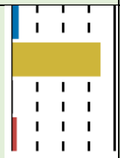
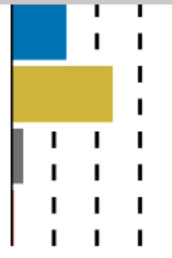
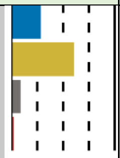
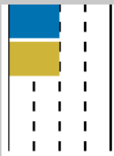
4.4.5 Emerging themes from qualitative analysis surrounding attitudes to range shift

Our thematic coding of the free text responses highlighted several recurring themes in our respondents' answers. We identified four themes which cut across both respondents' explanations for their attitudes to the species themselves (Supp. Table C.2) and their attitudes to species management (Table 4.2). However, the prevalence of each theme differed, and different sub-themes were identified for attitudes to species themselves and their management. With respect to attitudes to species, the most common theme was the potential direct costs and benefits of the arriving species, both socio-economic and ecological. There was a strong emphasis on social benefits here, often related to personal experiences. The second most recurrent theme was that of generalised principles about human intervention in nature and whether these range-shifters were arriving "naturally". Some respondents noted a mixed feeling: they felt positive about the species' establishment but worried about its perceived anthropogenic driver – climate change. The third theme, which only appeared infrequently for this question, was the respondents' perceived feasibility of managing range-shifters. The final theme was nativeness, where some respondents argued that native species should be prioritised over range-shifters.

With respect to species management, the most common theme was the species' costs and benefits. However, unlike responses on species themselves, respondents raised the potential costs of range-shifting species and most stated that they would consider management if range-shifters caused negative impacts. Those who thought range-shifters could have a positive impact were more likely to be range-shift supporters, while those who thought that a negative impact was possible were more likely to be neutral (Table 4.1). The theme around human intervention in nature was expressed more commonly in relation to management than to species themselves, revolving around ideas of letting a range-shifter develop its own path naturally without management. Animal rights emerged as a minor subtheme within this theme. The theme of costs and benefits of management action received attention, with considerable scepticism of the potential efficacy of management. On nativeness, there was a majority view that management should protect native species over range-shifters. However, a minority argued that all arriving range-shifters should be viewed as native and any negative impacts should be managed like those of any problematic native.

Table 4.2: Coding framework applied to responses to the question on range-shifters' management (see Table 4.1), each illustrated by a quote. RC indicates the number of references coded. The bar chart accompanying each theme and subtheme shows the percentage of references coded that were from each cluster of respondents (identified in the MCA) within each theme (support range-shifters = blue, non-intervention = yellow; neutral = grey, wary of range-shifters = red. Dashed lines show intervals of 25%).

Theme	Sub-theme	Summary	Example Quote
Cost/Benefit ratio from arrival of range-shifters  RC = 539	Positive effects on recipient ecosystems  RC=51	Range-shifters will affect the recipient ecosystem positively, via both ecological (e.g. more resilience) and social (e.g. eco-tourism) mechanisms.	"Climate change may mean native species can no longer tolerate conditions so better to have a replacement species rather than none"
	Minimal effects on recipient ecosystems  RC=150	Range-shifters will have minimal effects, either positive or negative, on the recipient ecosystem.	"There is no reason to control this species since it is not harmful."
	Negative effects on recipient ecosystems  RC=273	Range-shifters are perceived as having potentially negative effects on the recipient ecosystem, with a focus on risk rather than proven effects.	"As a non native species with potential to become invasive (I would assume) they shouldn't be actively encouraged to establish."
	Conservation status of the range-shifter  RC=65	Threatened range-shifters deserve conservation assistance, actions to promote the global conservation of a species are important.	"Species specific actions should only be prioritised against species that are threatened."
Human intervention in nature  (RC = 274)	Animals' rights  RC=14	Management must respect the rights of sentient creatures to exist.	"Every living thing has the right not to be persecuted."
	Allowing nature to take its course is preferable to human intervention.  RC=260	Allowing natural processes to shape range-shifts will result in better outcomes than trying to manage them directly.	"Let things alone and Mother Nature will look after itself without any interference"

Cost/Benefit ratio of management actions  RC = 197	Management to control range-shifters will have negative ecological costs  RC=27	Management to control range-shifters will have associated negative effects on the recipient ecosystem, e.g. insecticide use.	"It seems likely that reduction by 'management' would have unforeseen undesirable implications for other species."
	Management to help range-shifters will have additional positive benefits  RC=23	Management to help range-shifting species will have additional positive effects on the recipient ecosystem, e.g. habitat improvement.	"Providing habitat for these colonisers often provides much needed habitat for other struggling UK species."
	Management to assist range-shifters gives no additional benefit  RC=90	Management to assist range-shifters establish will not convey any additional benefit to the chances of establishment success.	"There is no need to actively conserve / increase the species as it is spreading naturally and numbers are rising."
	Management to reduce risk from range-shifters is too difficult  RC=57	Management attempts to control range-shifters will be very expensive and ineffective, or infeasible.	"I suspect it's pretty impossible to do anything to stop (or help) this species."
Nativeness  RC = 57	Natives should be prioritised for support  RC=46	Native species should be our priority. We should conserve native species rather than support range-shifters.	"I think we should be focusing our conservation efforts on our native species first"
	Range-shifters should be managed as if they were native  RC=11	There should be no difference in treatment from native species as arrival of range-shifters is "natural" so they should be equal.	"As they arrived of their own accord might as well be considered native and managed as native wildlife"

With respect to whether respondents thought that a causal effect of climate change on species range-shifts had implications for management we found a range of perspectives (Supp. Table C.3). Some respondents thought that climate-driven range-shifters deserved specific attention as they: a) might be losing range elsewhere; b) would be important for future climate adaptation, and c) due to a moral responsibility arising from humanity's culpability for climate change as "they are being pushed out of their range, and it's our fault!". A similar number of respondents thought that management to restrict climate-driven range-shifters was futile, arguing that the focus should be on the climate change "cause" not the species “symptoms”; preventing the arrival of even harmful species was too difficult and, even though climate change was anthropogenic, the species dispersal response to it was natural and should be accepted:

> *“I think that this is a paradox as global warming is a direct result of human impact yet in species colonisation context[s] humans should stay out of it.”*

Finally, around a third of references coded suggested that climate change was not the most important factor in forming a management response to these species. Instead, these participants thought that the impact of range-shifting species on the recipient ecosystem should shape the response, or that people’s responsibility is to protect biodiversity as a whole rather than to focus on specific cases.

4.5 Discussion

This study aimed to discover how range-shifting species are viewed by wildlife recorders in the UK. We found that awareness of the presence of range-shifting species was high. Moreover, most recorders had positive attitudes towards these species establishing. Both the species in question and recorder familiarity with the species predicted recorders’ attitudes to its establishment. However, this positivity did not manifest as favouring active forms of management to assist establishment. Instead, most recorders favoured non-intervention in the range-shift process. Recorders were also strongly against efforts to hinder range-shift.

These positive responses indicate that wildlife recorders value range-shifters. The sources of this value emerged in the qualitative comments. Many respondents talked about personal experiences with the species, for example “fabulous bird, what a joy to see them”, others about ecosystem services (principally pollination) and reduced extinction risk (Supp. Table C.2). This value suggests that people perceive socio-ecological benefits from the arrival of range-shifters.

The variation that we found amongst recorders’ attitudes towards different species suggests that there will be winners and losers in the battle for positive public reception. This finding supports the existing literature on taxonomic biases which finds that invertebrates are often perceived more negatively than vertebrates when considering reintroductions (Seddon et al, 2005) and invasions (Bremner and Park, 2007). This effect is lessened for aesthetically attractive species like dragonflies and butterflies (Shipley and Bixler, 2017), as we found.

In fact, it is perhaps surprising that attitudes were mostly neutral rather than negative for less aesthetic invertebrates. This probably reflects recorders' desire for further information on which to base their judgements. Their opinions were often balanced, for instance recognising that some scary or unpopular species such as wasps also provided important ecosystem services such as pest control. This more reserved stance is unlikely to be shared by less informed groups. Species charisma has been shown to be very influential in both the management and spread of invasive species (Jaric et al., 2020) and our results suggest that this may also be the case for range-shifters. Further research could refine the attributes to which people are responding in distinguishing better and less popular species, so as to better inform management decisions. For instance, by highlighting which harmful species would be likely to represent a risk of public resentment against control efforts or, conversely, which species might be used to attract funding or public engagement.

Our results may not generalise to less ecologically informed publics or other demographic groups (Supp. Fig. C.4). In the future, it would be useful to compare these results with those of other stakeholders, such as landowners, land-managers, and scientists to better understand potential differences. The UK is an outlier compared to most countries in its human population density and GDP. Evidence suggests that more established economies have greater environmental concern (Franzen and Vogl, 2013) and distance to wildlife (mediated by population density) also affects attitudes (Karlsson and Sjöström, 2007). Therefore, it would be valuable to compare how attitudes might vary across different regions, including developing countries with less influential conservation movements. The possibility of a defensive 'island mentality" from the presence of a geographic barrier (such as the English Channel) may also create more negative attitudes to range-shift than in more connected regions like North America or mainland Europe.

Our finding that participants were more positive about species with which they had some experience suggests that familiarity can make it easier to mobilise support. Public engagement, through recording or events such as BioBlitz, may therefore be a powerful tool to increase positive public opinion (Postles and Bartlett, 2018). We interpreted both having seen the species and recording the species' taxonomic group as linking to the same latent construct: familiarity. This is important as familiarity is unlikely to have a fixed relationship with attitude over time. For example, as Lynx continue re-establishing in Eastern Europe, attitudes to them appeared to have worsened as they became more abundant and more negative impacts appeared (Červený, et al. 2019). Similarly, changes have occurred in the case of non-native parakeets establishing in the UK, with some groups hardening views as impacts emerge and some growing more tolerant as the parakeets integrate into their sense of place (Crowley *et al*, 2019). Future studies will be needed to investigate how attitudes may change over time and the extent to which familiarity might mediate these changes to produce complex dynamics. As well as range-shifters, the number of invasive alien species establishing is forecast to increase with climate change (Beaury et al., 2020). Wildlife recorders appeared able to distinguish these two different but related phenomena, but it may be that attitudes towards them could interact with each other. The relationship between attitudes to invasive species and attitudes to range-shifting species may be an important area of future research. The effects on attitudes found where the species matched the recorders' group of interest or had been seen by them might not have been mediated by familiarity but rather by other intermediate factors, such as physical proximity, species abundance, recorder behaviour or positive interactions leading to differing affective relationships (Lorimer, 2007). However, our first interpretation is supported by the qualitative data's emphasis on personal experience.

The climate change experimental treatment did not affect respondents' attitudes. This ties into the thematic analysis (Supp. Table C.3), where we saw 40 respondents argue that the focus should be on species impacts rather than cause of arrival, echoing previous research on attitudes towards invasive species (de Wal et al., 2015). However, it is also possible that the experimental treatment was ineffective as most respondents attributed range-shift to climate change, with or without the prompt. This interpretation is supported by the text responses given to the control treatment where there were frequent references to climate change without any prompt (Supp. Fig. C.11 The significant remaining individual variation in attitudes in our models hints that the complexity in predicting responses may be derived from highly personal factors such as individuals' belief systems.

Disentangling these factors is likely to require a mixed of quantitative and qualitative approaches. In addition researchers will need to recognize the subjectivity that they bring to their studies and implement approaches to account for this in research practices (Brittain et al., 2020). We suggest that more direct metrics such as risk perception (Taylor, Dessai, & Bruine de Bruin, 2014) and views on the ‘dynamism vs balance of nature’ (Ladle & Gillson, 2008) may be a productive avenue in future research exploring individual variation. For applied regional studies, the local contexts and respondents’ sense of place may also be important (Masterson et al., 2017). Understanding the different lenses with which people view range-shifting species would allow bespoke communications to different stakeholders and potentially a predictive model for potential for conflict (McCleery, 2009).

The metrics we used to categorise respondents’ engagement with recording had little apparent effect on attitudes, though this could be because small differences were not detectable with our obtained sample size. Our study focused solely on wildlife recorders and there are likely to be differences between our findings for this group and the views of other publics. An important distinction is that wildlife recorders are likely to be more scientifically aware of nature than the general public (Figure S4). Therefore, they may be more likely to hold views on range-shifting species, one way or the other compared to others who have not previously considered the issue. Even if the latter use and enjoy the same natural spaces, other public groups may be more likely to draw from more indirect material when forming their opinions such as media articles or attitudes to wildlife in general (Brossard and Nisbet, 2007). Wildlife recorders may also be more aware of the ecological roles of less popular species like wasps and therefore happier to tolerate arriving range-shifters (Schönfelder and Bogner, 2017). Most wildlife recorders in our sample aligned with “stewardship” in their relationship with nature and other alignments might indicate different attitudes towards range-shifters. For example, we could imagine supporters of “compassionate conservation” such as animal rights activists taking a stronger stand against controlling harmful arrivals, or against assisted translocation if it were seen to compromise welfare (Callen et al., 2020; Griffin et al., 2020). Those who derive payment from ecosystem services such as developers or farmers could seek to incorporate these species into such schemes such as biodiversity offsets with ramifications for broader conservation.

The strong relation between attitudes to species and to their management is intuitive but not inevitable (Lindemann-Matthies, 2016). The demonstration of this relationship shows that changing views of species are likely to have knock-on effects on management through changes in public support. However, our study did not cover all management scenarios and some information that could have informed respondents' attitudes towards management was not available, for example estimates of cost, feasibility, effectiveness, species impact and welfare implications. It will be important to investigate in the future how these self-reported attitudes translate when respondents are given more detailed scenarios, or real case-studies. But there is some evidence that experimental surveys such as this can align well with real world behaviour (Hainmueller *et al*, 2015).

The predominance of support for non-intervention echoes Ohsawa and Jones (2017) who found a majority of surveyed park managers preferred not to intervene at the prospect of species range-shifting through the Japanese archipelago. However, our finding of support for the non-interventionist management option is striking as it sits at odds with the typical style of conservation management in the UK, which is frequently characterised as interventionist (Adams, 1997). It leads us to suggest the finding that most respondents expressed a 'stewardship' relationship with nature could be further deconstructed in the future into two more precisely defined 'stewardship'-type relationships. The first more traditional aspect of stewardship is the archetype of the pragmatist farmer-manager who inventories and actively supervises nature. The second is a more passive stewardship, protecting nature as its own agent for future generations. The thematic analysis suggests that respondents' preferences for non-intervention could be aligned to both of these aspects of stewardship. Many aligned with the pragmatic stewardship approach, believing that intervention would be ineffective and "there is no point being like King Cnut and trying to hold the tide back" and seeing "no need to throw money into trying to increase numbers of a naturally increasing species". Others aligned with the more passive process-orientated view of stewardship, emphasising the importance of allowing "nature" to choose its own path, espousing "Nature ebbs and flows, … - that's just how it is", and "if we intervine (sic) then it is being farmed". The prevalence of passive stewardship ideals, in contrast to the UK's typical pragmatic style of conservation, could be linked to the increasing discourse around rewilding and a desire to reduce the intensity of management (Root-Bernstein *et al*, 2018). A need for wild agency emerges from another comment on range-shifting little egrets:

“No huge sums of money thrown at them, none of this rubbish as per White Storks at Knepp or Ospreys at Rutland - this was the real deal, they colonised by themselves”

Finally, rather than indicating a pragmatic or passive stewardship perspective a preference, support for non-intervention could represent a non-committal “sitting on the fence” option. This interpretation is supported by qualitative responses from respondents who feel they lack necessary information to make a decision at this time (Sturgis *et al*, 2014). Untangling these perspectives and their prevalence will help conservationists to understand the public mood in their management of range-shifters.

The lack of support for interventions to support range-shifters could hinder future attempts to translocate species that are unable to move fast enough to track their climatic niche. A previous study on assisted translocation found opposition to transporting species outside their current ranges amongst the British Columbian public (Peterson St-Laurent *et al*, 2018). In both Peterson’s and our qualitative results (where respondents indicated they were aware of past presence), interventions to reintroduce locally extinct species were not opposed. In our study, attitudes to management often favoured native species over range-shifters when there was a conflict, for example: “If it's [the range-shifter is] having a deleterious effect on native wildlife then I would support action against it”. We interpret this attitude as an aspect of a “balance of nature” paradigm, where respondents feel we should protect the natural world from anthropogenic change (a common belief expressed by our respondents, Table 2). However, this paradigm contains implicit value judgements often using a fixed historical baseline as pointed out by another respondent; “There is an innate compulsion to resist change, to turn the clock back, to control and label species as good or bad”. Conservationists may therefore need to communicate more clearly the alternate paradigm of chaotic, dynamic nature, which is now relatively widespread in academia (Wu and Loucks, 1995) but may be less prevalent amongst recorders and the wider public. Recognition of this dynamism will be vital to allow range-shifts to protect vulnerable species from extinction while mitigating the threat to endangered natives (Scheffers and Pecl, 2019).

The opposition to measures to remove range-shifters (Figure 4.3) superficially suggests that managers may face opposition if they take such action. However, the text responses elucidate this feeling as being contingent on the perception that range-shifters pose little threat. Many respondents were willing to intervene if a threat became apparent. This focus on demonstrated threat appears in conflict with the precautionary principle often invoked with respect to invasion , i.e. better not to introduce taxa just in case there is a risk (Finnoff *et al*, 2007). This suggests that respondents perceive the threat range-shifters pose to recipient ecosystems is lower than the perceived benefits of action, and points to the need for urgent research into such threats. Respondents favoured adapting recipient ecosystems more than controlling range-shifters themselves, thus they might be more supportive of management if presented with information on vulnerability of recipient ecosystems rather than the riskiness of range-shifters.

In summary, we found that wildlife recorders viewed range-shifters more as vulnerable ecological refugees than as threatening climate opportunists. However, they were willing to shift their opinions in response to evidence of harm to native species. These findings form an important benchmark to measure future changes and to make comparisons to other areas and populations. They could also form the basis for future scenario planning for policy makers. The strong support for non-interventionist management should provoke consideration amongst conservationists on their management approaches. These attitudes also indicate a need for stronger scientific advocacy for vulnerable species of minimal risk – if, in the future, conserving them requires active measures including assisted translocation.

Chapter 5: General Discussion

5.1 Introduction

5.1.1 Revisiting thesis aims

In Chapter 1:, I laid out three key research gaps in our understanding of species redistribution. First, I argued that while we have many predictive models of range-shift but have few examples of these being applied and tested against recent range-shifts. Without testing and refining theoretical models, we will not be able to evaluate their usefulness or validity until we have the full benefit of hindsight. I suggested in particular that deepening our understanding of the roles of climate, habitat and movement processes would contribute to a better understanding of recent species range expansions.

Second, I suggested that we lack a framework to evaluate the consequences of range-shifting species for the ecosystems into which they are arriving. I acknowledged that as well as potential risks there might be prospective benefits but suggested that until these were better understood a pragmatic approach was to monitor range-shifters' effects on a per species basis. I argued that given limited resources, a useful tool to do this would be a modelling approach able to exploit widely available occurrence data and sufficiently flexible to work across different spatial scales.

Finally, I echoed (Bonebrake et al., 2018)'s call that responding to species redistribution will require integration of both ecological and social sciences. I argue that while there is an increasing amount of ecological research on range-shift consequences, and the feasibility of managing them, there are few examples of this literature engaging with societal perceptions of range-shift. I contend in particular that understanding public attitudes to range-shift will be crucial for charting future scenarios down which range-shifts may progress.

5.1.2 Summary of findings

In Chapter 2:, I explored the species redistribution process and found that climate cSDMs were poor predictors for newly arrived range-shifters distributions in the UK, and so also were habitat suitability and proximity to source populations. This could be partially explained by contingent absences; that is, that these species have not yet dispersed to reach all climatically suitable areas in the UK. However, the absence of a strong relationship between the species' time since arrival and number of occupied cells suggests that more complex processes may be shaping the species' redistribution.

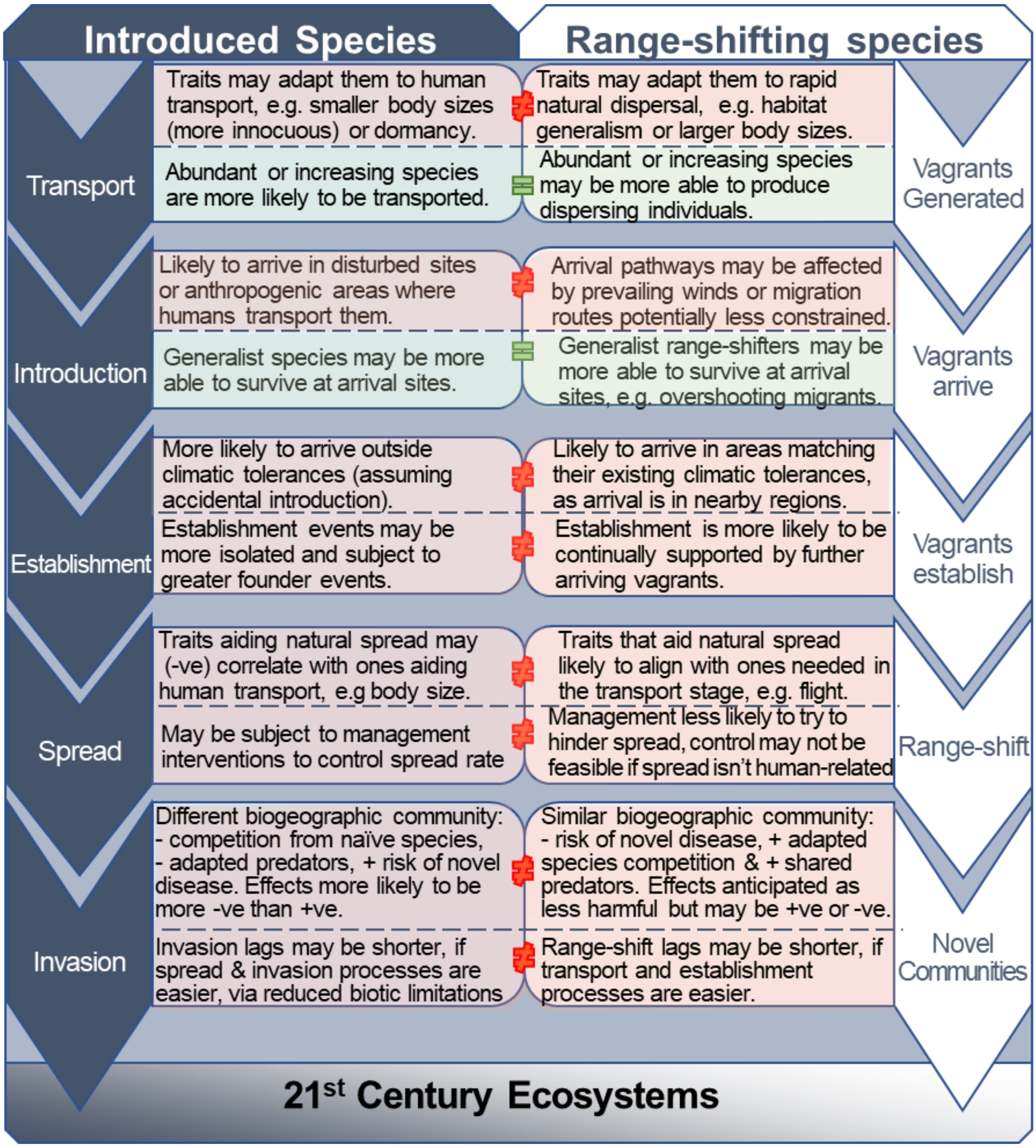
In Chapter 3:, I looked at the consequences of range-shift. Overall, there was no strong pattern of negative associations between the arrival of a range-shifting damselfly, *Erythromma viridulum*, and currently native species. Most species had slightly positive or indeterminate associations. Only two native species had a negative association, including the range-shifters' congener, *E. najas*. While this is positive news from a conservation perspective, a caveat is that these findings can be interpreted in at least three ways. First, habitat quality or another unmeasured variable may be positively correlated with the probability of both native persistence and range-shifter arrival. Second, range-expansions of the native species may be creating ephemeral populations outside the core range areas where the natives and range-shifter overlap. And third, it is possible that there are genuine facilitative interactions by a currently undetermined mechanism.

In Chapter 4:, I investigated perceptions of range-shift. Wildlife recorders viewed range-shifting species positively but were averse to managing for or against them. Whether the range shift was attributed to climate change did not seem to influence respondents' attitudes to either the species or its management. However, there were considerable differences in perceptions of different taxa, with preference shown for charismatic vertebrates. The qualitative data showed that respondents preferred to let "nature take its course" unless a native species or human interests were threatened.

5.2 Thesis implications for future research on range-shift processes

5.2.1 Probabilistic models of species occurrence conflate multiple range-shift processes

In my thesis introduction, I suggested in section 1.2.2 that a difficulty for understanding range-shifts was that the initial founder events, when a range-shifter is still a "vagrant", are quite stochastic (Wood et al., 2016). However, once a species is an established breeder we have a much better deterministic understanding of how it might spread, i.e. waders are likely to be found spreading to other estuaries, rather than woodlands, but which river they might arrive on may be very challenging to anticipate. In other words, the range-shift process involves multiple steps that may vary in predictability. Occurrence data may be sufficient to track the later stages of range-shift but is unlikely to be as useful in the more stochastic initial stages. A useful model to compare the multistage range-shift process to is the invasion pathway, as discussed by Hoffmann and Courchamp, (2016);(Figure 5.1).



Traits may adapt them to human transport, e.g. smaller body sizes (more innocuous) or dormancy.

Traits may adapt them to rapid natural dispersal, e.g. habitat generalism or larger body sizes.

Abundant or increasing species are more likely to be transported.

Abundant or increasing species may be more able to produce dispersing individuals.

Likely to arrive in disturbed sites or anthropogenic areas where humans transport them.

Arrival pathways may be affected by prevailing winds or migration routes potentially less constrained.

Generalist species may be more able to survive at arrival sites.

Generalist range-shifters may be more able to survive at arrival sites, e.g. overshooting migrants.

More likely to arrive outside climatic tolerances (assuming accidental introduction).

Likely to arrive in areas matching their existing climatic tolerances, as arrival is in nearby regions.

Establishment events may be more isolated and subject to greater founder events.

Establishment is more likely to be continually supported by further arriving vagrants.

Traits aiding natural spread may (-ve) correlate with ones aiding human transport, e.g body size.

Traits that aid natural spread likely to align with ones needed in the transport stage, e.g. flight.

May be subject to management interventions to control spread rate

Management less likely to try to hinder spread, control may not be feasible if spread isn't human-related

Different biogeographic community:
- competition from naïve species,
- adapted predators, + risk of novel disease. Effects more likely to be more -ve than +ve.

Similar biogeographic community:
- risk of novel disease, + adapted species competition & + shared predators. Effects anticipated as less harmful but may be +ve or -ve.

Invasion lags may be shorter, if spread & invasion processes are easier, via reduced biotic limitations

Range-shift lags may be shorter, if transport and establishment processes are easier.

Figure 5.1: Blackburn et al. (2011)'s invasion pathway compared to range-shift. I highlight important potential differences (red) and similarities (green) between the two pathways at each stage and link these differences to potential divergence in ecological outcomes.

5.2.2 Using occurrence data to disentangle elements of the range-shift process

Implications for future study of climate's effects on range-shifts

My climate cSDMs anticipated large areas of Britain climatically suitable for range-shifters which were not present at those sites (possibly due to movement processes - see below). This finding is interesting because it does not match an assumption that it is climate which limits these range-shifting species from establishing in the UK (which anecdotally appears to be a dominant media narrative). If this is the case, it suggests further research is needed on how climate limits species from shifting and what other factors may be involved, such as biotic interactions or population variability (Section 5.2.3). An important area to explore may be historic data to understand the extent to which the European range that our models were based on could be assumed to be at equilibrium with climate (Faurby and Araújo, 2018; Tingley and Beissinger, 2009; Vellend et al., 2013). Another aspect that could be related is whether the temporal scale of the climatic modelling was well matched to the available range-shift data. For example, climate extremes were not captured by my chosen climate variables, and it may be these which restrict range-shifters in poleward areas (Barton et al., 2019; Lynch et al., 2014). Mechanistic data on thermal tolerances may complement efforts to model current range-shifters by helping to solidify which species are limited by climate and where (i.e. where extremes in climate may exceed thermal tolerances), thus helping to estimate how much any remaining observed deviations may be attributable to other factors (Birkett et al., 2018).

Movement processes as an explanation for poor specificity in the novel range

One plausible reason for a lack of specificity in climate suitability projections is dispersal limitations. Future research could focus on how movement processes might be incorporated into the study of the range-shift process (Boulangeat et al., 2012). Our understanding of the factors limiting a species as it range-shifts will increase if we are able to distinguish otherwise suitable sites in the novel range which the range-shifter cannot or is very unlikely to be able to reach. To tackle this issue, further empirical research on dispersal could be fruitful, and new technologies such as insect flight mills (Robinet et al., 2019), entomological radar (Hüppop et al., 2019), and GPS and related telemetry techniques (Walton et al., 2018), may help us to achieve real world estimates of species dispersal. Figure 5.1 suggests that studies of the native range may also be helpful for understanding which areas are more probable sites of initial establishment. While these estimates may be more uncertain, they may improve understanding of where range-shifts will occur over short time scales. This could encompass looking at wind directions which are used by insects for long distance dispersal (Siljamo et al., 2020) and when these relate to peak abundances and dispersive events in the native range (Chapman et al., 2010). How such patterns may alter with ongoing climate change is also relevant to unravelling these first establishment events (Kling and Ackerly, 2020). Models may be able to exploit this data by incorporating mechanistic components such as dispersal kernels (Robinet et al., 2009) or even more complex processes such as Allee effects (Drake and Lodge, 2006; Roques et al., 2008), (Allee effects necessitate a certain number of individuals to be present before establishment can occur and hence is mediated by dispersal).

Implications for future study of habitat’s effects on range-shifts

Habitat is a particularly key factor when considering range-shift as, unlike climate, it can be directly managed and improved (Milsom et al., 2000), to create space for range-shifters. However, our findings suggest that, at least at the broad level associations we used it was not particularly useful for anticipating where range-shifters had established. As with climate, this could be partially attributed to dispersal limitations but there are several further interpretations to consider.

Firstly, habitat itself is an ill-defined construct with various conceptualisations, representing a mix of characteristically present species (e.g. eel grass beds) and hence biotic interactions, microclimates and other abiotic factors such as drainage, topography and soil chemistry (Turlure et al., 2019). Available data meant that it was necessary to relate species to habitat via using quite a coars categorisation of landcover as a proxy (Redhead et al., 2016), for example both a spruce plantation and an ancient scots pine forest would be mapped as coniferous forest landcover, despite being potentially very different in their ecological suitability for a given range-shifter (Tomaselli et al., 2013). This issue is compounded by a lack of internationally aligned fine-scale class definitions for habitat. This increases the difficulty of relating habitat classification between different administrative areas making it challenging to identify the full range of potentially suitable habitat. For example, heather grassland in the UK LCM2015

(Rowland, 2017) does not map clearly to any of the landcover categories in the EU Corine Landcover 2018 map. In the future, we may need to consider habitat more directly from the perspective of species, e.g. a species requiring riparian woodland will be more challenging to model if habitat classes include only forest or freshwater rather than a more precisely matched habitat class. Future attempts to incorporate the work done by the IUCN habitat classification scheme to standardize and refine habitat classification could benefit the study of redistribution (Jung et al., 2020).

Secondly, species habitat preferences may not be consistent in space or time. For example, the Duke of Burgundy butterfly (*Hamearis lucina*) was historically associated with woodland but now is found through more open habitats (Hayes et al., 2018). Across the range, species may occupy less restricted habitats in the range core than at the range edge, indicating a possible interaction between habitat quality and thermal tolerance (Pearce-Higgins et al., 2008). The degree of habitat fragmentation might also drive this pattern (Guo et al., 2005). We also have to consider that species habitat “preferences” may reflect displacement from optimal habitat onto more marginal areas due to anthropogenic pressures (Faurby and Araújo, 2018). For these reasons, habitat data should ideally be collected alongside occurrence data in the novel range (avoiding the space-for-time assumption). By verifying in high spatial resolution the habitat, a species is actually using when an occurrence is reported, changes in preferences can be identified more rapidly. In addition, when using habitat classes in cSDMs, habitat associations could first be more mechanistically explored (Meineri et al., 2015) to verify their biological realism as a constraint on the species range. For example, is habitat acting as a proxy for specialist needs such as the presence of a key host plant? Or is that the habitat may reflect a more general need? E.g. for nesting sites for birds, coniferous plantations may be as good (for some species), as other woodland or at least represent a smaller reduction in habitat suitability than in the scenario described for the specialist species.

5.2.3 Future research directions on the range-shift process

Occurrence data may miss the effects of population variability on range-shift processes

Species range-shift is an emergent property of the movement of populations, individuals and ultimately genes. There can be considerable intraspecific population variability in range-limiting traits, e.g. thermal tolerances (Tonione et al., 2020). Thus, individuals from a particular population might not be able to persist in all of the locations occupied by that species. Evidence of local adaptation appears frequently in populations (Aitken and Whitlock, 2013; Moran et al., 2016), and affects considerations of range-shift. Climatic limitations of locally adapted populations may need to be modelled rather than assuming fixed climatic tolerances across the species' range (Peterson et al., 2019). Though population climate limitations should all nest within the species' overall limitations (Journé et al., 2020), geographic or climate barriers (Burrows et al., 2014; Butikofer et al., 2020) could mean that the most climatically adapted population to range-shift is not in fact the population at the range-front. Failing to recognise genetic variability is also important because understanding starting genetic population structure is vital for knowing how it might change during range-shifts. Evidence shows significant genetic changes can occur over range-shifts (Rehm et al., 2015), perhaps adaptively with regards to shift (Dudaniec et al., 2018; Therry et al., 2014).

Do species traits matter for range-shifts and if so which ones?

The discussion above of population variability in traits relating to climatic and habitat tolerances as well as movement processes suggests a renewed focus on how these may be predictable without detailed study. The invasion literature has grappled extensively with this problem through attempts to identify ecological traits which predict invasiveness (Van Kleunen et al., 2010). Similar research has focused on traits associated with successful range-shift. Interestingly, it appeared that habitat generalism rather than dispersal ability better predicted how well species were able to shift (Estrada et al., 2016). As I explored above, both habitat generalism and dispersal ability may be challenging to define. So work to standardise terminology and approaches to describe traits may be necessary to disentangle traits before applying them to predicting how and at what rate a species may range-shift. While there are many traits of potential interest, I choose to highlight two areas. First, a focus on behavioural traits for more complex animals such as vertebrates might help us to understand the likelihood of success in the establishment phase. For example, site and mate fidelity may shape Allee effects that species have to overcome to establish (Roques et al., 2008; Walter et al., 2017). Second, plasticity, a trait that is likely to be crucial for invertebrates, for example in insects the proportion of long-winged to short-winged individuals will mediate dispersal rates. Plasticity creates trade-offs for organisms at range fronts, for instance between dispersal ability and competitiveness, which may affect how they spread. Potential evolutionary traps might exist (Hale et al., 2016), for example Odonata have been shown to evolve greater dispersal ability but with compromised immune and pesticide resistance, leaving them at risk of possible impacts in the future (Dinh et al., 2016; Therry et al., 2014). Traits are likely to continue being an important research area as a resource-efficient way to attempt to predict intraspecific and inter-specific variation in the range-shift process, as increasing amounts of trait data become aggregated in global databases, including historic trait data facilitate by the digitisation of museum collections.

Biotic interactions could facilitate or constrain species ranges

As well as intraspecific traits such as vulnerability to Allee effects, interspecific interactions are another important area to consider more explicitly (Zurell et al., 2018). Biotic interactions may limit species ranges. For example, parasitoids and many herbivorous insects will require their host species and hostplants respectively (Smith et al., 2007; Thierry et al., 2019). If we fail to account for limiting interactions in the host range, we might underpredict the areas to which range-shifters may be able to expand (Svenning et al., 2014; Early and Keith, 2019). However, biotic interactions might also extend species ranges. An interesting parallel to consider range shift against is the concept of “invasive meltdown”, which suggests that the resilience of an ecosystem to resist invaders decreases as more of them arrive and facilitate each other (Simberloff, 2006). It is unclear to what extent it might be the case that range-shifters also facilitate each other. However, there are some examples such as two UK range-shifters, Spoonbills and Little Egrets, commensally feeding in mixed flocks (Hamza and Selmi, 2016), and this could be an interesting area to explore further.

5.3 Thesis implications for future research on range-shift consequences

5.3.1 Using occurrence data to identify real biological interactions

When applying DMSOs to understand consequence I found positive associations between *E. viridulum* and native species which were unanticipated. In interpreting these findings, I identified three main areas where further research could help future models to infer biological interactions with greater confidence: identifying whether true co-occurrences exist in range-shifter occupied cells, accounting for habitat quality and range-shift in native species, and detecting/inferring which cells range-shifters have occupied and when.

Distinguishing true co-occurrences from shared cell occupancy

One important constraint which future models will need to consider is how "sites" are described in DMSO models. I used 1km^2 cells. However, as discussed in Chapter 3, this is quite large relative to the area a larval or even an adult damselfly might roam (Dolný et al., 2014). Therefore, the model assumes that every co-occurrence within a 1km^2 cell indicates a potential interaction (negative or otherwise) when in fact the two species may be occupying completely different sectors of the cell, particularly as in the UK freshwater habitats are often quite fragmented. Species could also be falsely inferred to not co-occur if the site they occupy spans a grid cell boundary and the different species are (by chance) only recorded on either side. The risk of false inference is likely to be most problematic for specialist species with small home ranges, where identifying overlap is challenging and could lead to impacts being misattributed to species which do not in fact interact (Bar-Massada, 2015).

Two approaches would help to address this concern in future DMSOs. A first and most self-evident approach is to increase the spatial resolution of both habitat and occurrence data. The risk of falsely identifying interactions will be much smaller for most species at 30m than at 1km resolution (Blanchet et al., 2020). Increased remote-sensing capability for gathering landscape data (Cord and Rödder, 2011) and GPS tagging for biological records will help to tackle this issue. A second and complementary approach, is to reduce spurious inference of interactions by increasing the resolution of other variables. For instance, temporal overlap in flight season may be a good indicator of the potential for competition in pollinators (Stone et al., 1998), and host plant range a good indicator for larval lepidopteran competition (Friberg and Wiklund, 2009). If we reduce the number of species which we test for interactions between to those with stronger cases *a priori* then we reduce the risk of identifyin false positives.

The more these approaches can be linked together the stronger they could be in allowing us to model associations based on genuine interactions. Ideally a model would *a priori* identify areas constituting a unique site from the biological perspective of the focal species (Girvetz and Greco, 2007), i.e. a distinct area the whole of which, once present, the species would swiftly occupy. Considering *E. viridulum,* this might be isolated patches of ponds. Once sites had been clearly defined, aspects of site quality could be controlled for in the model, akin to how we controlled for climate anomaly. A potential candidate could be the size of a pond, which potentially suggests increased permanence and a broader array of habitat. However, this example highlights the difficulty of defining a site in this way as not all areas are as discrete as pond, e.g. linear rivers, along these site allocation would have to be more ad hoc, to a subjective size (Efford and Dawson, 2012). This highlights an inherent weakness of the DMSO, that it relies on closure assumptions (Otto et al., 2013), i.e. that sites are isolated from each other between model time steps, in this case this assumption may not only be violated but it may be deviated from in different ways across sites. Violations of this assumption complicates interpretation of the model by confounding colonisation and persistence.

Integrating habitat quality and native range-shift as potential confounders

The issue above is inherent to all DMSO models (though it may be more acute for species with small home ranges like damselflies). Similarly, for all correlative models it is impossible to eliminate all potentially confounding effects, as controls are lacking. However, I suggest two factors in Chapter 3 that may be particularly relevant for range-shifting species: habitat quality and native range-shift.

The way in which habitat quality varied across our study sites is unknown. However, if it increased both a) the chance of *E. viridulum* arriving and b) native persistence, then it could drive a spurious positive correlation between them. Similar to the problem of delimiting sites, discussed above, a productive approach is to source fine resolution data on habitat quality where it exists. This is likely to be challenging in practice (Gilioli et al., 2018). As discussed in Section 5.2.2, we can only imprecisely identify a species' habitat preferences. Therefore, I suggest that a valuable approach is to encourage data collectors to tie occurrence observation directly to habitat observations in the novel range and to develop data infrastructures which support this (Sutherland et al., 2015). Such an approach might also incorporate variables to help modellers estimate effect detectability (for example solar radiance for Odonata or moon-state for moths).

British native dragonflies were also range-shifting over the study period (Hickling et al., 2005; Powney et al., 2015), which may be an important factor to consider as an effect in future models. If native species expand, causing new ephemeral populations to exist beyond the range-front (Angert, 2006; Mats et al., 2019) and also outside the area through which range-shifters such as *E. viridulum* spread, this could lead to spurious correlations. This problem that range-shifting species are arriving into areas whose natives are themselves range-shifting is likely to be widespread (Gillings et al., 2015). Future models based solely on occurrence may struggle to address this concern. As a result, we may need more and richer data such as species abundances, explored in Section 5.3.2. In the absence of such data, one option might be to attempt to describe the range-shift process through metrics such as date the species was first recorded in the cell. This variable might help to distinguish the native historic range from the novel range, if sufficient data is available to overcome noise (Botts et al., 2012).

Identifying where the range-shifter occurred at each time-step

In Chapter 3, I considered the potential impacts of assumptions about where *E. viridulum* was present. As discussed in Section 1.3.1, there are gaps in our knowledge about how well range-shifting species are recorded, whether they are over or underrepresented in occurrence datasets. The decisions about where *E. viridulum* is present affects the model outputs via assumed patterns of co-occurrence (Croft and Smith, 2019). We compared an assumption of *E. viridulum* being only present at sites where it was detected in that year with an assumption that once it was detected it then persisted *ad infinitum*. However, neither of these two assumptions is likely to be biologically realistic. In the future, when considering consequences, DMSOs, rather than using raw range-shifter occurrence data as direct effects on native persistence, could attempt to infer where range-shifters are probably present with associated uncertainty (Barbosa et al., 2013; Real et al., 2017). For example, by making assumptions about dispersal rates of varying complexity (Crowther, 2017) and time since arrival (Catterall et al., 2012). DMSOs could then relate inferred range-shifter presences to native persistence rates. These assumptions would require validation and empirical data but could increase the realism and hence usefulness of DMSOs for conservation.

5.3.2 Can occurrence tell us all we need to know?

Often occurrence data is used to address questions which ideally would be addressed using abundance data. For example most ecosystem services, such as pollination, pest control and carbon sequestration, arise as a function of species abundance (Harrison et al., 2014; Winfree et al., 2015) though species richness can also be important (Dainese et al. 2019). The more individuals are present the higher the service level and the greater its potential resilience (Sundstrom et al., 2018). Therefore, as the greater the number of individuals the more likely they are to be encountered, occurrence is often used as a proxy for species abundance. However, our understanding of abundance-occurrence relationships is limited (Bradley, 2016). These relationships could be non-linear or exhibit thresholds. For example, when considering consequences using DMSOs, when using occurrence, we assume a binary effect of *E. viridulum (*Figure 5.2*).* However, in fact the range-shifters effects are likely to depend on its abundance (Parker et al., 1999). Further research is necessary to understand how effective a proxy occurrence may be combined with knowledge of arrival time for determining local range-shifter abundance and subsequent impact (Doody et al., 2009; Phillips and Shine, 2004; Strayer et al., 2006).

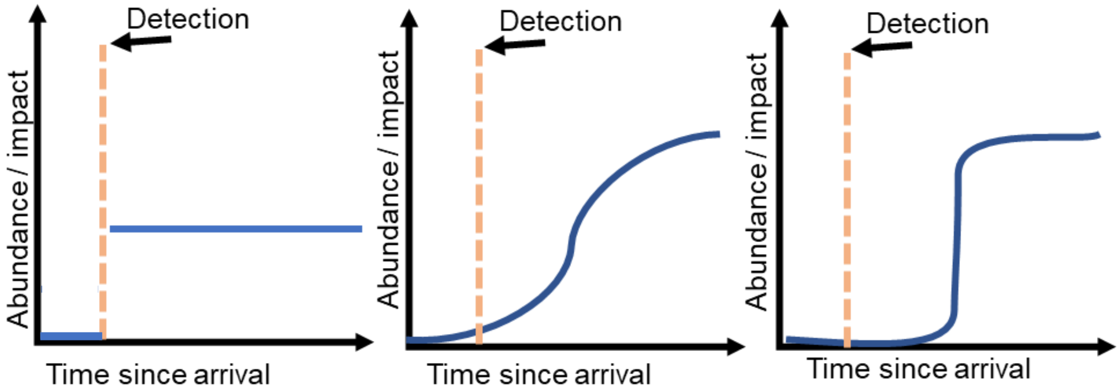


Figure 5.2: The occurrence-impact relationship is complicated by abundance. The left most graph replicates my Chapter 3's DMSO model assumptions: once detected the range-shifter at once exerts its full effect. In reality, assuming a fixed per capita impact, impacts might be expected to grow over time. Variance in the shape of this growth will affect our model's estimates of the range-shifters impact unless/until an equilibrium abundance is reached. For example, abundance might grow almost linearly (middle) or threshold effects could require a critical mass before rapid growth (right).This means that if we discount abundance we might be averaging very different impacts / abundances occurring in different sites.

5.4 Thesis implications for increasing the value of occurrence data

5.4.1 Targeted data collection for range-shifters

To understand the multiple stages of range-shift we need to consider the data we collect and recognise that different approaches may be needed for each stage of range-shift. In particular, I recognise a divide between the first three steps from vagrant generation to establishment and the subsequent two steps of range-shift and its consequences (Figure 5.1). In the latter two steps, macroecological modelling is more useful as range-shifters have established and are spreading, and sufficiently large datasets are available to give the statistical power to detect effects (Blanchet et al., 2020). However, the first three steps are likely to be characterised by smaller datasets and stochastic processes. Therefore, there is a need to consider how to collect data to study the first three range-shift steps. This is important because anticipating sites of establishment allows them to be protected and appropriately managed. On the other hand, for species we may be concerned about, interventions to control spread are usually cheaper and more effective when executed earlier (Eschen et al., 2021). With the building of human capacity and recorder networks, local knowledge could provide early detection of range-shifters (Pettorelli et al., 2019), as has been done for introduced species through the Non-Native Species Information Portal (NNSIP);(Roy et al., 2012). A recommendation for policymakers would be to create a parallel portal for range-shifters or to fold them into the NNSIP, while clearly distinguishing range-shifters from introduced species.

5.4.2 Encouraging volunteers to provide high quality data

Once establishment has occurred, modelling spread, and impacts become the next priority to understand. Though these processes may be more amenable to probabilistic modelling (Section 5.2.1), there are still important actions to improve data quality that would support stronger model inferences, such as associating habitat data with occurrence records (Section 5.2.2) and increasing spatial precision (Section 5.3.1). In addition, there is a need to incorporate estimates of recorder effort into models. This need is long established but progress on achieving it has been slow. Current efforts to identify recorder characteristics such as mean recording effort directly from available datasets are constrained both by inconsistency in recorder identity between datasets and seemingly intractable privacy concerns (Isaac and Pocock, 2015). Social scientists may be able to help bridge this gap by identifying recorder motivations (Boakes et al., 2016; Ganzevoort et al., 2017; Ganzevoort and van den Born, 2020; Hobbs and White, 2012).

5.4.3 Speeding the flow of data

There are several steps between occurrence data collection and occurrence data being used as summarised by the NBN’s data flow pathway (Figure 5.3). Increasing the timeliness of data availability would be very useful for range-shift management at all its stages. Every year counts when monitoring for the effects of novel species, as previously discussed. Ideally both Chapters 2 and 3 would have been able to rely on even more recent data than 2015. In particular, Chapter 3 may have benefited, as *E. viridulum* is still spreading, suggesting that more confirmed presences might have been added. A current choke on data flow is the quality assurance process. Verification of records is time consuming and there are far fewer experienced verifiers than there are recorders (Faith et al., 2013; Guralnick et al., 2007). This leaves considerable amounts of potentially useful data in limbo. A possible solution is developing automated verification processes, at least for less challenging taxa, through machine learning (August, 2020; Tabak et al., 2019; Toivonen et al., 2019). This could create time for verifiers to focus on more difficult groups and also to train future verifiers. An implication of machine learning is that records of species ID may become more probabilistic statements rather than a binary of correctly or falsely identified (Bush et al., 2017). If this change occurs, future modellers should consider both the risks and opportunities of using this new type of data.

Figure 5.3: The NBN's six stage data flow pathway between recorders and users (National Biodiversity Network, 2015).

5.4.4 Building a more integrated UK network

Data collection and verification are only the first of two steps in the data pathway, albeit where the vast majority of individual stakeholders are involved (Figure 5.3). It is also important to consider how the wider data network affects the availability of occurrence data (Judge, 2019). Frequently data are curated and aggregated locally (particularly historic datasets), such as by Local Environmental Record Centres in the UK, or in datasets of narrow taxonomic groups, such as the Bees, Wasps and Ants Recording Society (Roy et al., 2012). These groups may have concerns about sharing data, perhaps because they fear data misuse, concerns about recorders' consent or reliance on commercial use of the data for financial sustainability (Pearce-Higgins et al., 2018). However, surveys of citizens scientists suggest that recorders on the ground generally favour making the records they collect more openly available and want their impact for conservation to be maximised (Fox et al., 2019). Addressing these concerns is a vital step in making available the necessary data for managing range-shift across more taxa. Many taxa, for example Hymenoptera, are poorly represented in the species redistribution literature (Platts et al., 2014) but play significant ecological and economic roles such as pollination. The focus of Chapters 2 and 3 on charismatic observable species was partly a product of data availability.

Looking at latter stages of the NBN pathway, it is important to consider how macroecological modelling can maximise its impact on conservation policy (Rapacciuolo, 2019). Dynamic multi-species occupancy models may be a particularly useful tool for managing range-shifters due to their scale flexibility, allowing them to tackle both national and local questions, for example identifying the potential vulnerability of specific resident species in a protected area. However, achieving this will require developing DMSOs as a usable tool for a wider range of users (Ponisio et al., 2020); (e.g. as SPARTA (August et al., 2020) has done for inferring species trends from occurrence data). In the future DMSOs could also be applied to look at changes in ecosystem function (Stewart et al., 2020) or community composition (Soroye et al., 2020).

5.4.5 Shared global datasets are needed for modelling range-shift

One reason this thesis focused solely on the UK was its rich biodiversity data. Occurrence data are becoming increasingly available, but data are not evenly distributed across the globe. They are concentrated in North America and Europe (Cayuela et al., 2009; Meyer et al., 2015). These regions are predominantly temperate and at high latitude (Perez et al., 2016) and so have greater annual climatic variation and projected climate velocities than much of the world's surface (Williams et al., 2007). Regions could also show topographic particularity; palynological data suggests that species shifted faster in postglacial reestablishment in North America than in Europe (Giesecke et al., 2019). Genetic evidence in several European mammal species suggests that this could be due to Europe's mountains being primarily orientated East-West rather than North-South as they are in North America, forming more of a barrier to poleward dispersal (Badgley, 2010). This historic evidence implies that there will be regional differences in range-shift processes which cannot be understood without wider spatial data coverage.

5.5 Thesis implications for future research on perceptions of range-shift

5.5.1 Stakeholders requested further ecological knowledge

The three key knowledge needs identified in Chapter 4: link strongly to the other two data chapters. First, attitudes to range-shifters appeared to be affected by the conservation status of the relevant species. Conservation assessments rely on an understanding of range loss as well as range-expansion – on a species basis. Thus, it is important to estimate, reduce and communicate current uncertainty about retracting range edge processes to stakeholders at the expanding range edge. A concern is that range-expansions may be easier to detect than retractions, as presences are often easier to infer than absences (Section 1.3; (Jump et al., 2009; Svenning and Sandel, 2013; Talluto et al., 2017)). Thus, evidence of endangerment could be missed by stakeholders in novel parts of the range. Second, some respondents wanted further information on species historic ranges and possible human impacts on them. They believed that historic residents had a better claim for conservation. Further research on historical sources of ecological data is one avenue to supply this information (Tingley and Beissinger, 2009; Vellend et al., 2013), as touched on by Chapter 2's mention of medieval egret records. Finally, respondents wanted to know about evidence of impacts, showing more research akin to Chapter 3 is useful.

A concerning pattern in these three knowledge needs is that they all align with a very traditional paradigm of conservation as prevention of extinction: i.e. prioritize the most threatened range-shifters, restore past ranges of restricted species, restrict "impactful" species. A noted risk in conservation is that of tunnel vision focused on preventing the extinction of rare species working to the detriment of declining common species (Lunney, 2017; Neeson et al., 2018). These common species are the ones that we most frequently interact with. Our "everyday" wildlife is as important for our sense of connection with nature as rare iconic species (Brock et al., 2017) and also for ecosystem services. Local knowledge of species abundances is lost in time as generations pass, as recognised by the shifting baseline paradigm (Soga and Gaston, 2018). Range-shifts might also mean that local knowledge is lost as range-shifters decrease in their historic range whilst society in the novel range is unaware of historic baseline abundance. In other words, in recipient regions people's attitudes may shape a new perceived baseline abundance for the range-shifter, which could be below the levels in the historic range. Reduced abundances might also mean reduced resilience and ecosystem service provision accompanied by a lost ecological awareness of the past state of nature.

5.5.2 The importance of potential factors influencing future attitudes

Chapter 4 captured factors which might influence attitudes at a single snapshot in time. It is also useful as a baseline for comparison with which to understand future influences that may change attitudes over time. Future research to understand the wider environment shaping stakeholder needs and views may be beneficial. One reason is that latitudinal studies can potentially draw stronger causal inferences by accounting for temporal sequence. Species abundance and media framing are two factors which may be potentially important in shaping future attitudes.

When range-shifter populations appear to be increasing rapidly to a naïve human society, there is an elevated risk of invasiveness and “human-wildlife” conflicts being perceived (Steen and Jachowski, 2013). If considerations of the species’ impacts are allowed to influence classification (i.e. if having harmful impacts increases the risk of misidentification of a range-shifter as an introduced species), faulty inferences may be drawn about the relative incidence and impact of introduced species and range-shifters (McGeoch et al., 2012). As discussed in Section 1.2.2, even at present within the UK, we have an incomplete understanding of our ecological communities’ history. Newly arrived range-shifters have not always been distinguished from historic residents (Lancaster, 2020, 2016). As discussed in Section 5.5.1, the loss of ecological knowledge in the societies of the historic range may compound this problem. An interesting approach to this could be to consider these historic range societies as stakeholders in managing expanding range-shifters and integrate their perspectives into conservation planning. This might be achieved, for example, through interregional community forums, a parallel to intergenerational forums for discussing shifting baseline syndrome (Jones et al., 2020).

Another focus for factors shaping attitudes could be media content which might help identify possible leverage points for change (Chan et al., 2020). How the media frame issues has been shown to strongly influence attitudes (Siemer et al., 2007; Triezenberg et al., 2011), with associated impacts on public perceptions of risk and judgements on management (Houston et al., 2010;

Landon et al., 2020; Slagle et al., 2012). A concerning negative frame would be to cast range-shifters as opportunistic “climate invasives” (Lakoff, 2010). On the other hand, a media framing that downplayed the risk of all novel species as part of modern nature could weaken conservation messaging on the danger of introduced alien species (Hobbs et al., 2006; Simberloff, 2015). On a more positive note, new species could also be framed as a potential rallying point for conservation efforts (Forgrave, 2019), inspiring fresh engagement, similar to one argument for rewilding (Jepson, 2016).

5.5.3 Different international perspectives may split range-shift governance

Range-shifting species have no regard to political boundaries so global agreements are required to support their conservation (Mason et al., 2020). Island states may experience fewer range-shifters than continental states due to relative difficulty of arrival and may therefore perceive less risk. On the other hand, they may be more cautious, because they may be less familiar with newly arriving species, have more unique fauna, or more delicate ecosystems (D’Antonio and Dudley, 1995). Coordinating these multiple perspectives on biodiversity will require complex negotiation but will be essential for good management of range-shift.

Biodiversity conservation orientated to cultural services

The UK represents a quintessential example of conservation in Europe. Conservation is carried out mostly to preserve the semi-natural habitats of pre-industrial agricultural landscapes (Adams, 1997; Cooper, 2000). Many management activities such as coppicing and clearing reed beds and bracken are a continuation of medieval resource extraction. It is easy to underestimate the embeddedness of this “stewardship” mindset in the European conservation movement. But these views arise from the very origins of modern western conservation in the romantic movement (Meine, 2013). The modern era saw nature used in the construction of national identity, from “manifest destiny” in the USA (Patin, 1999) to the post-war national parks in Britain (Lunney, 2018). These constructions archetype nature at approximately the same baseline period that I used to delimit range-shifters in Section 1.2. An implication of this is that we might expect possible resistance to range-shift as it could be perceived as eroding this archetype, and therefore the value of nature to both a “mastery” and “stewardship” perspective.

Indeed, range-shifting species are a challenge to reconcile with strict preservation in practice. Controversy over tree-planting in the Lake District (UK national Park but also a highly modified working landscape (Hanley et al., 2009)) and the return of carnivores to western Europe, suggests that if consensus cannot be reached – even for species which occurred recently in the areas which range-shifters are newly arriving into – then range-shifters may face even greater potential difficulties. Similarly, the American public trust doctrine (where the state is entrusted to protect natural resources for the public benefit – both present and future generations); (Sagarin and Turnipseed, 2012) may struggle to balance the potential loss of public resources (in the form of current species), with the risk of harming the potential value of future public resources (in the form of newly arriving range-shifters).

The potential for range-shifters to hybridise with native species (Chunco, 2014) may pose a particular challenge to a preservationist culture of conservation which focuses on species composition. If a range-shifting species hybridizes with species in the recipient ecosystem, then a novel entity has been created at the species level. Different perspectives might consider only “pure” individuals to be range-shifters, or instead use genetic markers (resident individual with particular alleles derived from the range-shifter species/population);(Ellstrand et al., 2010). Conservation debates around hybridisation have often become heated, consider, past examples such as culling of ruddy ducks in Europe (Guiașu, 2016; Muñoz-Fuentes et al., 2006) and the killing of coyote-wolf hybrids in the US (Bohling and Waits, 2015). Such controversy might have the potential to harm range-shifters.

Biodiversity conservation orientated to provisioning services

In contrast to Europe, North America and more developed economies, in the global South conservation often plays second fiddle to the urgent needs to raise people’s standards of living. But development and conservation are not necessarily contrasting goals. Ecosystem services are vital for lifting people out of poverty sustainably. For instance, in Costa Rica, a system of payment for ecosystem services is credited with the prevention of large-scale watershed deforestation (Pagiola, 2008), a successful example of broader global frameworks such as REDD (Mahanty et al., 2013). This functionalist view on species may be quite adaptable to species range-shift, so long as the incoming species are able to maintain current ecosystem services. From this viewpoint, a healthy ecosystem is one that resiliently provides services, not one that contains the “right” species (Mace, 2014).

There are potential downsides for this approach flowing from an approach based on instrumental values (Section 1.5.1). Range-shifters which create disservices or are not “cost-effective” will lose out. Moreover, there is some evidence that this instrumental framing of nature can harm conservation attitudes (Rode et al., 2015). This may be particularly dangerous for range-shifting species, which unlike residents, often lack a statutory footing for national protection. Economics (and consequently politics) enter the conservation of range-shifting species when instrumental values are centre-stage (Collard, 2013). For example, an important source of income for many developing countries is ecotourism and trophy-hunting, which relies on the presence of charismatic megafauna. Shifting ranges mean that this potential revenue is also moving and with it the potential for human and wildlife’s interests to conflict, for example in South African game reserves where tourism relies primarily on the presence of large charismatic vertebrates (Blackmore, 2020). Protected areas, particularly in areas of potential human wildlife conflict, are frequently fenced and so species may not be able to range-shift as required (Thuiller et al., 2006) without human mediation or political interest (Brennan et al., 2020). This may not be forthcoming if the fauna is perceived as necessary to generate important funds for development. Current international legal frameworks attempt to address these problems (Trouwborst et al., 2016) but without sufficient political will may be hard to enforce.

5.6 Conclusion

My thesis contributes to a growing literature on species redistribution which challenges current conservation paradigms. Beyond cSDMs, there is now an urgent need to focus on processes beyond climatic limitations to predict how species will expand with anthropogenic climate change. Attempting to describe a range-shifting damselfly’s impacts in Chapter 3 revealed the challenges remaining in using occurrence data to develop effective modelling tools for conservation. My survey revealed positive attitudes towards range-shifters which suggests UK wildlife managers will operate (at least initially) in the context of perceptions broadly supportive of range-shifters amongst wildlife recorders. It also suggested that policymakers in the future may have to weigh potentially conflicting perspectives on conservation management. We identified perspectives focused on ecosystem composition and others focused on ecosystem function, reflecting a contrast between preservationist conservation and more modern movements such as rewilding. I believe that only a holistic exploration of the social and ecological implications of species redistributions will help to fill these research gaps. There will be a need as much to examine the societal reasons why we are modelling range-shift as to consider which ecological processes we are modelling to identify needed research. To quote John Tukey:

> *“An approximate answer to the right problem is worth a good deal more than an exact answer to an approximate problem” (Tukey, 1962).*

For species redistribution, we have advanced our problem definition in great strides and now is the time to reach for answers – even approximate ones.

Appendices

Appendix A: Chapter 2 (Supplementary Materials)

Supplementary Methods

Supplementary Method A.1: Mesh Construction for INLA

INLA aims to estimate a parameter in continuous space (in our case species occupancy) by solving a Stochastic Partial Differential Equation (SPDE) . The solution of this equation is requires constructing a triangular mesh to link observed point process data to continuous space, (modelled as a Gaussian Markov Random Field). We created this triangular mesh using the centroids of each British 10km cell as vertices. We specified an inner and outer boundary for the mesh using two non-convex hulls around Great Britain (10 km buffer the inner domain and a 25 km buffer for the outer domain). The max edge length was constrained to 5km in the inner domain and 12.5km in the outer domain. The minimum allowed distance between vertices was 5km. The resulting mesh contained 7352 vertices. This number of vertices allowed a sufficiently fine grained spatial resolution for analysis while minimising computational resources required.

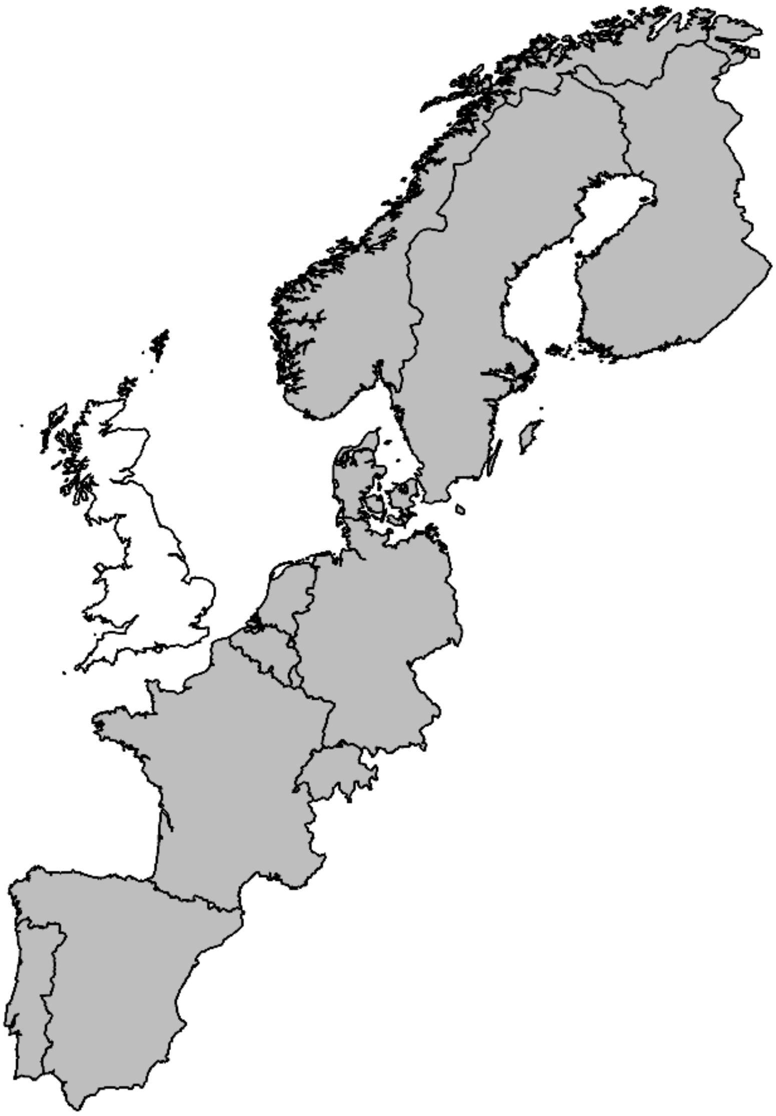
Supplementary Figures and Tables

Supplementary Table A.1: Range-shifter Data obtained. The Latin and Common Names are reported; the Vice-county and year of first breeding in the 20th Century are reported along with the Reference for the information; the number of UK 10km cells occupied in the British breeding Bird atlas (2011-2014). The Classification distinguishes species which are re-established: those which are believed to have bred in the UK before 1900 but subsequently went extinct prior to the establishment event recorded in the table, as a contrast to those species which are believed to have established in the UK for the first time in historical time in the last century. Species marked as excluded, appear regularly but do not breed in the UK, the remaining species appeared in too few (<10) 10km cells to be included in our analysis.

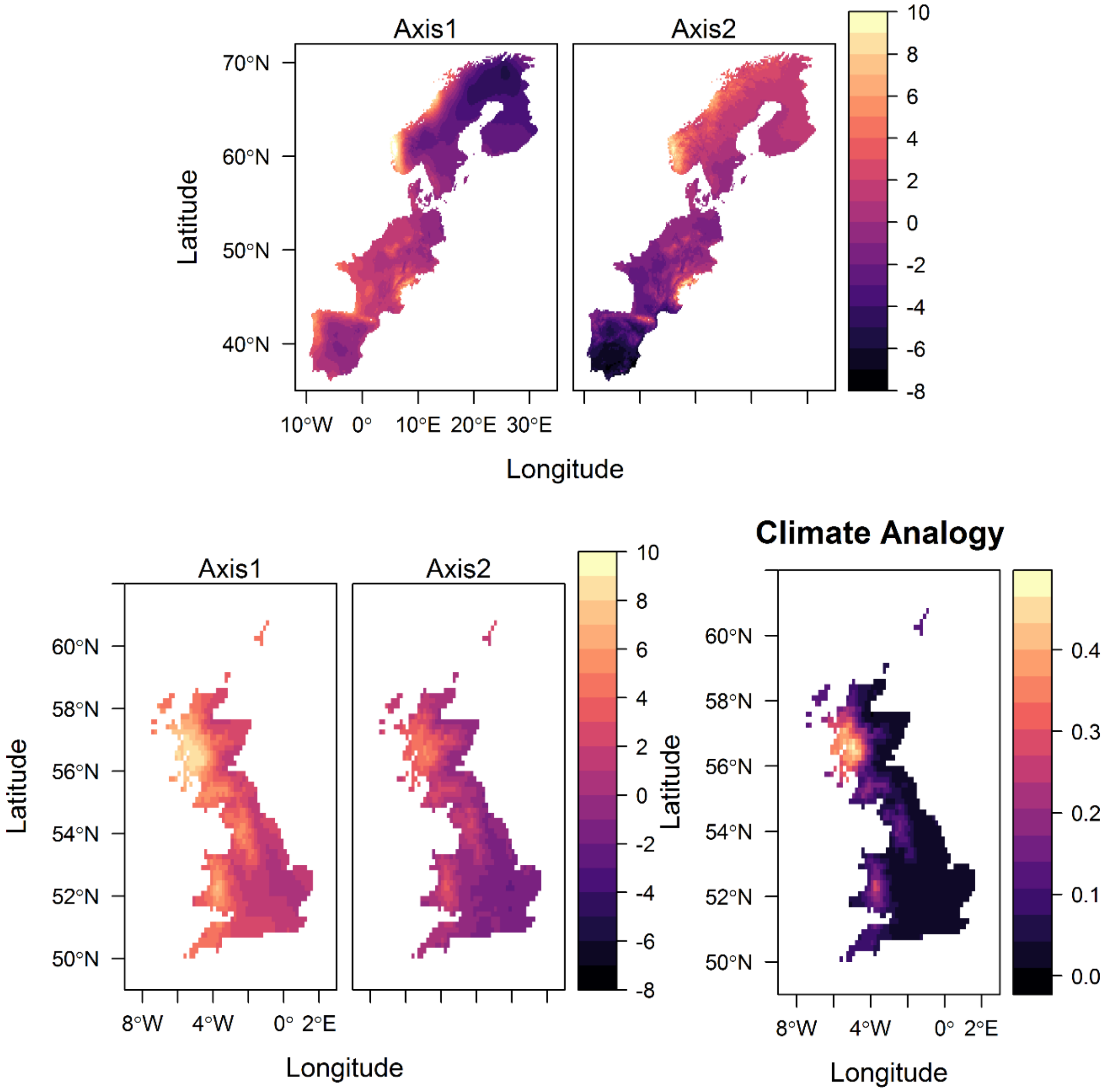
Latin Name	**Common name**	**Class**	**County of arrival**	**10km cells**	**Year**	**Ref**
Limosa limosa	Blacktailed Godwit	Re-established	Norfolk	30	1952	Cottier & Lea 1969
Locustella luscinioides	Savi's Warbler	Re-established	Kent	19	1960	Gurney 2015

Recurvirostra avosetta	Avocet	Re-established	Suffolk	141	1941	Gurney 2015
Cettia cetti	Cetti's Warbler	Established	Kent	417	1973	Robinson 2007
Egretta garzetta	Little Egret	Established	Dorset	327	1996	Gurney 2015
Charadrius dubius	Little Ringed Plover	Established	Hertfords.	597	1938	Gurney 2015
Larus melanocephalus	Mediterranean Gull	Established	Hamps.	90	1968	Taverner 1970
Streptopelia decaocto	Collared Dove	Established	Norfolk	2370	1955	Gurney 2015
Regulus ignicapilla	Firecrest	Established	Hamps.	212	1962	Adams 1966
Podiceps nigricollis	Black-necked Grebe	Established	Anglesey	53	1904	Martin & Smith 2007
Bucephala clangula	Goldeneye	Established	Inverness	44	1970	Dennis & Dow 1984
Turdus iliacus	Redwing	Established	Sutherland	75	1953	Parslow 1967
Turdus pilaris	Fieldfare	Established	Orkney	23	1967	Frost & Shooter 1983
Phoenicurus ochruros	Black Redstart	Established	Sussex	131	1923	Morgan & Glue 1981
Calidris maritima	Purple Sandpiper	Established				
Grus grus	Common Crane	Re-established				
Podiceps auritus	Slavonian Grebe	Established				
Podiceps grisegena	Red-necked Grebe	Established				
Ixobrychus minutus	Little Bittern	Established				
Loxia pytyopsittacus	Parrot Crossbill	Established				
Botaurus stellaris	Eurasian Bittern	Re-established				
Platalea leucorodia	Eurasian Spoonbill	Established				
Larus michahellis	Yellow-legged Gull	Established				
Ardea Alba	Great White Egret	Established				
Tringa glareola	Wood Sandpiper	Established				
Puffinus mauretanicus	Balearic Shearwater	Excluded				
Serinus serinus	European Serin	Excluded				
Stercorarius longicaudus	Long-tailed Skua	Excluded				

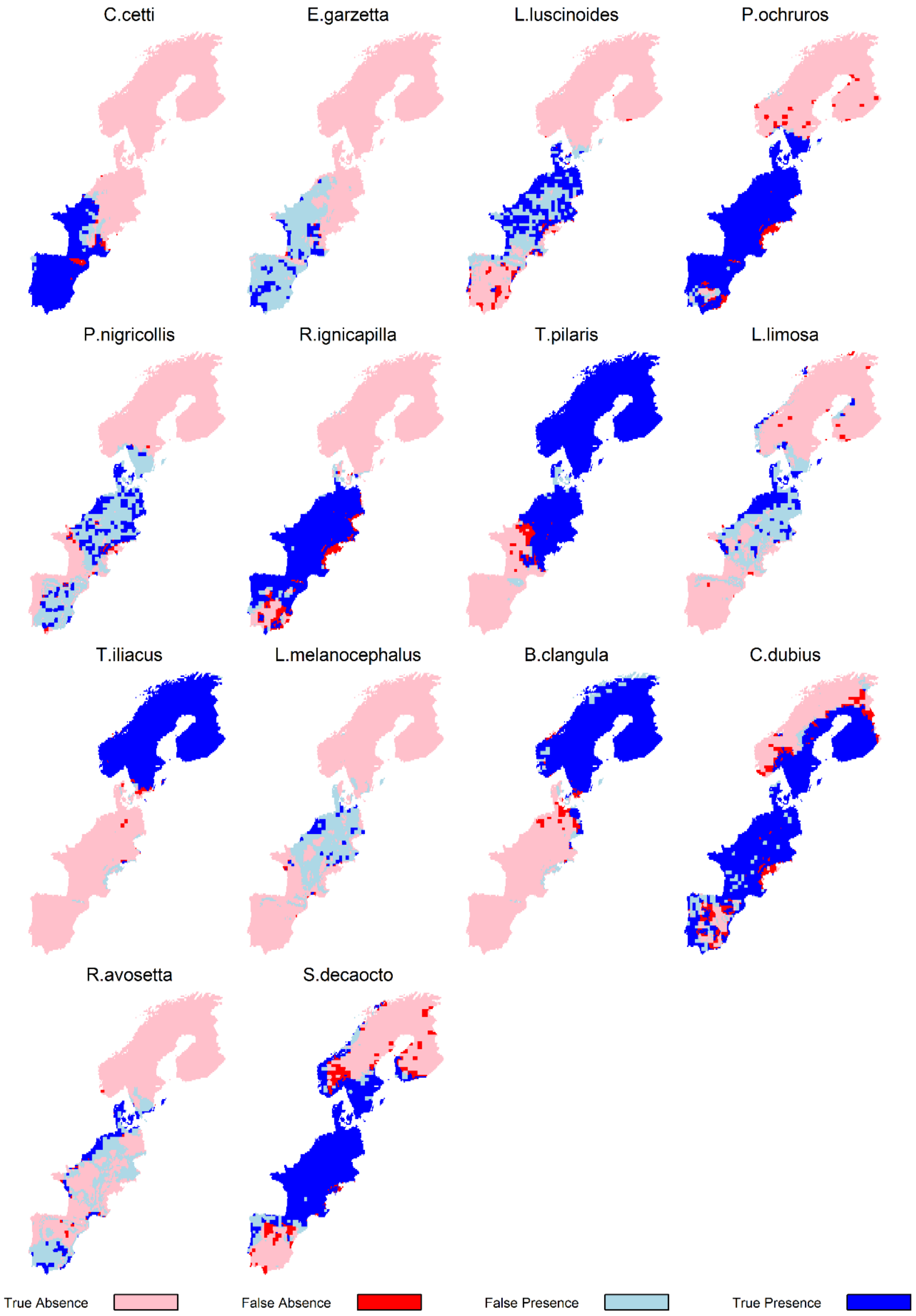
Eremophila alpestris	Shore Lark	Excluded				
Bubo scandiacus	Snowy Owl	Excluded				
Larus cachinnans	Caspian Gull	Excluded				



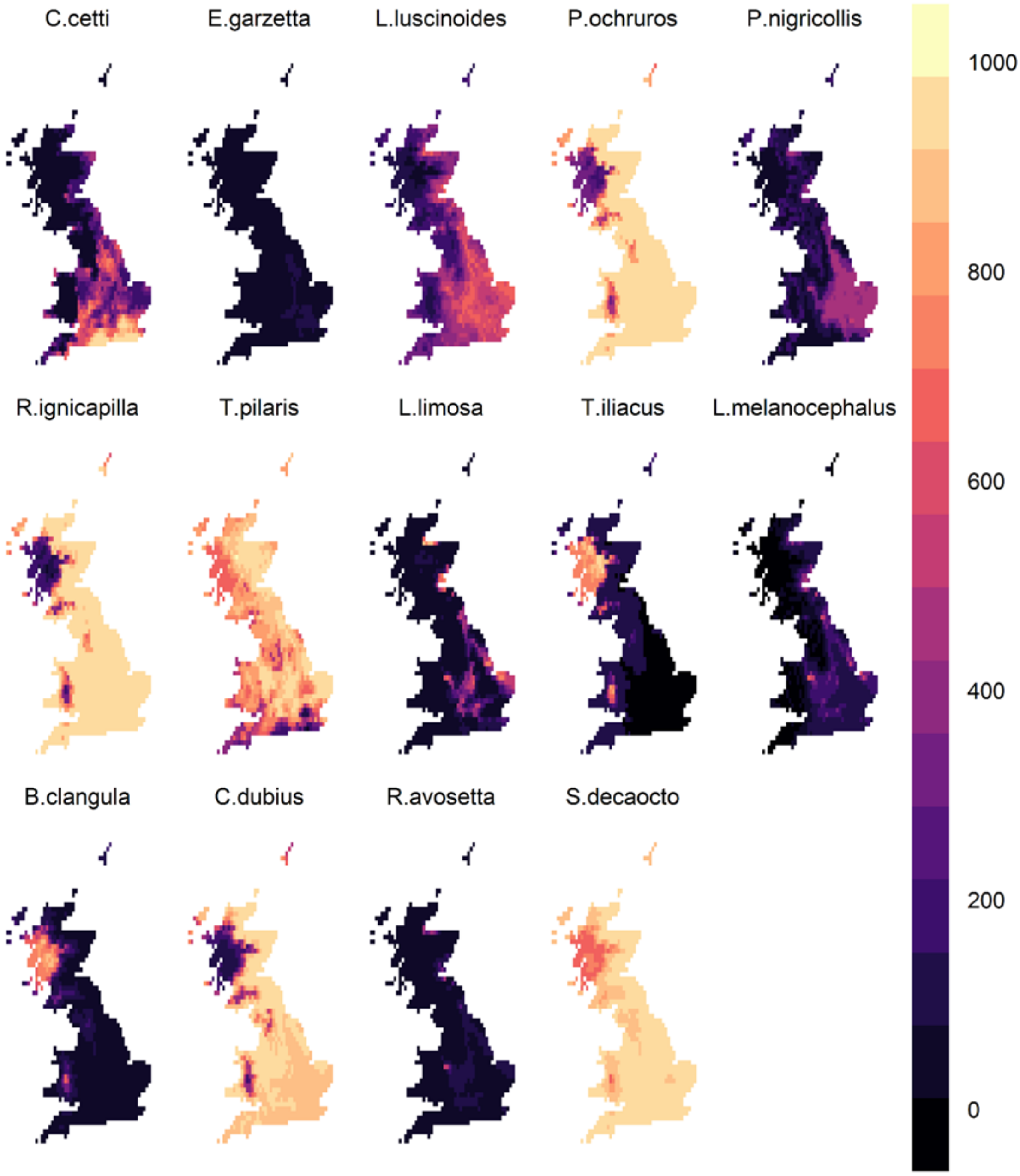
Supplementary Figure A.1: Map of the Study area. Countries included in the geographic extent for cSDMs and for which European Breeding Bird Atlas Data were taken used are shown in grey.



Supplementary Figure A.2: The first two principal components derived from a PCA of the values of 19 core bioclimatic variables (from Worldclim) across our study area are shown here, plotted for Europe (Top) and the UK (Bottom-Left).The extent of climatically analagous space within the UK derived using the r package ecospat::ecospat.climan, areas between 0 and 1 are climatically analog, see (Mesgaran et al. 2014).



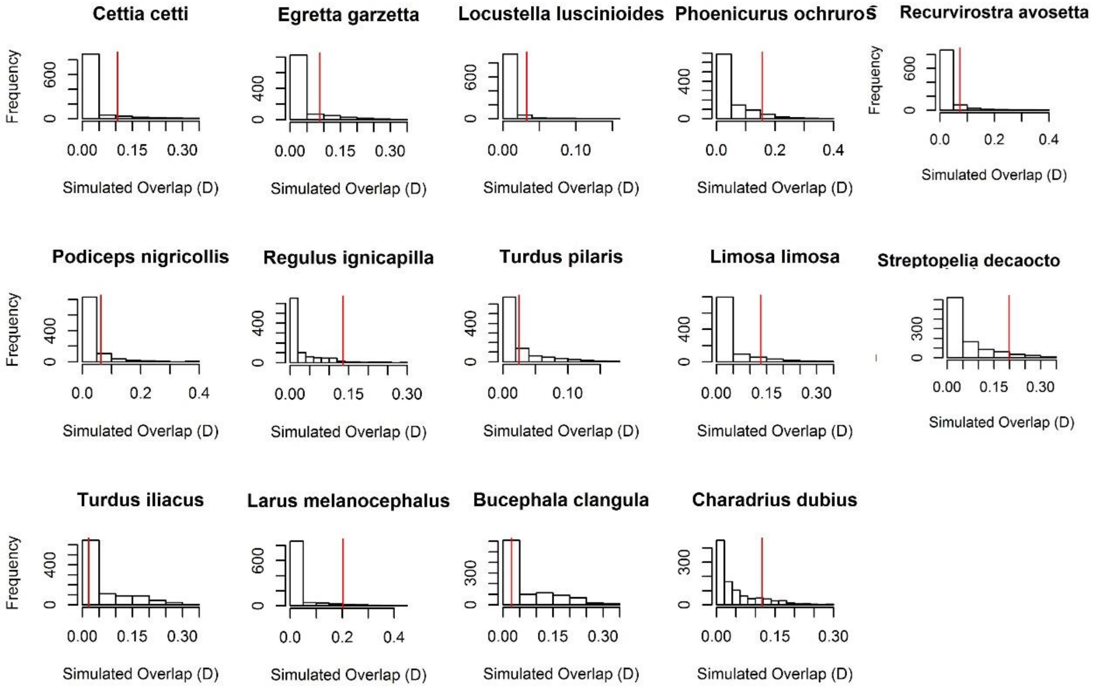
Supplementary Figure A.3: Maps of Climatic cSDM predictive performance for range-shifters' European Range. Presence data plotted represents the full European Atlas distribution.



Supplementary Figure A.4: European cSDM climatic suitability projected for the UK. Scale is ‰, i.e. 1000 = 100% probability of presence, 0 =0% probability of presence.

Supplementary Table A.2: True Skill Statistic (TSS), TSS threshold (‰), sensitivity (%) and specificity (%) of Climatic cSDMs for the range-shifters in the European range. See Supplementary Figure A.5.

Species	TSS Score	TSS Threshold	Sensitivity	Specificity
Turdus.iliacus	0.949	429	98.379	96.553
Cettia.cetti	0.920	210	96.198	95.754
Phoenicurus.ochruros	0.887	694	92.380	96.301
Turdus.pilaris	0.881	766	97.020	91.075
Bucephala.clangula	0.866	391	95.731	90.880
Regulus.ignicapilla	0.854	568	90.558	94.814
Streptopelia.decaocto	0.728	526	85.929	86.862
Larus.melanocephalus	0.709	119	91.422	78.342
Egretta.garzetta	0.692	44	96.552	72.749
Charadrius.dubius	0.682	627	89.130	79.044
Recurvirostra.avosetta	0.679	53	90.010	77.735
Locustella.luscinioides	0.669	196	87.586	79.253
Limosa.limosa	0.643	54	88.265	76.099
Podiceps.nigricollis	0.614	93	92.273	68.906

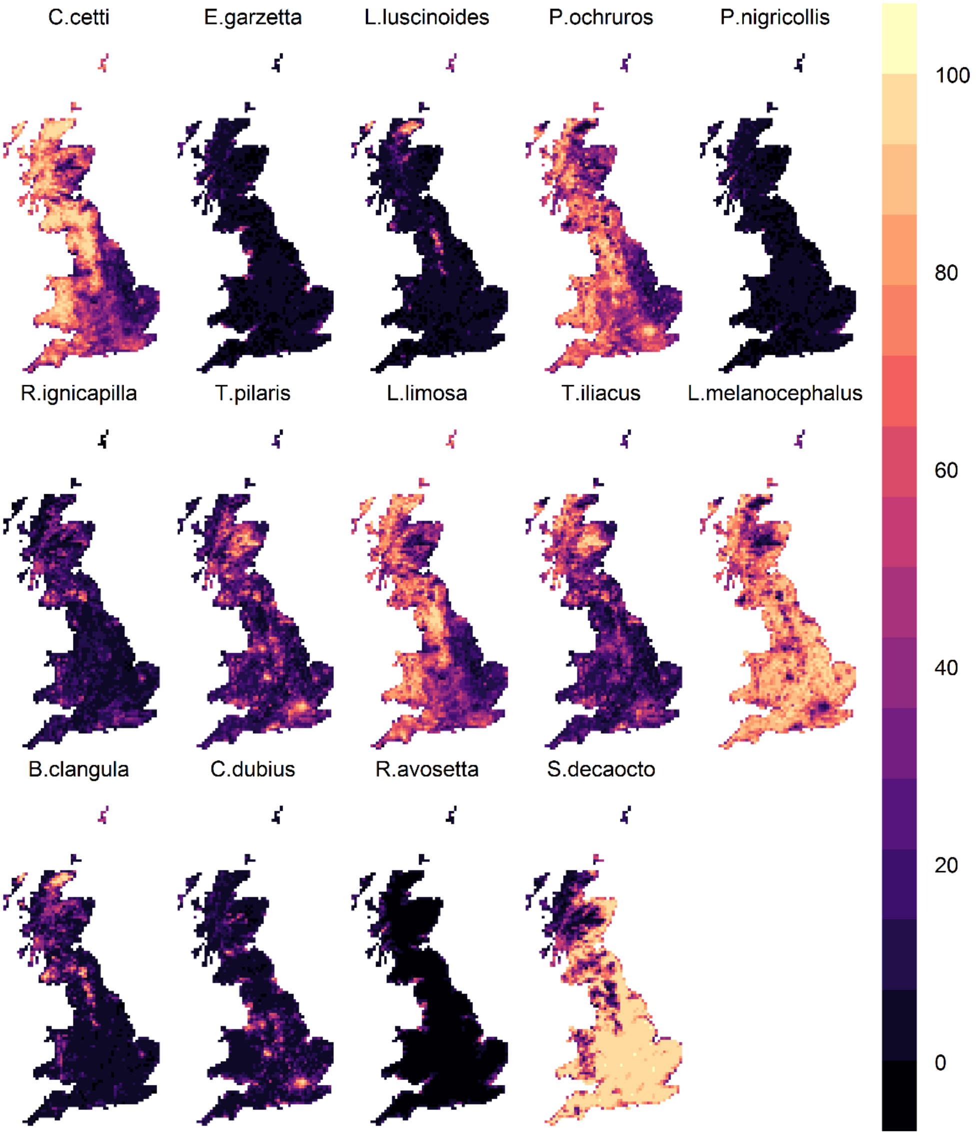


Cettia cetti
Egretta garzetta
Locustella luscinioides
Phoenicurus ochruros
Recurvirostra avosetta
Podiceps nigricollis
Regulus ignicapilla
Turdus pilaris
Limosa limosa
Streptopelia decaocto
Turdus iliacus
Larus melanocephalus
Bucephala clangula
Charadrius dubius

Supplementary Figure A.6: Range-shifters observed niche overlap in Europe & Britain compared to simulated data. Observed overlap (red line) against 1000 simulated overlaps (histogram). Overlaps between the European range and random niches as available in the range of the UK. The Uk simulated range has the same pattern as the true uk range but the center is randomly translatated in *the availabe UK PCA and weighted by UK PCA densities, (see https://rdrr.io/cran/ecospat/man/ecospat.niche.similarity.test.html).*

Supplementary Table A.3: British Range-shifters' observed niche expansion. ObsD is the observed niche overlap between the European and the native range and pD is the p-value for the niches being less similar than expected. Expansion, shows the proportion of cells where expansion was observed (i.e. the species was present) compared to the potentially climatically suitable cells.

Species	ObsD.	pD	Expansion	Expansion Observed Cells	Expansion Potential Cells
B.clangula	0.026	0.498	0.401	167	438
T.iliacus	0.019	0.564	0.625	226	513
T.pilaris	0.025	0.713	0.038	8	81
C.dubius	0.117	0.870	0.000	0	73
P.nigricollis	0.063	0.880	0.000	0	144
R.avosetta	0.074	0.895	0.000	0	308
E.garzetta	0.089	0.903	0.065	58	338
L.limosa	0.132	0.921	0.109	37	194
C.cetti	0.105	0.926	0.017	24	216
S.decaocto	0.199	0.939	0.024	27	27
P.ochruros	0.157	0.942	0.016	21	130
R.ignicapilla	0.135	0.945	0.001	2	143
L.luscinoides	0.033	0.962	0.000	0	168
L.melanocephalus	0.203	0.969	0.089	38	426

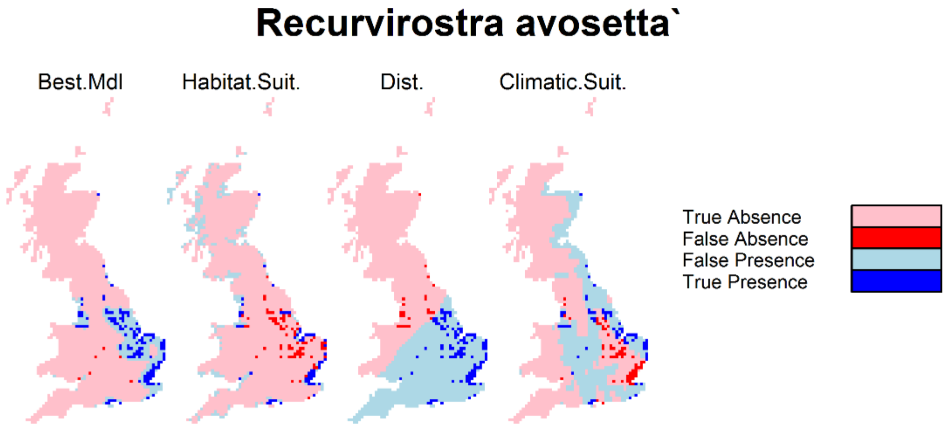


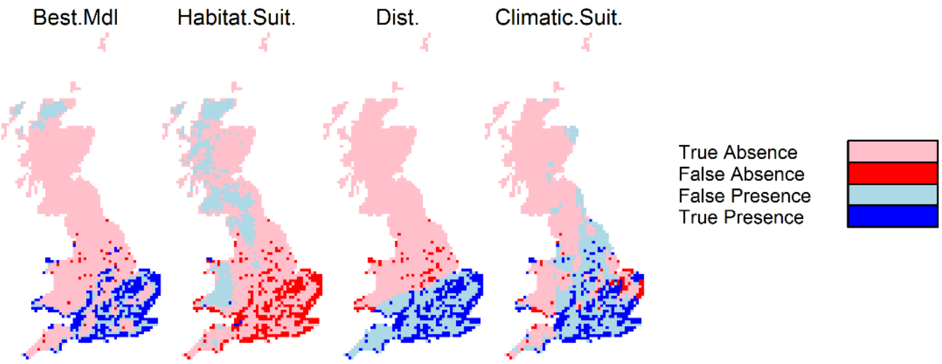
Supplementary Figure A.7: UK Habitat suitability(0% - 100% suitable landcover)

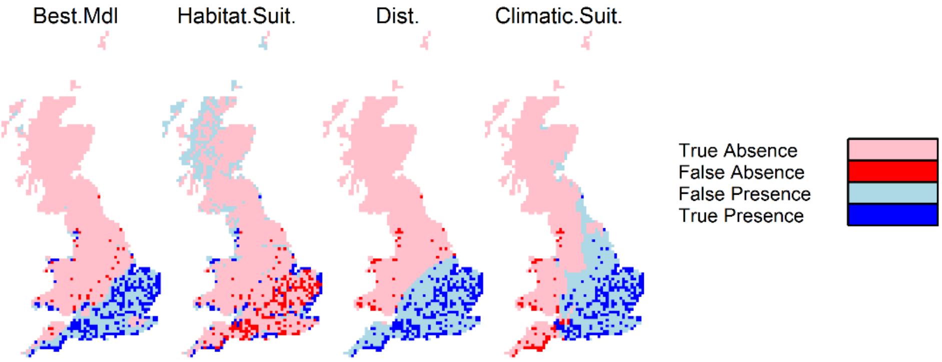
Supplementary Table A.4: Target Class Suitability for the modelled UK range-shifters(0 = Unsuitable, 1 = Suitable)

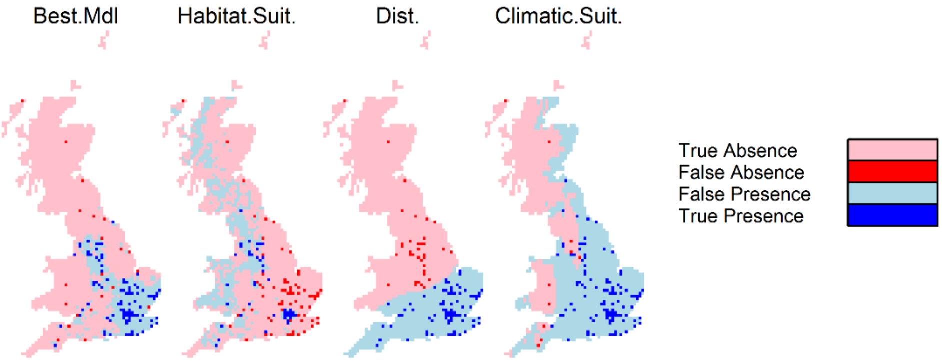
	B. clangula	C. cetti	L. limosa	P. ochruros	T. iliacus	L. melanocephalus	R. avosetta	S. decaocto	E. garzetta	L. luscinioides	P. nigricollis	T. pilaris	C. dubius	R. ignicapilla
Broadleaved woodland	0	0	0	0	1	0	0	1	0	0	0	1	0	1
Coniferous woodland	1	1	0	0	1	0	0	1	0	0	0	1	0	1
Arable and horticulture	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Improved Grassland	0	1	1	1	0	1	0	1	0	0	0	0	0	0
Neutral Grassland	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Calcareous Grassland	0	1	1	1	0	1	0	0	0	0	0	0	0	0

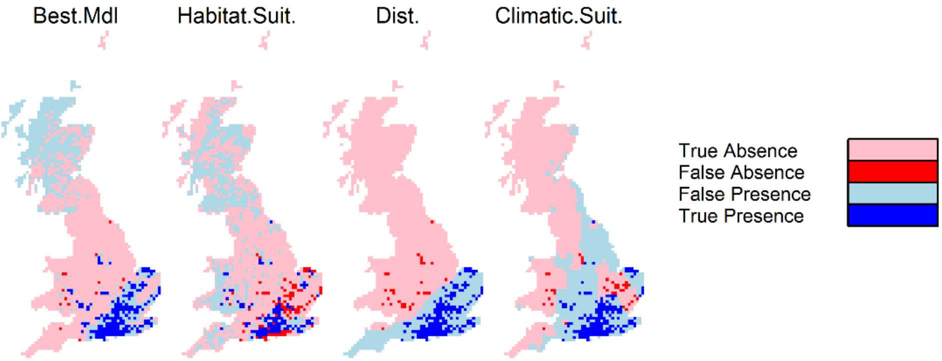
Acid Grassland	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Fen, Marsh and Swamp	1	1	1	0	0	1	0	0	1	1	0	0	0	0
Heather	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Heather grassland	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Bog	1	1	1	0	0	0	0	0	0	1	0	0	0	0
Inland Rock	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Saltwater	0	0	0	0	0	1	1	0	1	0	1	0	0	0
Freshwater	1	1	0	0	0	1	0	0	1	1	1	1	1	0
Supra-littoral Rock	0	0	0	1	0	1	0	0	1	0	0	1	1	0
Supra-littoral Sediment	0	0	0	0	0	1	1	0	1	0	0	0	1	0
Littoral Rock	0	0	0	1	0	1	0	0	1	0	0	0	1	0
Littoral Sediment	0	0	0	0	0	1	1	0	1	0	0	0	1	0
Saltmarsh	1	1	1	0	0	1	1	0	1	1	0	0	1	0
Urban	0	0	0	1	0	0	0	1	0	0	0	1	1	0
Suburban	0	0	0	1	1	0	0	1	0	0	0	1	1	0

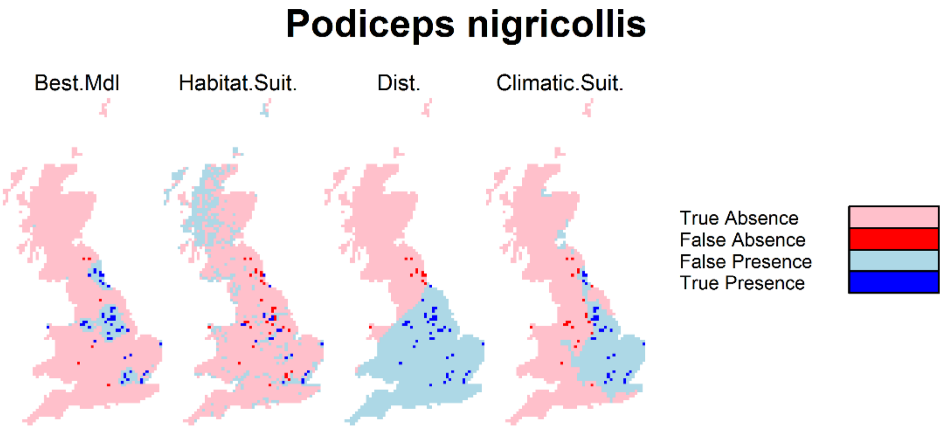



Cettia cetti


Egretta garzetta


Phoenicurus ochruros


Streptopelia decaocto


Podiceps nigricollis
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Dist.
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True Absence
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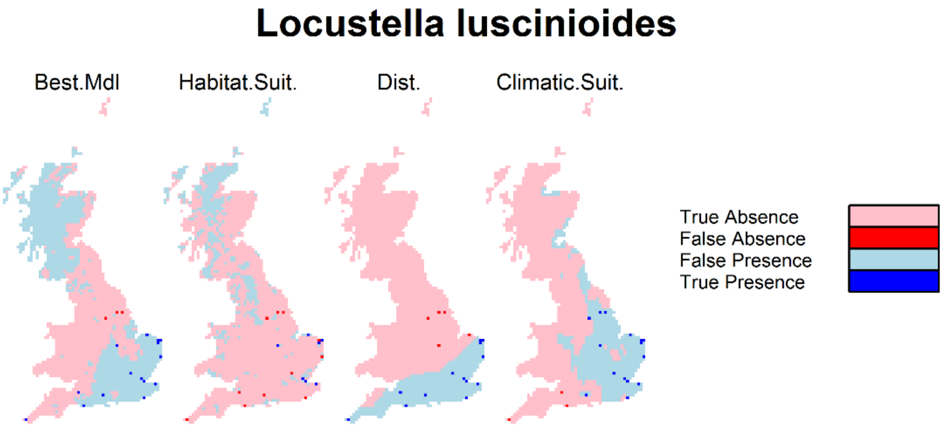
True Presence


Locustella luscinioides
Best.Mdl
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True Absence
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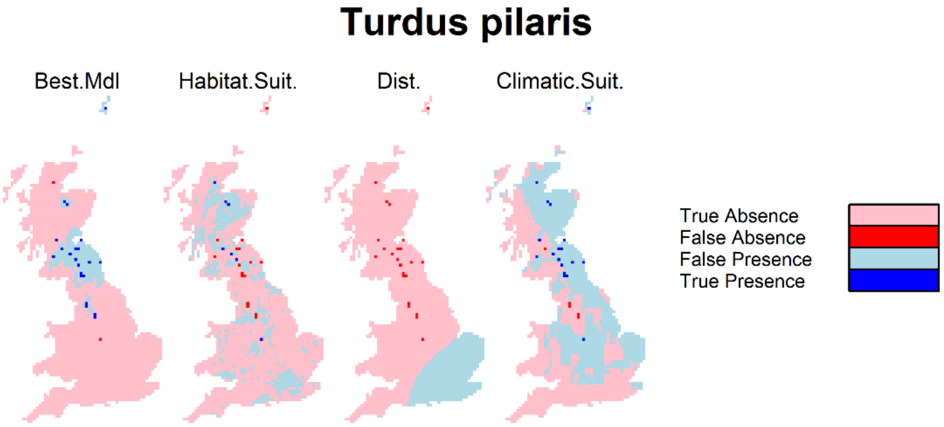
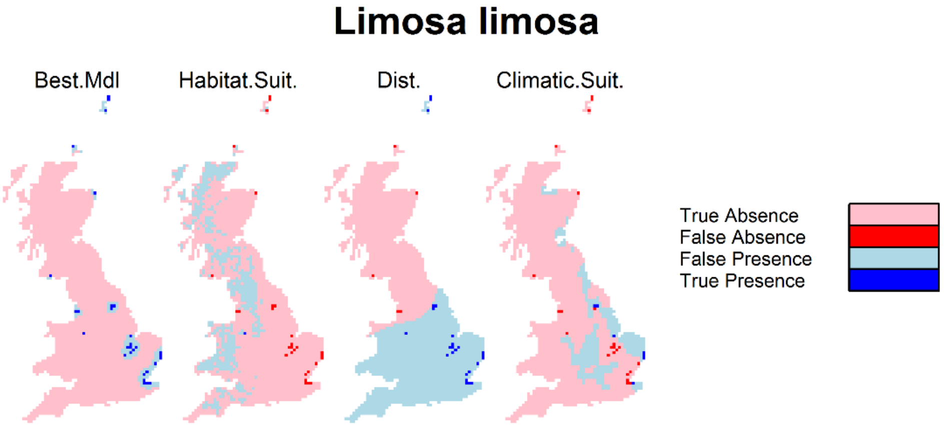
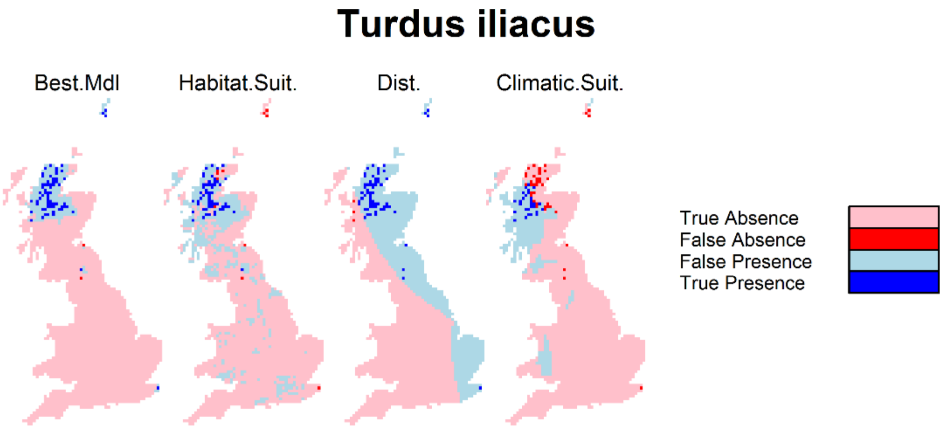
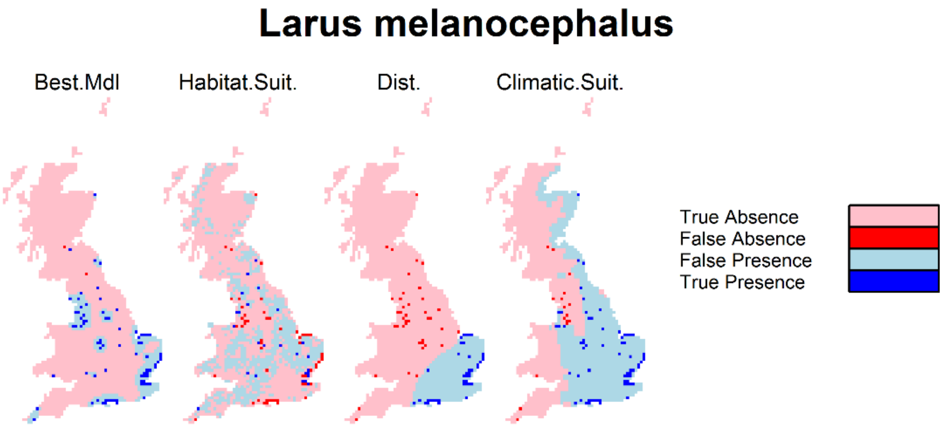
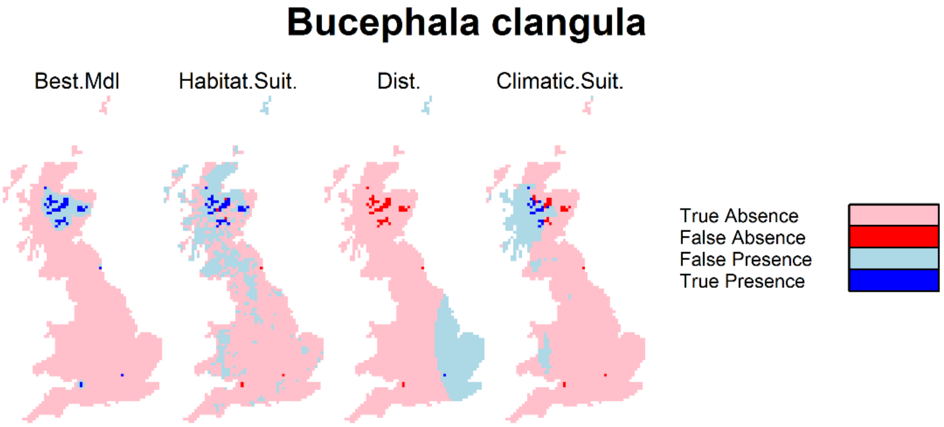
True Presence

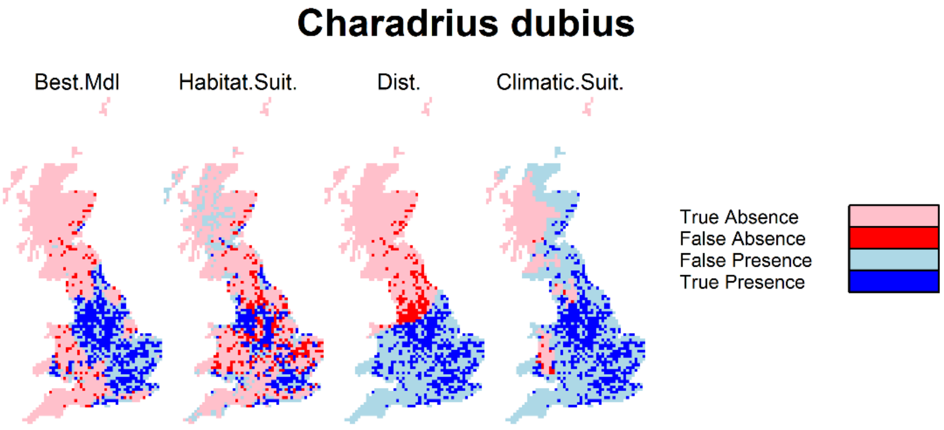

Turdus pilaris
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence

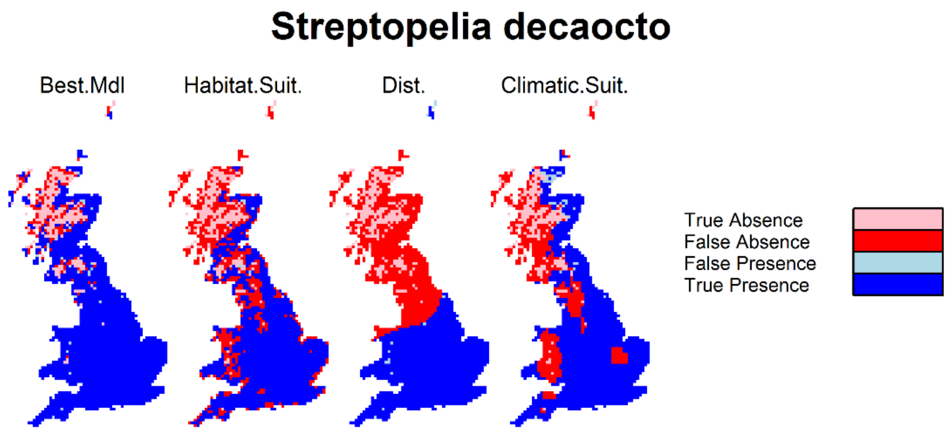

Limosa limosa
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence


Turdus iliacus
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence


Larus melanocephalus
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence

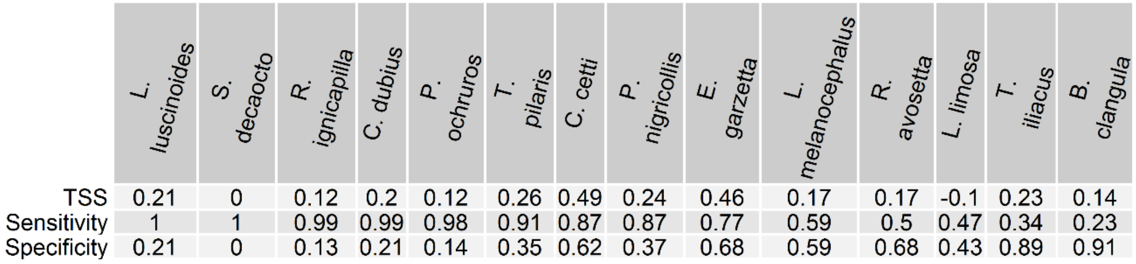

Bucephala clangula
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence


Charadrius dubius
Best.Mdl
Habitat.Suit.
Dist.
Climatic.Suit.
True Absence
False Absence
False Presence
True Presence

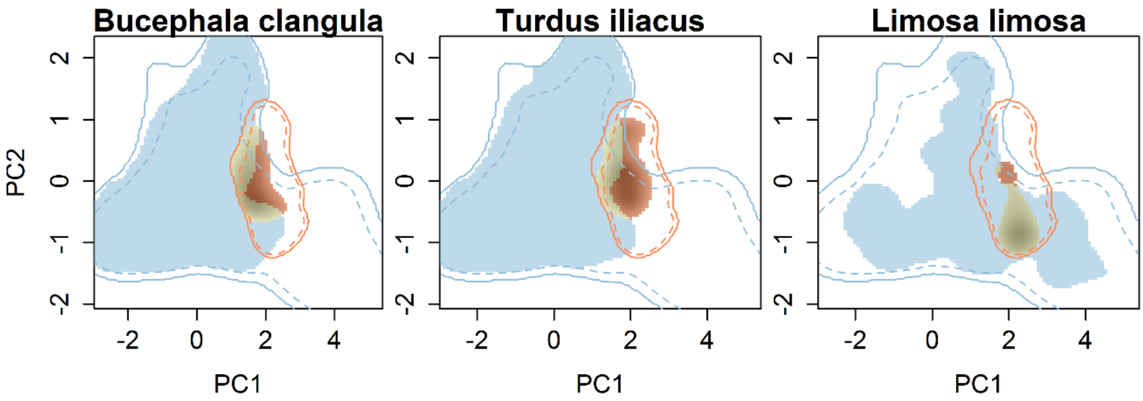


Supplementary Figure A.8(a-n): Maps showing predictive performance of the best INLA model compared to models with no spatial effect. The best models for each species are shown in Supplementary Table A.5, i.e. the model with the lowest Wantanabe-Akaike Information Criterion WAIC). The three adjacent models show the classification accuracy of the three explanatory variables with no spatial effect, i.e. logistic regression.

Supplementary Table A.6: TSS, Sensitivity & Specificity of the European climatic cSDM applied to the range-shifters' British distributions. I.e. what is the classification accuracy of the cSDM trained on the range-shifters in the European range for the British distributution at the same TSS threshold as optimal in the European Range.

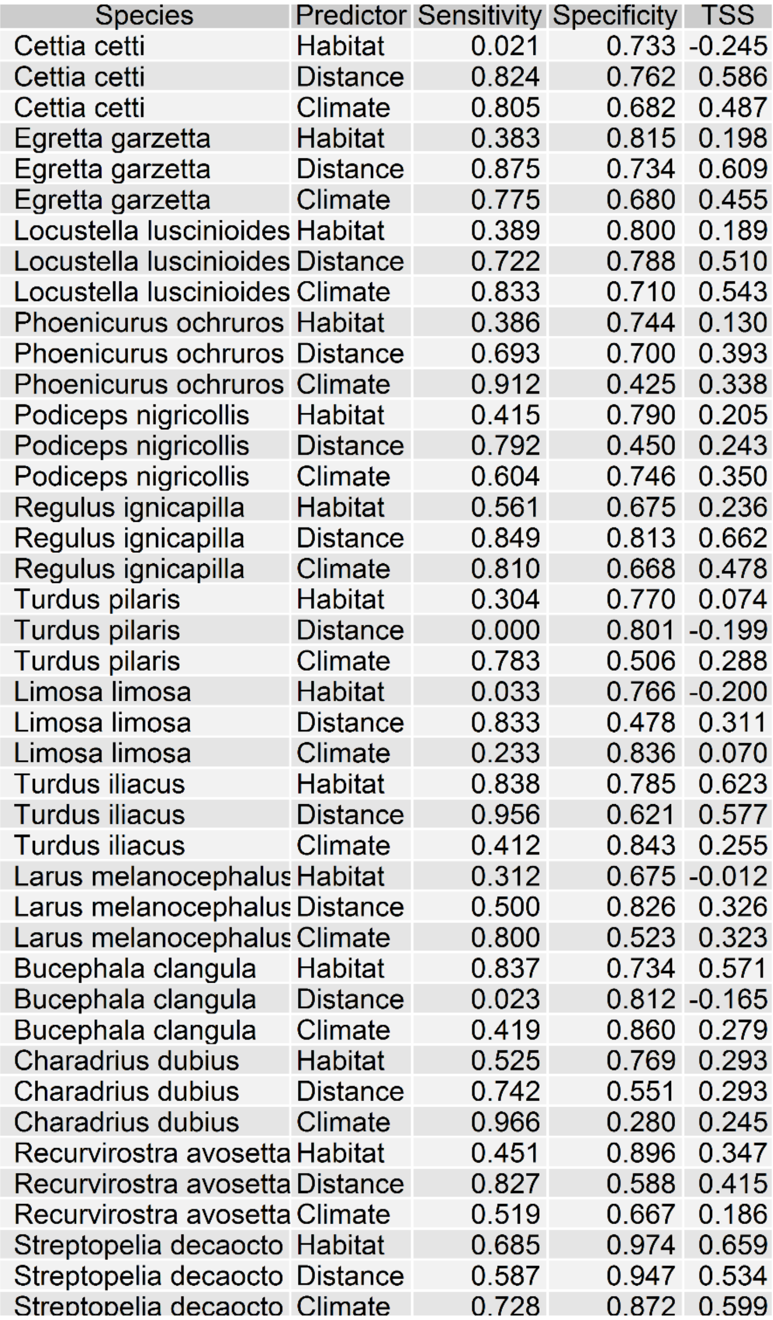


	L. luscinioides	*S. decaocto*	*R. ignicapilla*	*C. dubius*	*P. ochruros*	*T. pilaris*	*C. cetti*	*P. nigricollis*	*E. garzetta*	*L. melanocephalus*	*R. avosetta*	*L. limosa*	*T. iliacus*	*B. clangula*
TSS	0.21	0	0.12	0.2	0.12	0.26	0.49	0.24	0.46	0.17	0.17	-0.1	0.23	0.14
Sensitivity	1	1	0.99	0.99	0.98	0.91	0.87	0.87	0.77	0.59	0.5	0.47	0.34	0.23
Specificity	0.21	0	0.13	0.21	0.14	0.35	0.62	0.37	0.68	0.59	0.68	0.43	0.89	0.91



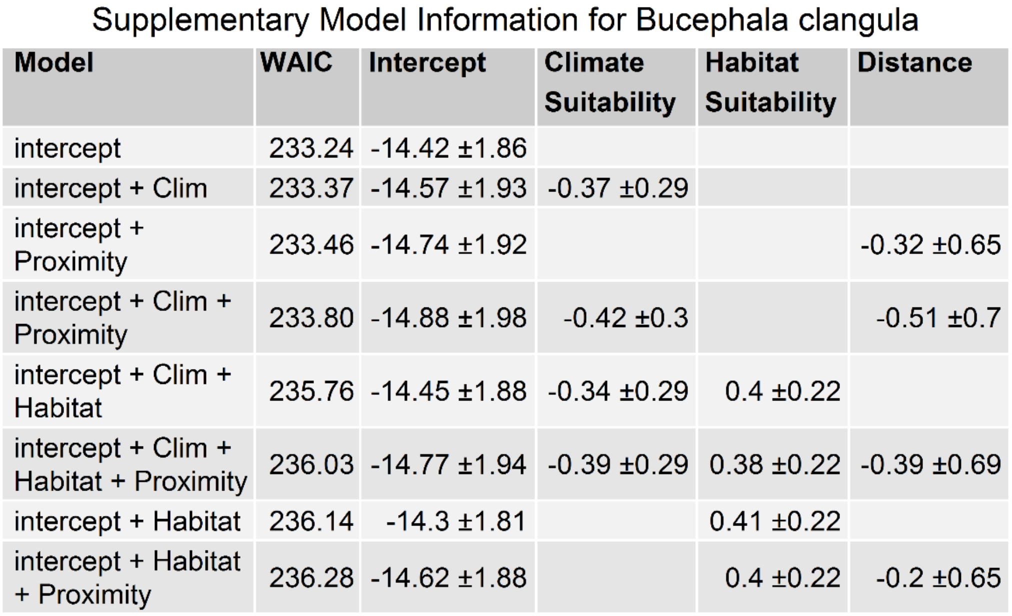
Supplementary Figure A.9: Niche models of the 3 species with >10% expansion. Areas of PCA environmental space only occupied in the European range are *shown shaded in blue, in the British range in red and both ranges in yellow. The solid outer lines show the total available PCA environmental space in each range and the dotted lines contain 75%.*

Supplementary Table A.7: TSS, Sensitivity and specificity of the spatial INLA models fitted using each one of the three predictors for the range-shifters in the British range in isolation in univariate models.



Species	Predictor	Sensitivity	Specificity	TSS
Cettia cetti	Habitat	0.021	0.733	-0.245
Cettia cetti	Distance	0.824	0.762	0.586
Cettia cetti	Climate	0.805	0.682	0.487
Egretta garzetta	Habitat	0.383	0.815	0.198
Egretta garzetta	Distance	0.875	0.734	0.609
Egretta garzetta	Climate	0.775	0.680	0.455
Locustella luscinioides	Habitat	0.389	0.800	0.189
Locustella luscinioides	Distance	0.722	0.788	0.510
Locustella luscinioides	Climate	0.833	0.710	0.543
Phoenicurus ochruros	Habitat	0.386	0.744	0.130
Phoenicurus ochruros	Distance	0.693	0.700	0.393
Phoenicurus ochruros	Climate	0.912	0.425	0.338
Podiceps nigricollis	Habitat	0.415	0.790	0.205
Podiceps nigricollis	Distance	0.792	0.450	0.243
Podiceps nigricollis	Climate	0.604	0.746	0.350
Regulus ignicapilla	Habitat	0.561	0.675	0.236
Regulus ignicapilla	Distance	0.849	0.813	0.662
Regulus ignicapilla	Climate	0.810	0.668	0.478
Turdus pilaris	Habitat	0.304	0.770	0.074
Turdus pilaris	Distance	0.000	0.801	-0.199
Turdus pilaris	Climate	0.783	0.506	0.288
Limosa limosa	Habitat	0.033	0.766	-0.200
Limosa limosa	Distance	0.833	0.478	0.311
Limosa limosa	Climate	0.233	0.836	0.070
Turdus iliacus	Habitat	0.838	0.785	0.623
Turdus iliacus	Distance	0.956	0.621	0.577
Turdus iliacus	Climate	0.412	0.843	0.255
Larus melanocephalus	Habitat	0.312	0.675	-0.012
Larus melanocephalus	Distance	0.500	0.826	0.326
Larus melanocephalus	Climate	0.800	0.523	0.323
Bucephala clangula	Habitat	0.837	0.734	0.571
Bucephala clangula	Distance	0.023	0.812	-0.165
Bucephala clangula	Climate	0.419	0.860	0.279
Charadrius dubius	Habitat	0.525	0.769	0.293
Charadrius dubius	Distance	0.742	0.551	0.293
Charadrius dubius	Climate	0.966	0.280	0.245
Recurvirostra avosetta	Habitat	0.451	0.896	0.347
Recurvirostra avosetta	Distance	0.827	0.588	0.415
Recurvirostra avosetta	Climate	0.519	0.667	0.186
Streptopelia decaocto	Habitat	0.685	0.974	0.659
Streptopelia decaocto	Distance	0.587	0.947	0.534
Streptopelia decaocto	Climate	0.728	0.872	0.599

Supplementary Table A.8(a-n): Model comparison showing the Wantanabe-Akaike Information Criterion (WAIC) of each of the 8 INLA models tested for each *species. The model coefficients with 95% credible intervals are also shown for the parameters included in the relevant model. The model with the lowest WAIC represents the most likely model of those compared given the data.*



Supplementary Model Information for Bucephala clangula

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept	233.24	-14.42 ±1.86			
intercept + Clim	233.37	-14.57 ±1.93	-0.37 ±0.29		
intercept + Proximity	233.46	-14.74 ±1.92			-0.32 ±0.65
intercept + Clim + Proximity	233.80	-14.88 ±1.98	-0.42 ±0.3		-0.51 ±0.7
intercept + Clim + Habitat	235.76	-14.45 ±1.88	-0.34 ±0.29	0.4 ±0.22	
intercept + Clim + Habitat + Proximity	236.03	-14.77 ±1.94	-0.39 ±0.29	0.38 ±0.22	-0.39 ±0.69
intercept + Habitat	236.14	-14.3 ±1.81		0.41 ±0.22	
intercept + Habitat + Proximity	236.28	-14.62 ±1.88		0.4 ±0.22	-0.2 ±0.65

Supplementary Model Information for Cettia cetti

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat + Proximity	1171.79	-8.4 ±1.16	0.82 ±0.18	-0.54 ±0.17	3.13 ±0.68
intercept + Clim + Proximity	1175.17	-8.29 ±1.23	0.91 ±0.18		3.34 ±0.72
intercept + Habitat + Proximity	1183.28	-8.7 ±1.03		-0.66 ±0.16	3.75 ±0.61
intercept + Clim + Habitat	1185.06	-6.73 ±1.67	1.08 ±0.18	-0.58 ±0.17	
intercept + Proximity	1187.00	-8.74 ±1.16			4.21 ±0.68
intercept + Clim	1187.98	-6.53 ±1.77	1.16 ±0.18		
intercept + Habitat	1193.56	-6.91 ±2.04		-0.71 ±0.17	
intercept	1195.01	-6.74 ±2.22			

Supplementary Model Information for Charadrius dubius

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat + Proximity	1878.17	-6.22 ±1.49	0.68 ±0.22	0.44 ±0.06	1.02 ±0.53
intercept + Clim + Habitat	1881.03	-6.12 ±1.57	0.71 ±0.22	0.44 ±0.06	
intercept + Habitat + Proximity	1887.08	-6.33 ±1.68		0.46 ±0.06	1.25 ±0.57
intercept + Habitat	1890.36	-6.25 ±1.85		0.46 ±0.06	
intercept + Clim + Proximity	1907.68	-6.15 ±1.38	0.82 ±0.23		1.07 ±0.52
intercept + Clim	1910.93	-6.09 ±1.46	0.85 ±0.23		
intercept + Proximity	1917.01	-6.16 ±1.53			1.36 ±0.56
intercept	1920.99	-6.17 ±1.7			

Supplementary Model Information for Egretta garzetta

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat + Proximity	1152.24	-7.86 ±1.07	0.16 ±0.16	0.69 ±0.08	3.04 ±0.54
intercept + Habitat + Proximity	1153.01	-7.91 ±1.03		0.7 ±0.08	3.15 ±0.52
intercept + Clim + Habitat	1156.32	-6.65 ±2.66	0.24 ±0.15	0.68 ±0.08	
intercept + Habitat	1157.23	-6.74 ±2.82		0.69 ±0.08	
intercept + Clim + Proximity	1201.08	-7.48 ±1.05	0.29 ±0.17		2.86 ±0.56
intercept + Proximity	1204.84	-7.55 ±0.97			3.04 ±0.52
intercept + Clim	1209.53	-6.27 ±2.06	0.42 ±0.17		
intercept	1215.63	-6.32 ±2.26			

Supplementary Model Information for Larus melanocephalus

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Proximity	516.12	-9.77 ±0.86			1.44 ±0.4
intercept + Clim + Proximity	516.99	-9.79 ±0.86	0.19 ±0.18		1.37 ±0.4
intercept + Habitat + Proximity	517.55	-9.8 ±0.87		-0.02 ±0.18	1.45 ±0.4
intercept	518.00	-9.57 ±0.99			
intercept + Habitat	518.49	-9.62 ±0.99		0.06 ±0.18	
intercept + Clim + Habitat + Proximity	518.60	-9.81 ±0.87	0.19 ±0.18	-0.04 ±0.18	1.38 ±0.4
intercept + Clim	519.61	-9.53 ±0.94	0.32 ±0.17		
intercept + Clim + Habitat	520.32	-9.58 ±0.95	0.32 ±0.17	0.04 ±0.18	

Supplementary Model Information for Limosa limosa

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept	215.34	-12.37 ±1.55			
intercept + Clim	215.65	-12.47 ±1.62	-0.29 ±0.36		
intercept + Proximity	217.19	-12.56 ±1.53			0.92 ±0.56
intercept + Clim + Proximity	217.42	-12.71 ±1.62	-0.4 ±0.37		1.06 ±0.6
intercept + Habitat + Proximity	218.19	-12.67 ±1.56		-0.04 ±0.38	0.92 ±0.59
intercept + Habitat	218.60	-12.38 ±1.53		-0.18 ±0.37	
intercept + Clim + Habitat + Proximity	219.44	-12.76 ±1.63	-0.41 ±0.37	-0.1 ±0.39	1.03 ±0.62
intercept + Clim + Habitat	219.69	-12.44 ±1.59	-0.32 ±0.36	-0.24 ±0.37	

Supplementary Model Information for Locustella luscinioides

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat + Proximity	174.79	-15.5 ±1.94	1.37 ±0.48	1.02 ±0.31	2.46 ±0.75
intercept + Clim + Proximity	180.03	-14.15 ±1.72	1.15 ±0.44		1.87 ±0.67
intercept + Habitat + Proximity	182.25	-13.62 ±1.66		0.75 ±0.27	2.74 ±0.76
intercept + Proximity	185.34	-12.81 ±1.49			2.23 ±0.67
intercept + Habitat	185.63	-10.81 ±2.46		0.31 ±0.26	
intercept	187.41	-10.48 ±2.12			
intercept + Clim + Habitat	188.52	-11.97 ±1.12	1.66 ±0.42	0.42 ±0.22	
intercept + Clim	189.01	-11.66 ±1.02	1.49 ±0.39		

Supplementary Model Information for Phoenicurus ochruros

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Habitat + Proximity	710.75	-9 ±1.1		0.94 ±0.17	1.65 ±0.46
intercept + Clim + Habitat + Proximity	712.21	-9.08 ±1.09	0.08 ±0.39	0.94 ±0.17	1.63 ±0.48
intercept + Habitat	716.55	-8.53 ±2.09		0.95 ±0.16	
intercept + Clim + Habitat	718.65	-8.6 ±1.97	0.29 ±0.37	0.95 ±0.16	
intercept + Proximity	726.98	-8.62 ±0.67			1.46 ±0.3
intercept + Clim + Proximity	728.34	-8.71 ±0.68	0.04 ±0.38		1.46 ±0.33
intercept	740.65	-8.44 ±1.17			
intercept + Clim	741.79	-8.5 ±1.09	0.28 ±0.41		

Supplementary Model Information for Podiceps nigricollis

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Habitat + Proximity	384.56	-11.92 ±1.55		0.38 ±0.12	1.26 ±0.62
intercept + Habitat	387.18	-11.7 ±1.59		0.36 ±0.12	
intercept + Clim + Habitat + Proximity	389.30	-11.71 ±1.53	0.29 ±0.26	0.36 ±0.12	1.05 ±0.64
intercept + Proximity	389.47	-11.58 ±1.43			1.15 ±0.59
intercept	392.11	-11.29 ±1.43			
intercept + Clim + Habitat	393.52	-11.25 ±1.45	0.44 ±0.25	0.34 ±0.12	
intercept + Clim + Proximity	394.74	-11.33 ±1.39	0.33 ±0.25		0.91 ±0.6
intercept + Clim	398.75	-10.85 ±1.28	0.48 ±0.24		

Supplementary Model Information for Recurvirostra avosetta

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Habitat + Proximity	564.28	-11.92 ±1.51		0.68 ±0.11	2.7 ±0.68
intercept + Clim + Habitat + Proximity	564.81	-12.02 ±1.52	0.15 ±0.22	0.68 ±0.11	2.71 ±0.69
intercept + Habitat	571.43	-11.12 ±1.82		0.65 ±0.11	
intercept + Clim + Habitat	571.90	-11.19 ±1.81	0.15 ±0.21	0.65 ±0.11	
intercept + Proximity	582.63	-11.68 ±1.5			2.55 ±0.69
intercept + Clim + Proximity	583.36	-11.77 ±1.52	0.13 ±0.24		2.56 ±0.69
intercept	589.33	-10.92 ±1.65			
intercept + Clim	590.00	-10.98 ±1.65	0.16 ±0.22		

Supplementary Model Information for Regulus ignicapilla

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Habitat + Proximity	652.67	-14.56 ±1.78		1.28 ±0.17	4.64 ±0.82
intercept + Clim + Habitat + Proximity	653.58	-14.68 ±1.8	-0.19 ±0.5	1.28 ±0.17	4.76 ±0.84
intercept + Habitat	663.62	-12.69 ±2.49		1.19 ±0.17	
intercept + Clim + Habitat	664.90	-12.78 ±2.47	0.16 ±0.49	1.2 ±0.17	
intercept + Clim + Proximity	717.35	-12.65 ±1.56	-0.56 ±0.46		3.84 ±0.75
intercept + Proximity	717.71	-12.6 ±1.57			3.6 ±0.73
intercept	727.57	-11.47 ±2			
intercept + Clim	728.52	-11.59 ±2.04	-0.06 ±0.45		

Supplementary Model Information for Streptopelia decaocto

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat	765.94	10.36 ±0.86	0.59 ±0.16	2.38 ±0.21	
intercept + Clim + Habitat + Proximity	766.14	10.59 ±0.9	0.55 ±0.17	2.34 ±0.22	0.31 ±0.33
intercept + Habitat + Proximity	773.06	10.72 ±0.87		2.49 ±0.21	0.59 ±0.3
intercept + Habitat	774.28	10.42 ±0.85		2.59 ±0.21	
intercept + Clim + Proximity	910.26	8.34 ±0.92	1.2 ±0.17		1.26 ±0.41
intercept + Clim	913.82	7.77 ±1.1	1.33 ±0.17		
intercept + Proximity	942.37	8.68 ±0.85			2.03 ±0.37
intercept	944.52	8.25 ±1.37			

Supplementary Model Information for Turdus iliacus

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim + Habitat + Proximity	327.89	-14.58 ±2.05	-0.31 ±0.23	0.63 ±0.18	1.96 ±0.62
intercept + Clim + Habitat	330.60	-12.35 ±1.85	-0.42 ±0.23	0.57 ±0.18	
intercept + Clim + Proximity	331.88	-14.68 ±2.27	-0.33 ±0.24		1.91 ±0.67
intercept + Habitat + Proximity	332.67	-14.27 ±1.89		0.62 ±0.18	1.96 ±0.57
intercept + Clim	334.91	-12.4 ±1.99	-0.41 ±0.24		
intercept + Habitat	337.42	-12.02 ±1.74		0.55 ±0.17	
intercept + Proximity	337.57	-14.24 ±2.08			1.89 ±0.62
intercept	342.28	-11.96 ±1.86			

Supplementary Model Information for Turdus pilaris

Model	WAIC	Intercept	Climate Suitability	Habitat Suitability	Distance
intercept + Clim	229.63	-11.38 ±1.33	0.95 ±0.51		
intercept + Clim + Habitat	230.91	-11.49 ±1.35	0.96 ±0.51	-0.06 ±0.23	
intercept	231.17	-10.91 ±1.33			
intercept + Habitat	232.64	-11 ±1.35		-0.06 ±0.23	
intercept + Proximity	237.20	-10.89 ±1.26			-0.66 ±0.44
intercept + Habitat + Proximity	237.48	-11.04 ±1.28		-0.06 ±0.22	-0.66 ±0.45
intercept + Clim + Proximity	239.61	-11.19 ±1.21	1.07 ±0.48		-0.76 ±0.38
intercept + Clim + Habitat + Proximity	241.20	-11.28 ±1.23	1.1 ±0.49	-0.1 ±0.21	-0.78 ±0.38

Appendix B: Chapter 3 (Supplementary Materials)

Supplementary Figures and Tables

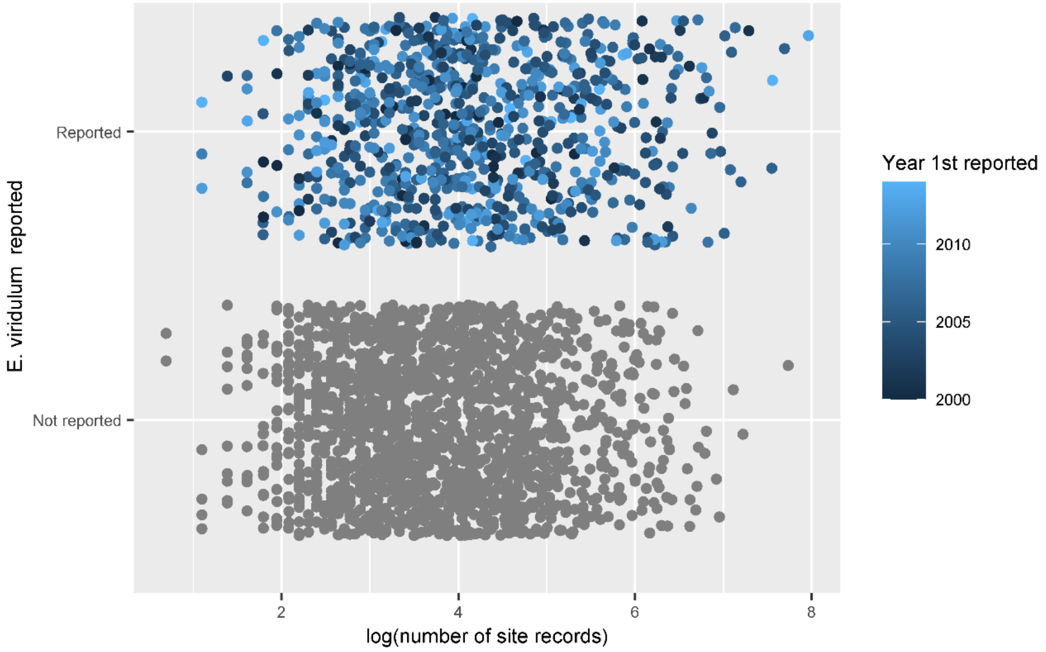
Supplementary Method B.1: JAGS model for E. viridulum's effect on native species. Native species are indexed by i, sites by j, year by t and suborder by f. The two models are shown by noting deviations from the model excluding climate with an asterisk and underlining sections of code used only for the model including climate.

```
#####
#Multi-Dynamic occupancy model with data in long format (one line per
visit)
Model {
#####State Priors

For (i in 1:nspecies){
  # FIXED EFFECTS
  init.occ[i] ~ dunif(0, 1) # vague prior on occupancy in year 1.

# RANDOM EFFECTS
alpha.phi[i] ~ dnorm(mu.alpha.phi, tau.alpha.phi)
logitgamma[i] ~ dnorm(mu.gamma, tau.gamma) # Colonisation
probabilities
logit(gamma[i]) <- logitgamma[i]

# EFFECTS THAT ARE RANDOM BUT SPLIT BY SUB-ORDER
beta1[i] ~ dnorm(mu.beta1[Aniso[i]], tau.beta1[Aniso[i]])
beta2[i] ~ dnorm(mu.beta2[Aniso[i]], tau.beta2[Aniso[i]])*
    *only present in Climate model
}
# State model hyperpriors
mu.alpha.phi ~ dnorm(0, 0.01) #persistence intercept
mu.gamma ~ dnorm(0, 0.01)
tau.alpha.phi ~ dt(0,1,1)T(0,)
tau.gamma ~ dt(0,1,1)T(0,)

for(f in 1:2){
beta1.mean[f] ~ dunif(0,1)
mu.beta1[f] <- logit(beta1.mean[f])
tau.beta1[f] ~ dt(0,1,1)T(0,)

beta2.mean[f] ~ dunif(0,1)
mu.beta2[f] <- logit(beta2.mean[f])
tau.beta2[f] ~ dt(0,1,1)T(0,)*
    *only present in Climate model
}
############################### Observation model priors
For (i in 1:nspecies){
dtype1.p[i] ~ dnorm(mu.d1.p, tau.lp1)
dtype2.p[i] ~ dnorm(mu.d2.p, tau.lp2)
dtype3.p[i] ~ dnorm(mu.d3.p, tau.lp3)
```

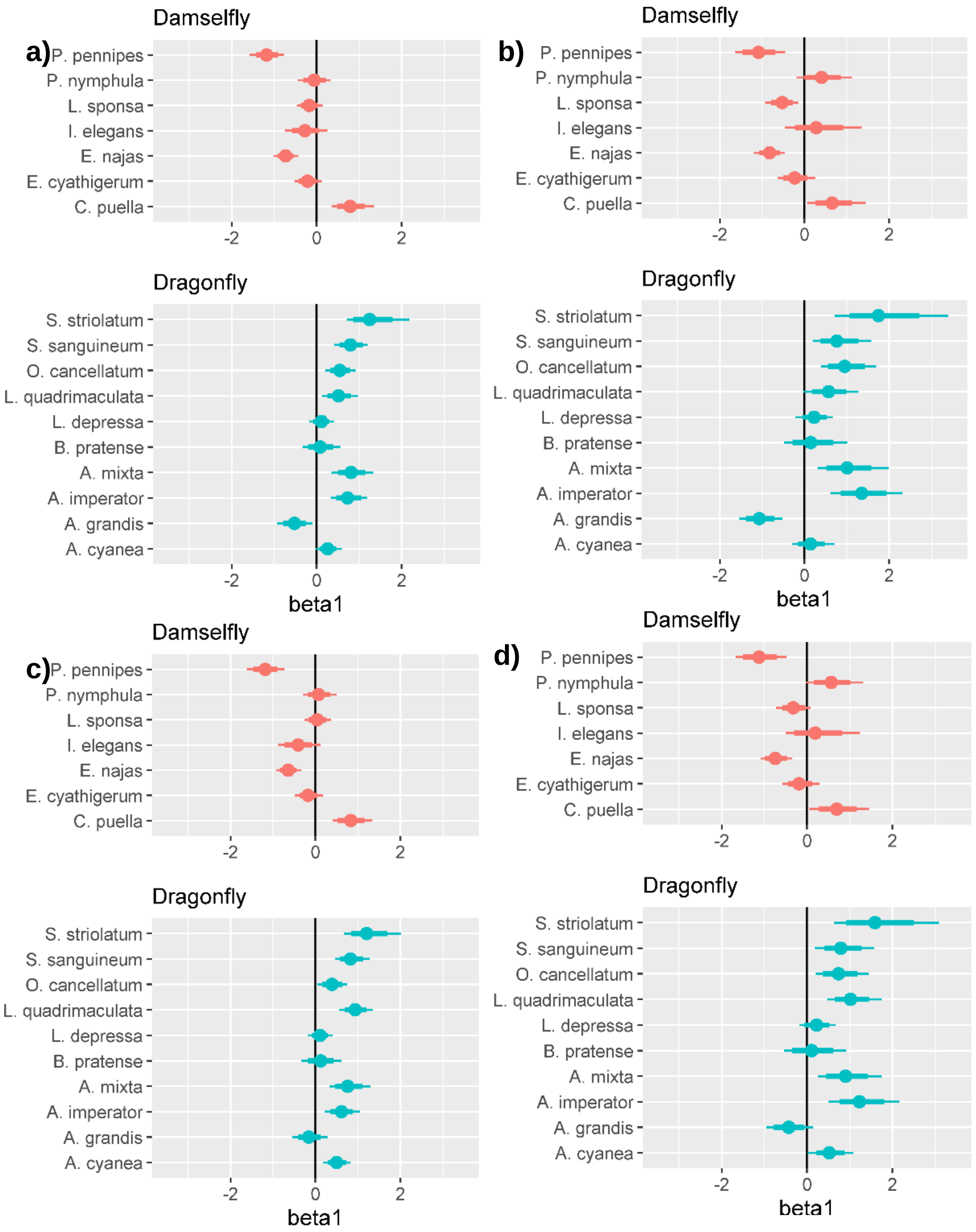
```
dtype4.p[i] ~ dnorm(mu.d4.p, tau.lp4)
}
# observation model hyperpriors
mu.d1.p ~ dnorm(-1.85, 0.01)
mu.d2.p ~ dnorm(0, 0.01)
mu.d3.p ~ dnorm(0, 0.01)
mu.d4.p ~ dnorm(0, 0.01)

tau.lp1 ~ dt(0,1,1)T(0,)
tau.lp2 ~ dt(0,1,1)T(0,)
tau.lp3 ~ dt(0,1,1)T(0,)
tau.lp4 ~ dt(0,1,1)T(0,)

################################
# State model
for (i in 1:nspecies){
 for (j in 1:nsite){ # j loop indexes the monad
  z[i,j,1] ~ dbern(init.occ[i])
  for (t in 2:nyear){
# Persistence at site i in year t is a function of covariates in year
t-1
    logit(phi[i,j,t]) <- alpha.phi[i] + beta1[i] * EV[j,t-1] +
beta2[i] * SpatAnol[j]*
    *only present in Climate model
# Dynamic Occupancy = previous occupancy, modified by persistence +
colonization
    muZ[i,j,t] <- z[i,j,t-1] * phi[i,j,t] + (1 - z[i,j,t-1]) *
gamma[i]

    # Simulated True occupancy z at site i in year t
    z[i,j,t] ~ dbern(muZ[i,j,t])

}}}

# Observation model:
for (i in 1:nspecies){
  for(k in 1:nvisit) {
  #for each visit, find the matching siteand year identities
logit(p[i,k]) <- dtype1.p[i] + dtype2.p[i]*DATATYPE2[k] +
dtype3.p[i]*DATATYPE3[k] + dtype4.p[i]*DATATYPE4[k]

  Py[i,k] <- z[i,Site[k],Year[k]] * p[i,k]
  y[k,i] ~ dbern(Py[i,k])
}}

######## DERIVED PARAMETERS
# difference between sub-orders
beta1.diff <- mu.beta1[1] - mu.beta1[2]
}
```

Supplementary Table B.1: Species habitat preferences from Powney et al (2014).The 17 species included in our analysis are highlighted in yellow plus E. viridulum in red.

Species	*Aeshna affinis*	*Aeshna grandis*	*Aeshna isosceles*	*Aeshna mixta*	*Anax imperator*	*Brachytron pratense*	*Coenagrion puella*	*Coenagrion pulchellum*	*Coenagrion scitulum*	*Enallagma cyathigerum*	*Erythromma najas*	*Erythromma viridulum*	*Ischnura elegans*	*Lestes dryas*	*Lestes sponsa*	*Lestes viridis*	*Libellula depressa*	*Libellula quadrimaculata*	*Orthetrum cancellatum*	*Pyrrhosoma nymphula*	*Sympetrum sanguineum*	*Ischnura pumilio*	*Lestes barbarus*	*Libellula fulva*	*Platycnemis pennipes*	*Sympetrum striolatum*
Lowland rivers & canals	0	1	0	1	1	1	1	1	0	1	1	1	1	0	1	1		1	1	1	1	0	0	1	1	1
Streams & upland rivers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Moorland, lowland wet heath & bog	0	1	0	0	1	1		0	0	1	0	0	1	0	1	0	0	1		1	1	1	1	0	0	1
Levels, fens & grazing marshes	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ponds & lakes	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1
Woodland	0	1	0	1	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1



Supplementary Figure B.1: Ln(records) at sites with or without E. viridulum records. At sites where it was recorded during the study period the year of arrival is indicated using a colour scale, darker points were recorded earlier. The *absence of a strong trend in the 1st year reported with number of records, suggests that E. viridulum was not detected in certain regions first simply due to recording effort.*



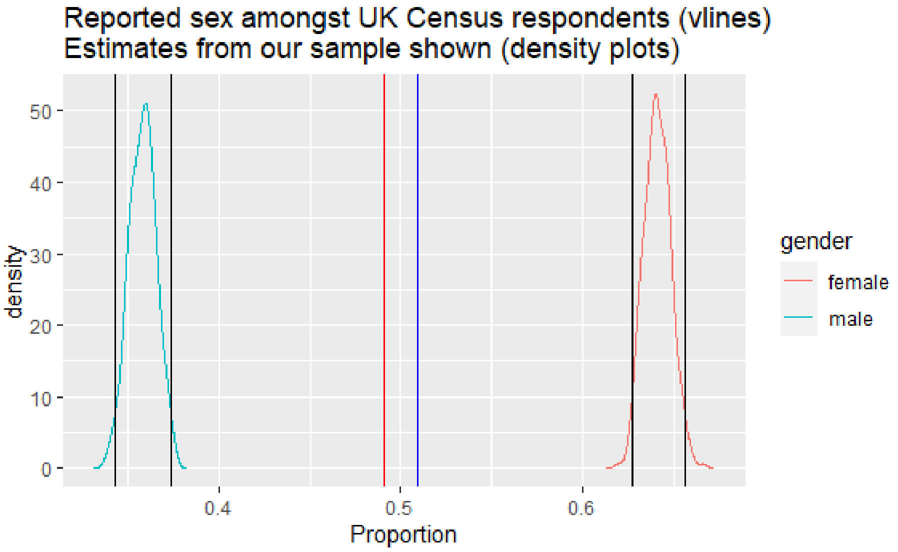
Supplementary Figure B.2: E. viridulum effect on species site persistence probabilty (β1) by model: a) Model assuming E. viridulum persisted as sites once established and no effect of climate anomaly, b) Model assuming E. viridulum was present at sites only in years it was reported and no effect of climate anomaly, c) Model assuming E. viridulum persisted as sites once established and including an effect of climate anomaly, d) Model assuming E. viridulum was *present at sites only in years it was reported and including an effect of climate anomaly (Credible intervals (point = median, thick band = 80% CI, thin band = 95% CI). A -ve coefficient indicates E. viridulum presence reduced the probability of species persistence and a +ve coefficient that presence increased it.*

Appendix C: Chapter 4 (Supplementary Materials)

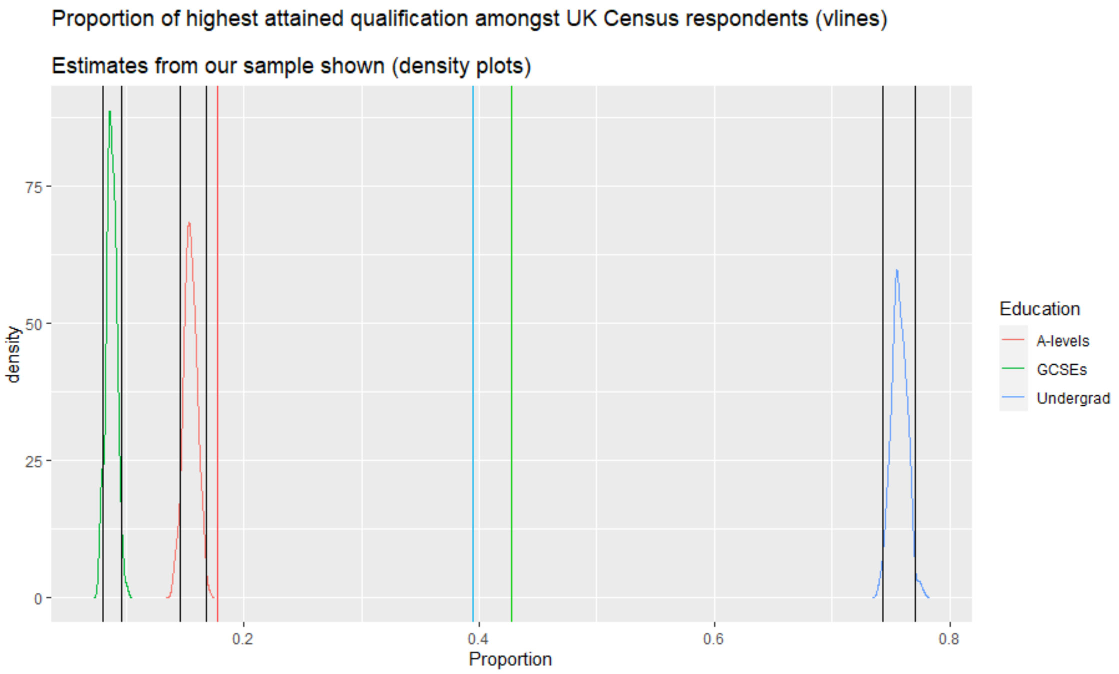
Supplementary Figures and Tables

Supplementary Table C.1: Latin and common names of species in the surveywith their respective taxonomic group.

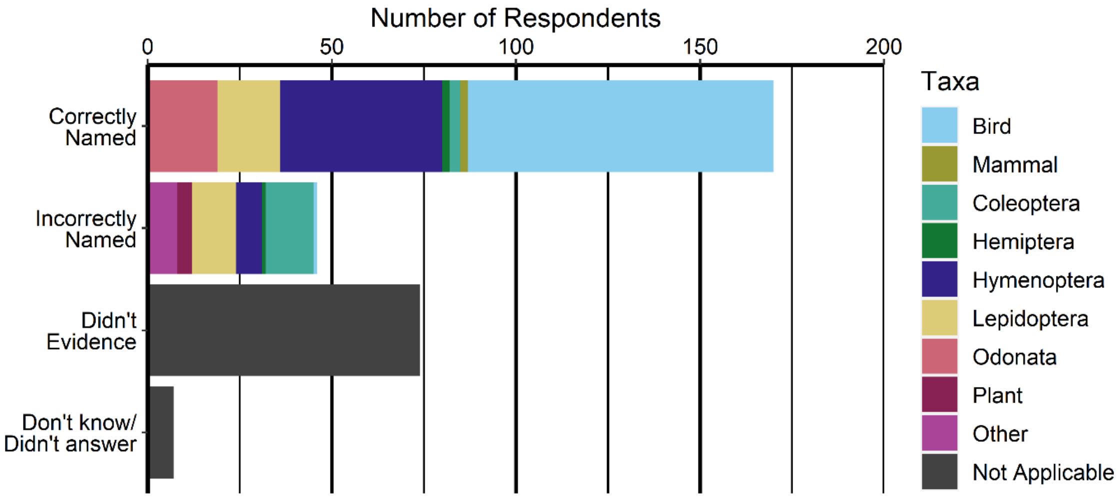
Latin Name	Common Name	Taxonomic group
Egretta garzetta	Little Egret	Bird
Ixobrychus minutus	Little Bittern	Bird
Ardea alba	Great White Egret	Bird
Bubulcus ibis	Cattle Egret	Bird
Plegadis falcinellus	Glossy Ibis	Bird
Ardea purpurea	Purple Heron	Bird
Platalea leucorodia	Eurasian Spoonbill	Bird
Himantopus himantopus	Black-winged stilt	Bird
Aeshna affinis	Southern Migrant Hawker	Dragonfly
Erythromma viridulum	Small Red-eyed Damselfly	Dragonfly
Cryphia algae	Tree Lichen Beauty	Moth
Platyperigea kadenii	Clancy's Rustic	Moth
Bombus Hypnorum	Tree Bumblebee	Bees and Wasps
Dolichovespula saxonica	Saxon Wasp	Bees and Wasps
Eurydema ornata	Ornate Shieldbug	Shieldbug
Rhaphigaster nebulosa	Mottled Shieldbug	Shieldbug



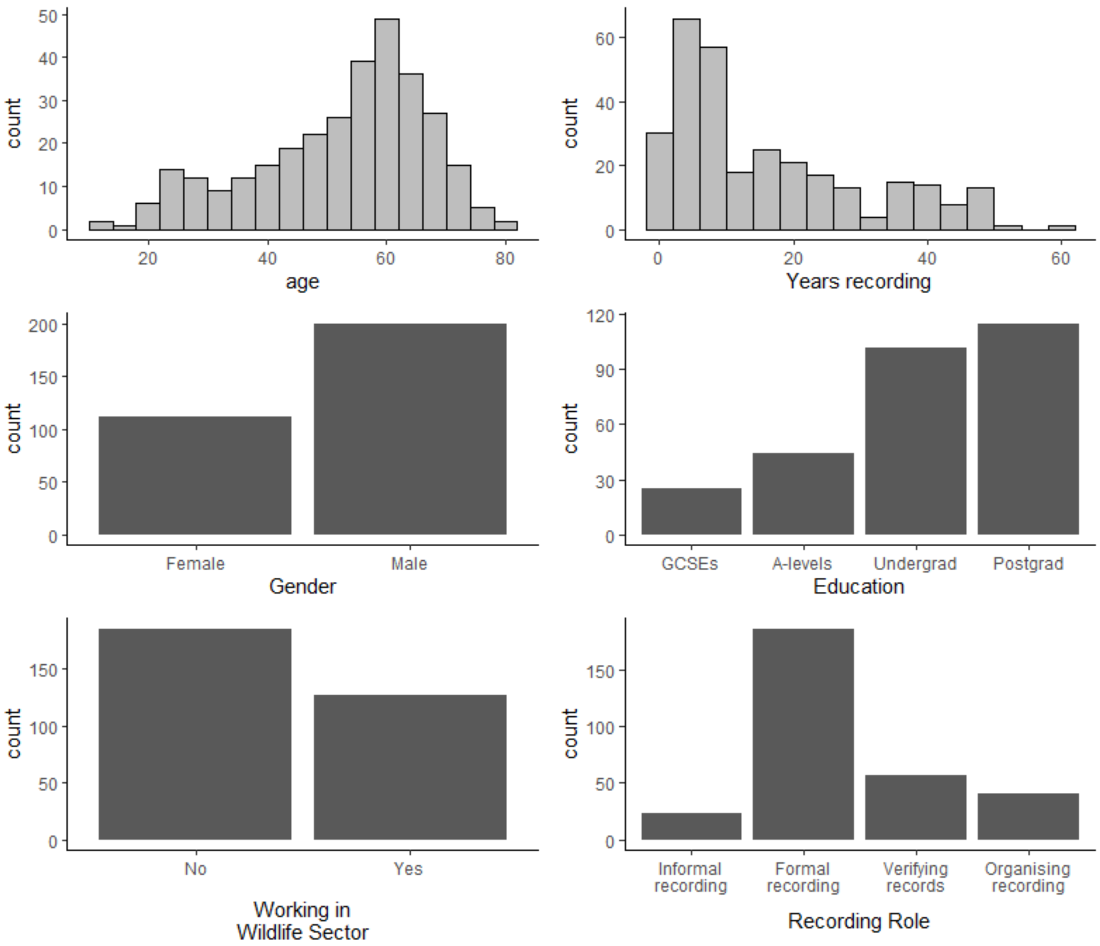
Supplementary Figure C.1: Posterior predictions for respondent's gender (95 % credible intervals are show in black). The proportion of each category in the UK 2011 census are coloured respectively. As the coloured lines fall outside the credible intervals there is a greater than 95% chance that proportions are different.



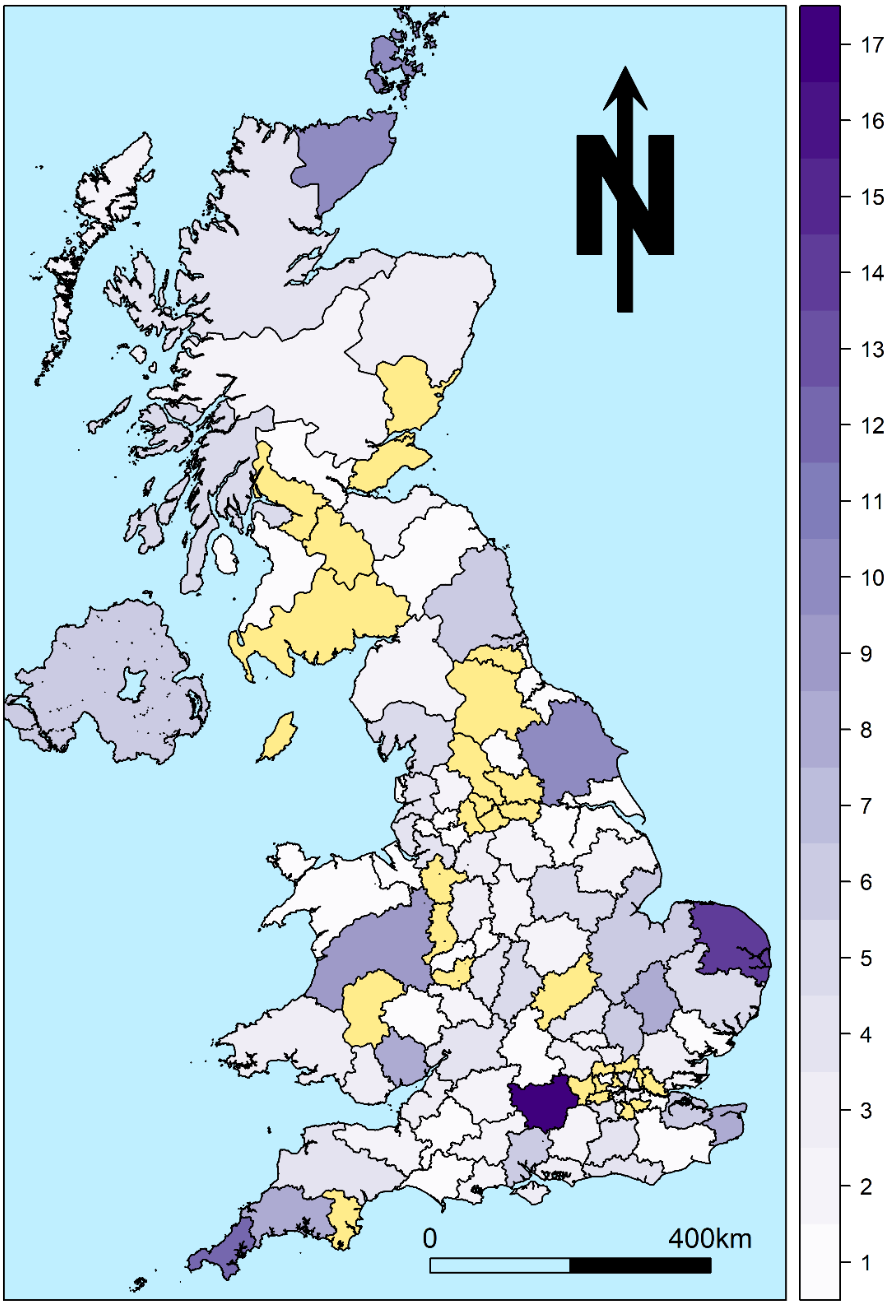
Supplementary Figure C.2: Posterior predictions for respondent's educational level (95% credible intervals are show in black).The proportion of each category in the UK 2011 census is shown in matching colours. As the coloured lines fall outside the credible intervals for all except A-Levels there is a greater than 95% chance that proportions are different.



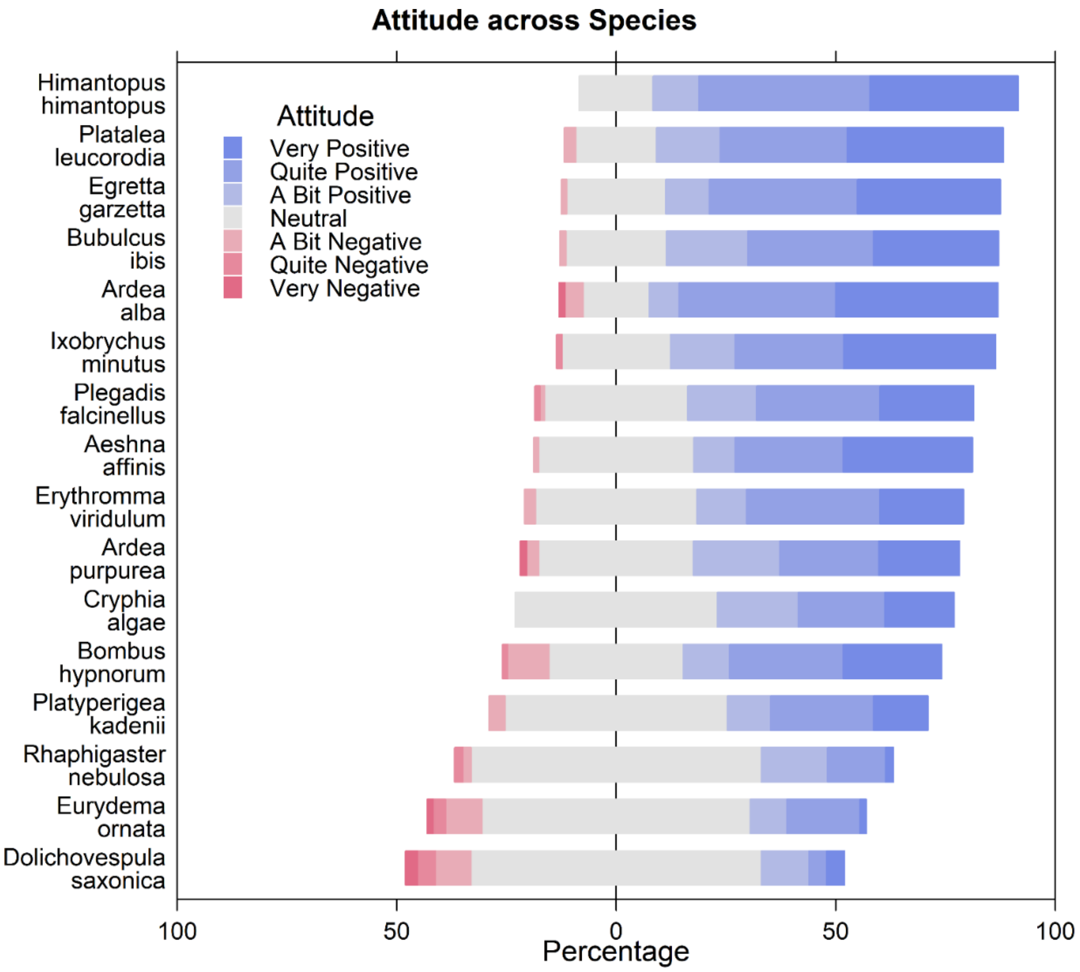
Supplementary Figure C.3: Number of respondents aware of and/or able to name a range-shifting species in the UK (see pg 3 of the survey in Appendix D). Resoonses are coloured by taxon group of the species named – NAs occur when respondents didn't respond naming a particular species.



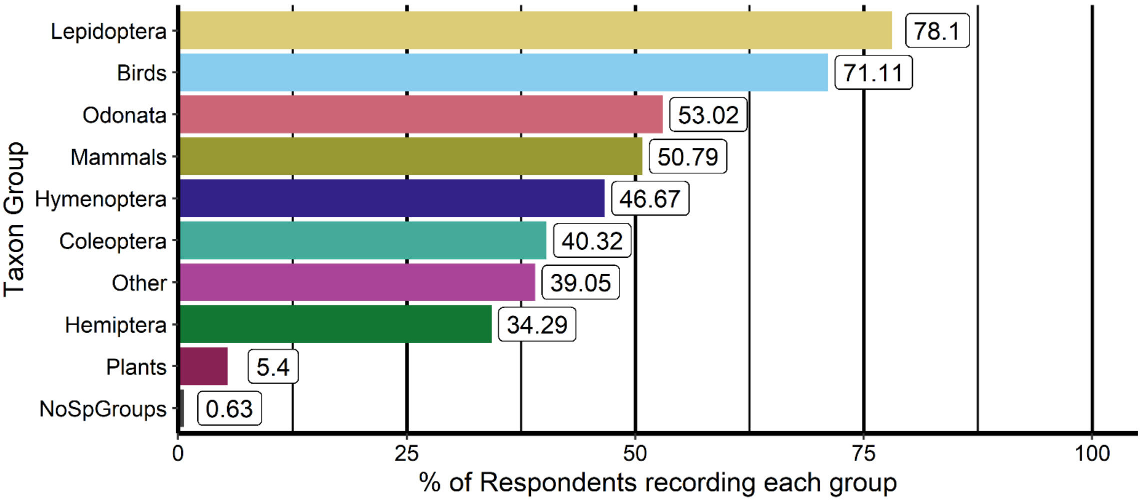
Supplementary Figure C.4: Distributions of respondent characteristicsas Histograms (continuous variables) and barcharts (discrete variables)



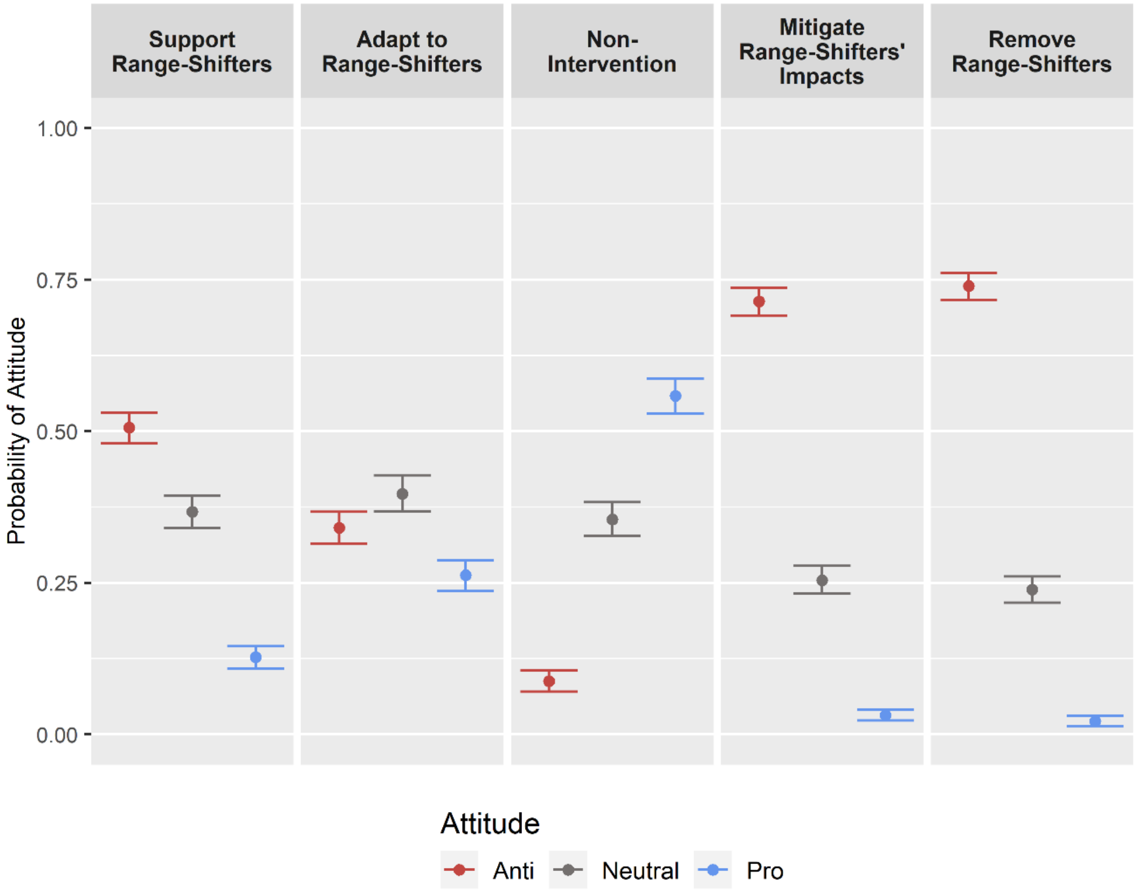
Supplementary Figure C.5: The frequency of respondents from each UK postcode outward code (e.g., for TR10 9FE -> TR) at the end of the survey, (yellow areas had no respondents)



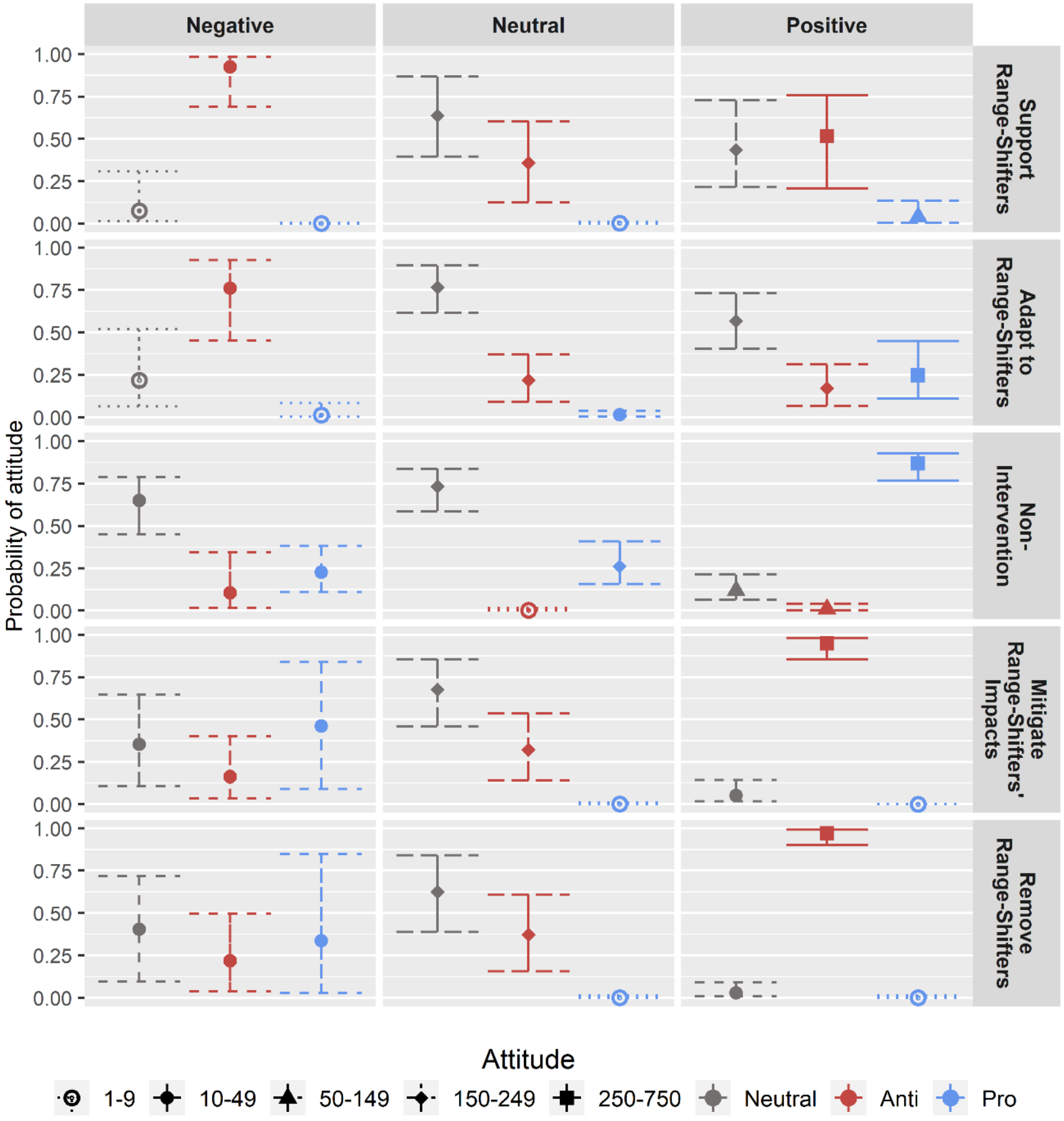
Supplementary Figure C.6: Likert plot of attitude responses for each species



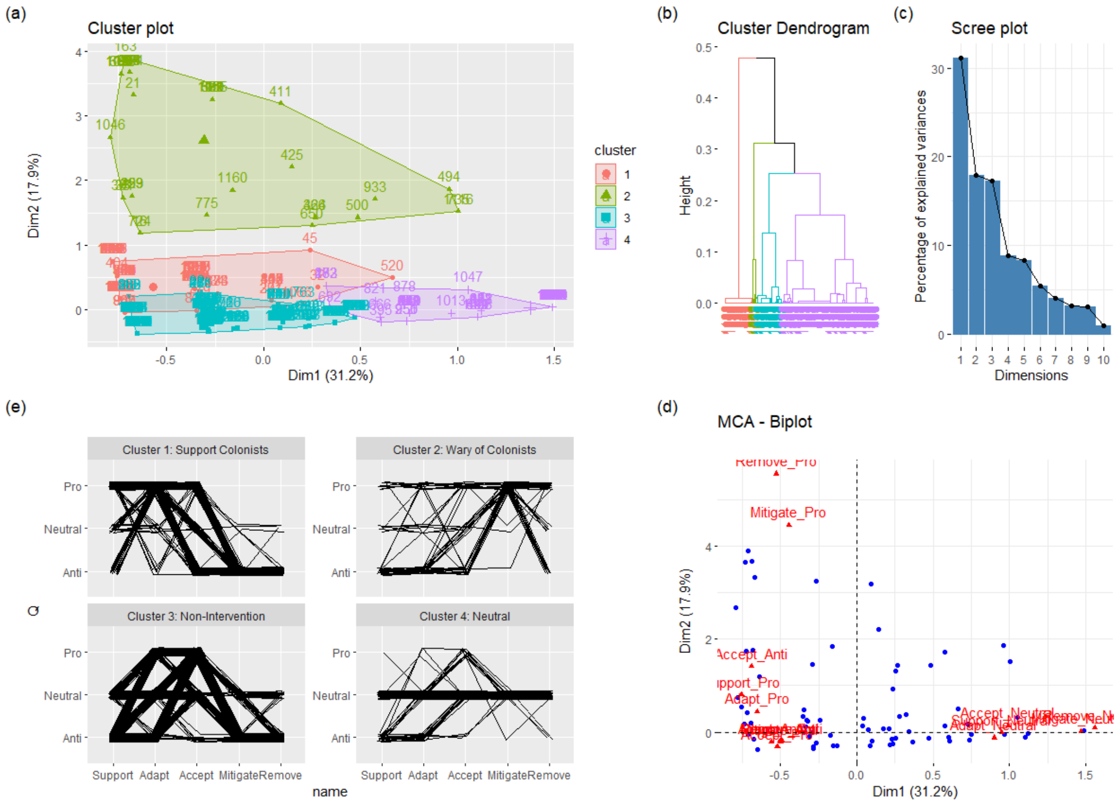
Supplementary Figure C.7: Percentage of respondents recording each taxon group



Supplementary Figure C.8: Posterior predictions for the probability of a respondent being neutral (grey), pro (blue) or anti (red) towards a given management option. Points show the median of the posterior and the error bars 95% credible intervals.

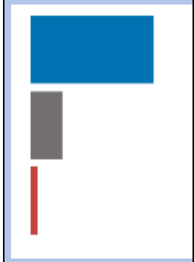


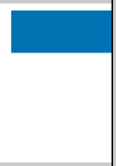
Supplementary Figure C.9: Posterior predictions for the probability of each attitude to a given management option(Y-axis facets), depending on their attitude to the species (X-axis facets). Neutral attitudes (grey), pro (Blue) or anti (red).The shape and linetype shows the number of responses for each Attitude to Management option. Points show the median of the posterior and the error bars 95% credible intervals.



Supplementary Figure C.10: Outputs of the MCA analysis. Figure C.10(a) shows the four clusters identified plotted against the first two principal components identified by the multiple correspondence analysis. Figure C.10(b) shows a scree plot showing the decline in variance explained as more components are added. Figure C.10(b) shows thehierarchical distance between clusters. The loadings of each variable onto the first two dimensions of the MCA are show in Figure C.10(d). Figure C.10(e) shows each respondents answers on attitudes to management (by species) with jitter to allow visualisation.

Supplementary Table C.2: Coding framework for respondent's attitudes to species (rather than their attitudes to their management Table 4.2). An illustrative quote accompanies a summary of what the sub-theme is intended to capture. RC stands for references coded. The bar chart accompanying each theme and subtheme shows the relative proportion references coded from respondents with attitudes that were: neutral = grey, positive = blue, negative = red).

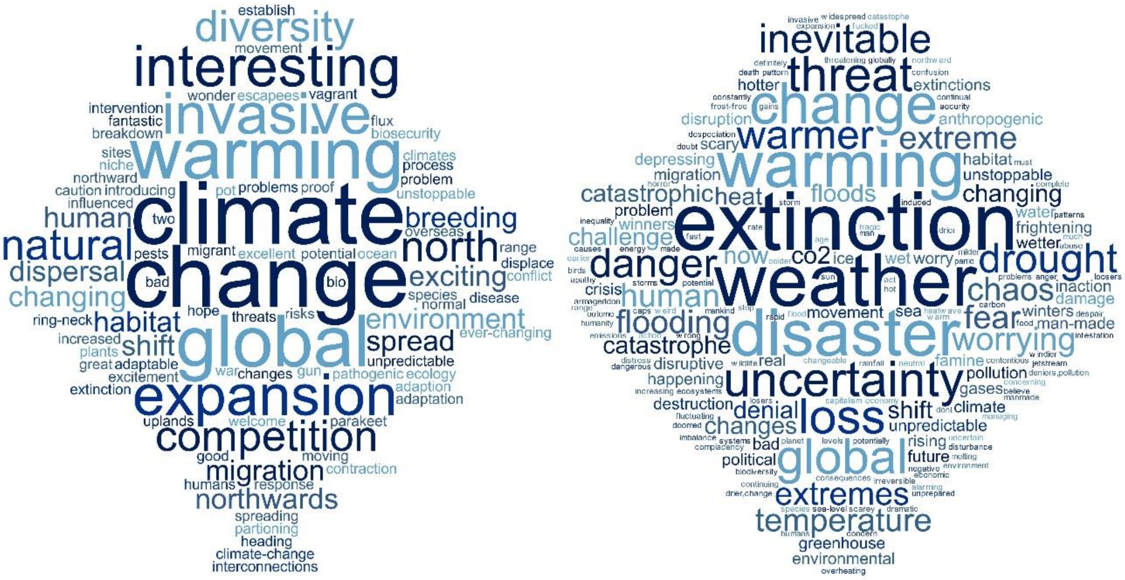
Theme	Sub-theme	Summary	Quotes
Cost / Benefit ratio of the Range-shifting Species  RC=1017	Positive effects on recipient ecosystems  RC=451	There will be positive effects from the range-shifter on the recipient ecosystem, both ecological such as increased resilience and social such as eco-tourism.	"They are exciting, beautiful birds and although they are not native, if they are range expanding naturally, it feels like a positive thing"
	Minimal effects on recipient ecosystems  RC=292	There will be minimal effects either positive or negative on the recipient ecosystem from the range-shifter.	"They are well established in our area and so far have little discernible effect on the local ecology"
	Negative effects on recipient ecosystems  RC=252	Concern about perceived or potential negative effects either positive on the recipient ecosystem from the range-shifter. Mostly focused on risks rather than proven effects.	"competition with native species such as heron could affect the survival of our wading birds."
	Conservation statuses of the range-shifter  RC=22	Threatened range-shifters deserve conservation assistance, actions to promote the global conservation status of a species is important.	"UK may be important in maintaining its global population in the future."
Human intervention in Nature  RC =178	Allowing Nature to take its course is preferable to human intervention  RC=146	Allowing natural processes to shape the outcomes of range-shift is sufficient to achieve better outcomes than trying to manage it directly.	"species arriving here without human interference are to be welcomed...it is part of the way the natural world has always worked"
	Range-shifters are positive but climate change is worrying  RC=32	We can distinguish between anthropogenic climate change which is worrying but still feel positive about species responding to their changed environment "naturally".	"I am 'positive' with regard to a new species becoming established but I am uneasy because the underlying reasons should be worrying all of us."

Cost / Benefit ratio of management actions	Too expensive / impossible to ameliorate risk through management  RC=13	Management to try to control range-shifters will be very expensive for their effect. Many actions may be infeasible.	“I also think that doing anything about it could be like King Canute trying to hold back the tide.”
Nativeness	Natives should be prioritised for support.  RC=12	Native species should be our priority. We should conserve native species rather than support range-shifters and protect native species if it is them or the range-shifter.	“Spoonbills were a British bird that became extinct due to human exploitation. We should work to restore them to the fauna.”

Supplementary Table C.3: Coding framework to classify responses about management implications dependent on if a species arrived due to climate change or not. An illustrative quote accompanies a summary of what the sub-theme is intended to capture. RC stands for references coded.

Theme	Sub-theme	Summary	Quotes
Climate driven range-shifters deserve sympathetic management (RC = 54)	Climate changes’ consequences are a human responsibility (RC = 14)	Since species are moving due to human caused climate change, humans have a responsibility to protect those species.	“If things are coming over due to climate change, then surely we have a responsibility to accept that this is likely our own fault and learn to live with it?”
	Climate driven range-shifters will be losing range elsewhere (RC = 11)	Specie moving due to climate change deserve special attention as they will be losing range elsewhere due to less favourable environmental conditions.	“They should be conserved because their range will be contracting southerly, especially if they have a small range of tolerance.”
	Climate driven range-shifters are necessary to future adaptation (RC = 29)	Species moving due to climate change deserve special attention as they are needed to maintain ecological resilience as we lose species in the UK.	“Introduction of species that could enhance biodiversity or fill the niched left by non successful natives that may be in decline, enriching species poor environments”
Climate driven range-shifters should not be directly managed	Climate change is unstoppable (RC = 36)	If species moving due to climate change, management to control them is unlikely to be effective as the forces are too powerful and ongoing.	“If climate change is the sole or main driver of the establishment, there cannot be any effective action as climate change is just too massive, and currently unstoppable.”

(RC = 60)	Climate change should be tackled directly (RC = 9)	Species moving due to climate change should not be the focus of action, as they are a symptom not a cause. We should tackle climate change directly.	“We need to respond to climate change and not respond to species taking advantage of climate change”
	Species’ responses to environmental change are natural (RC = 15)	Though climate change is human-caused, species have always moved with past environmental change. This response is “natural”.	“If species are refielding because of climate change, leave well alone as it's natural progression”
The driver of the range-shift should not determine management (RC = 46)	Focus should be on impact (RC = 40)	Climate change as a driver of species arrival does not have any specific implications. Management should focus instead on species impact on the recipient ecosystem.	“The reasons for the establishment of new species are immaterial. We need to look at the effects on the existing ecosystems of the arrival of new species.”
	All species are equal (RC = 6)	Climate change as a driver of species arrival does not have any specific implications. Our focus should be on nature and biodiversity rather than on specific species.	“I think we have a responsibility to help protect and conserve all species and nature as a whole, whether these species have arrived from another country or not.”



Supplementary Figure C.11: Word clouds showing the words associations of respondents in the control (left) and climate change treatments (right)

, i.e. “When you think about <range-shift> (50% of respondents) / <climate change> (50% of respondents) which words or words first come to mind (3

words max). The size of the words scales with the frequency with which that word appears in the responses.

Appendix D: Questionnaire sent to Wildlife Recorders

Supplementary Method D.1: Questionnaire sent to wildlife recorders. The survey logic is highlighted using annotations in red indicating where respondents would have received differing treatments or species. The welcome page is also shown where we obtained informed consent.

Range-shifting species establishing in the UK

Thanks for taking 10-25 minutes of your time to help me with this research. The timing varies by how long you choose to spend on the optional long answer questions.

My research explores the implications of new species arriving in the UK and in particular I'm interested in the views of wildlife recorders!

I aim to better understand public opinion on establishing range-shifting species to inform future research and policy, for more effective conservation.

This study has been ethically approved by University of Exeter.

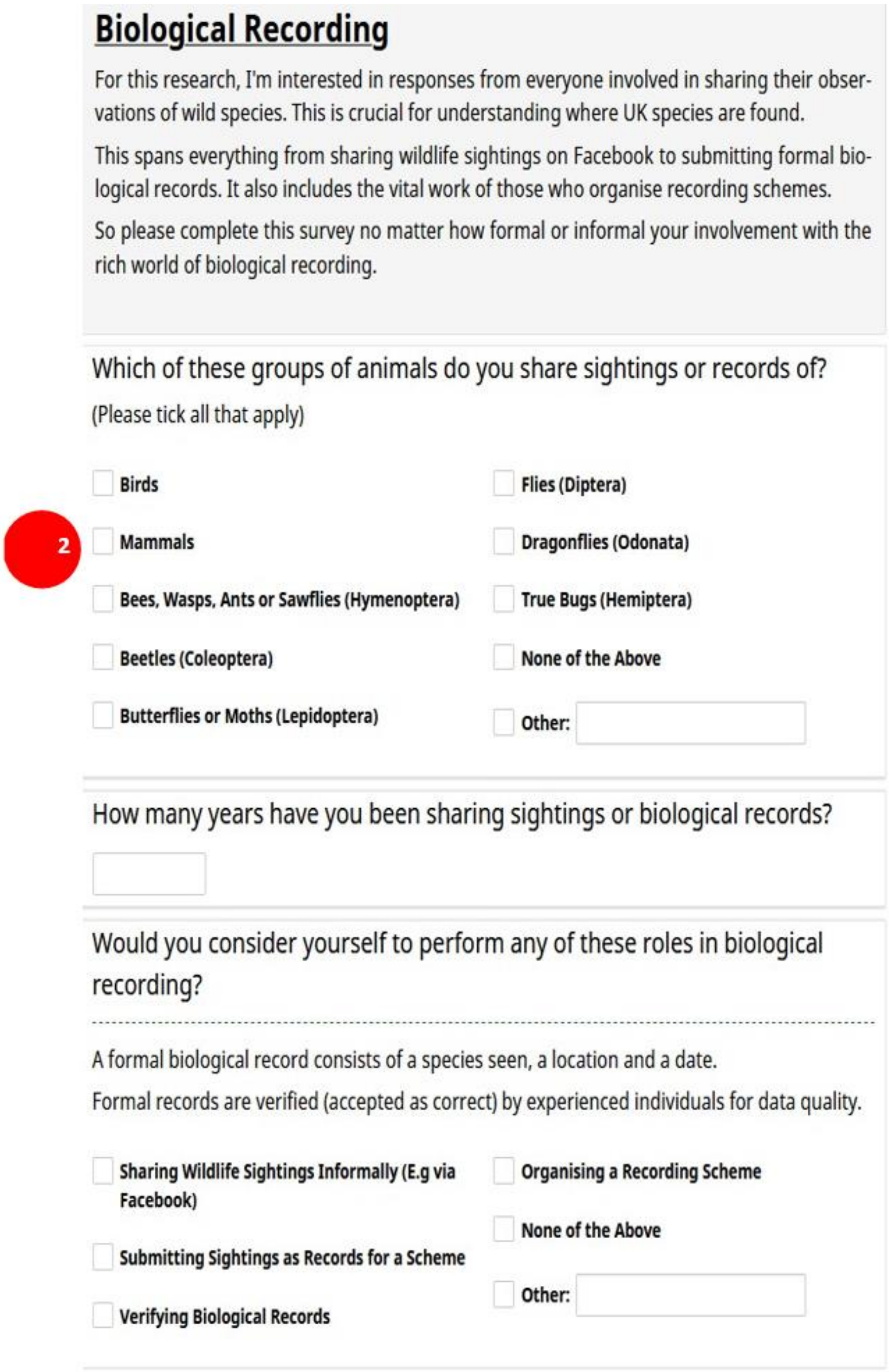
All questions are optional, your responses are all completely anonymous and can be withdrawn until 1st June by emailing myself, J.Cranston2@exeter.ac.uk.

Please tick the box below to consent for me to use your survey responses for my research.

Thanks again!

I have read the information above & consent for my response to be recorde ☐

Next Page -> Pg2



Biological Recording

For this research, I'm interested in responses from everyone involved in sharing their observations of wild species. This is crucial for understanding where UK species are found.

This spans everything from sharing wildlife sightings on Facebook to submitting formal biological records. It also includes the vital work of those who organise recording schemes.

So please complete this survey no matter how formal or informal your involvement with the rich world of biological recording.

Which of these groups of animals do you share sightings or records of?

(Please tick all that apply)

☐ **Birds**
☐ **Mammals**
☐ **Bees, Wasps, Ants or Sawflies (Hymenoptera)**
☐ **Beetles (Coleoptera)**
☐ **Butterflies or Moths (Lepidoptera)**
☐ **Flies (Diptera)**
☐ **Dragonflies (Odonata)**
☐ **True Bugs (Hemiptera)**
☐ **None of the Above**
☐ **Other:**

How many years have you been sharing sightings or biological records?

Would you consider yourself to perform any of these roles in biological recording?

A formal biological record consists of a species seen, a location and a date.

Formal records are verified (accepted as correct) by experienced individuals for data quality.

☐ **Sharing Wildlife Sightings Informally (E.g via Facebook)**
☐ **Submitting Sightings as Records for a Scheme**
☐ **Verifying Biological Records**
☐ **Organising a Recording Scheme**
☐ **None of the Above**
☐ **Other:**

Next Page -> Pg 3

Have you heard that new species are establishing **in the UK <u>after arriving under their own powers of dispersal</u>**?

***I.e.* NOT *introduced species which are transported into the UK through human activity*.**

○ Yes, I am familiar with this phenomenon & I can name **ONE** species which has established in the UK.

○ Yes, I am familiar with this phenomenon but couldn't name a specific example.

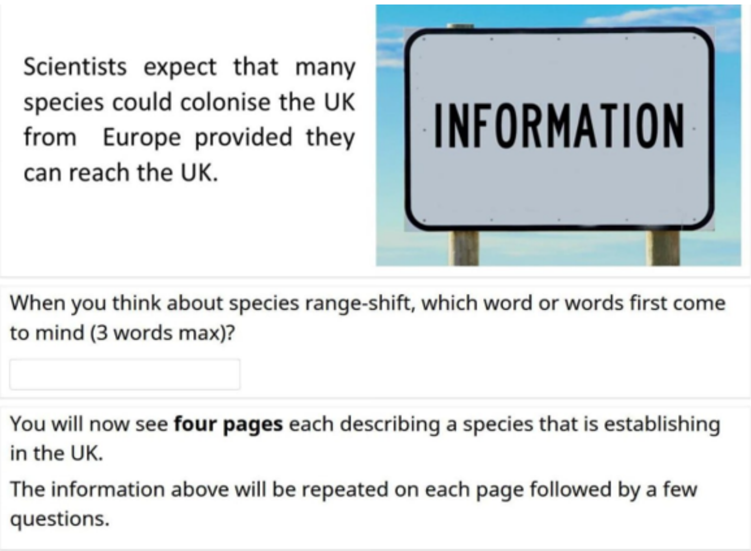
○ No, I haven't heard of this phenomenon.

Please enter your ONE species here (if applicable):

3

The text box on the right where respondents could type a response, naming a species only appeared if the respondent first ticked the option "Yes, I am familiar with this phenomenon & I can name ONE species which has established in the UK.

Next Page either (Pg4 – the Control treatment (50%) or Pg5 – the Climate change treatment (50%))) |



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

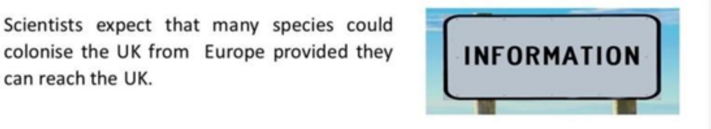
4

When you think about species range-shift, which word or words first come to mind (3 words max)?

You will now see **four pages** each describing a species that is establishing in the UK.

The information above will be repeated on each page followed by a few questions.

Next Page -> Respondents were then shown one of the 16 species pages (6.25%). After they completed that page they were shown 3 more species (i.e. 4 in total). They were shown 2 invertebrate species and two vertebrate species in a randomly assigned order. All 16 species are shown here for completeness, in the survey the open text questions only became visible after completing the multiple choice, hence they are shown filled in here, though in the original survey they would appear unselected at first.

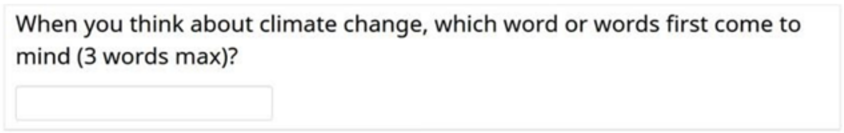


Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

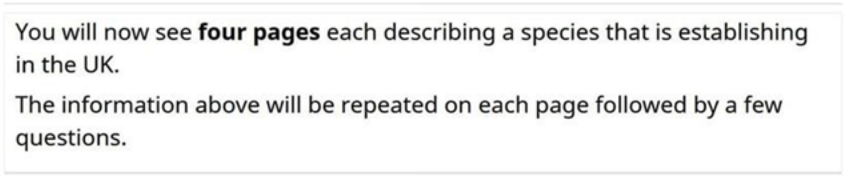
After completing the relevant questions for these four species, respondents were taken to page 22.

Scientists expect that many species could colonise the UK from Europe as global warming makes climate more suitable for them, provided they can reach the UK.

5



When you think about climate change, which word or words first come to mind (3 words max)?



You will now see **four pages** each describing a species that is establishing in the UK.

The information above will be repeated on each page followed by a few questions.

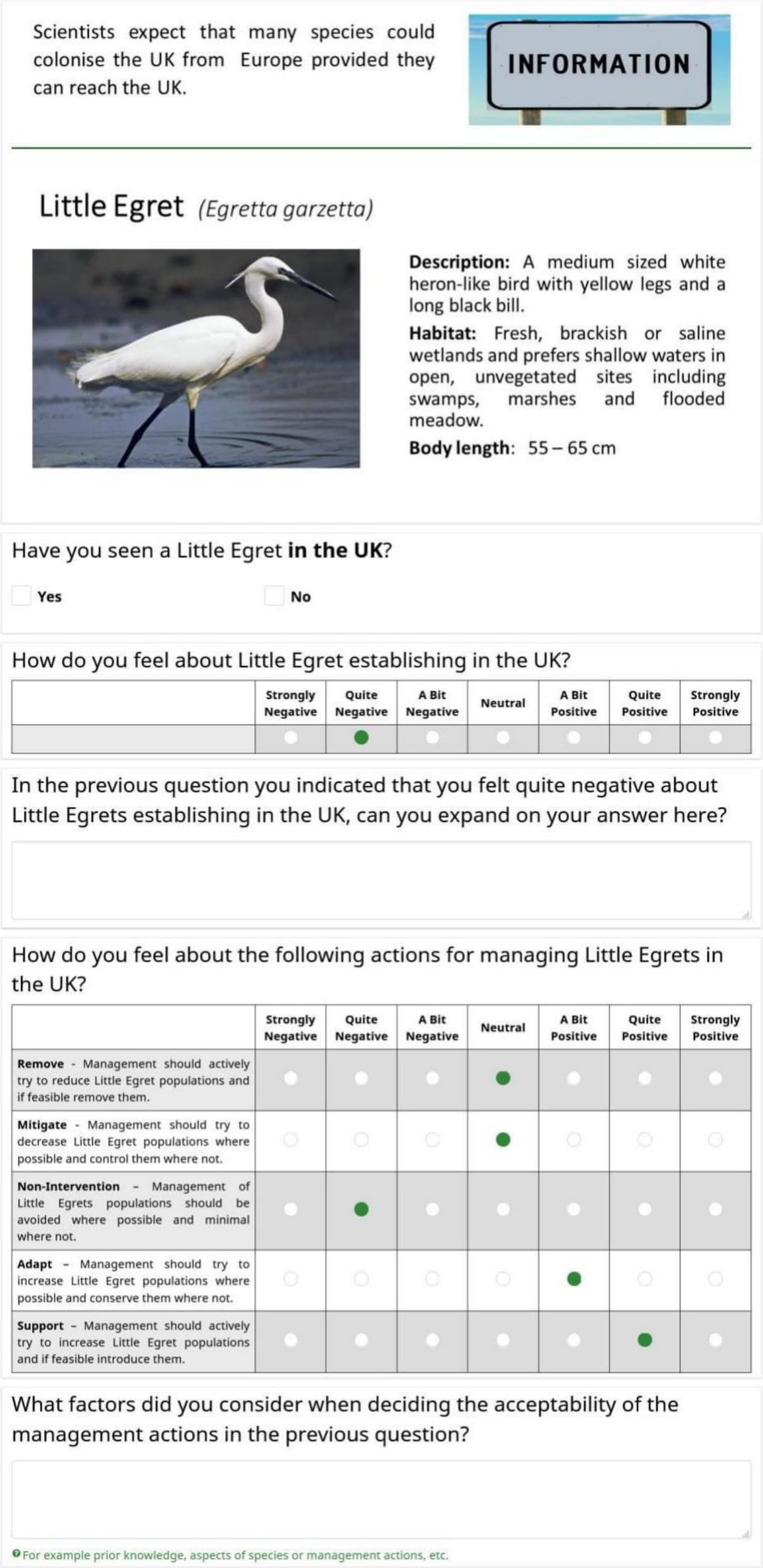
Next Page -> Respondents were then shown one of the 16 species pages (Pgs 6-21, 6.25% each). After they completed that page they were shown 3 more species (i.e. 4 in total). All respondents were shown 2 invertebrate species and two vertebrate species in a randomly assigned order. All 16 species are shown here for completeness, in the survey the open text questions only became visible after completing the multiple choice, hence they are shown filled in here, though in the original survey they would appear unselected at first.

All 4 species pages had a banner on top, as follows if they were in the climate change treatment (though the images presented below are all shown with a control treatment banner)

Scientists expect that many species could colonise the UK from Europe as global warming makes climate more suitable for them, provided they can reach the UK.

After completing the relevant questions for these four species, respondents were taken to page 22.

6



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Little Egret *(Egretta garzetta)*

Description: A medium sized white heron-like bird with yellow legs and a long black bill.

Habitat: Fresh, brackish or saline wetlands and prefers shallow waters in open, unvegetated sites including swamps, marshes and flooded meadow.

Body length: 55 – 65 cm

Have you seen a Little Egret **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Little Egret establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	●	○	○	○	○	○

In the previous question you indicated that you felt quite negative about Little Egrets establishing in the UK, can you expand on your answer here?

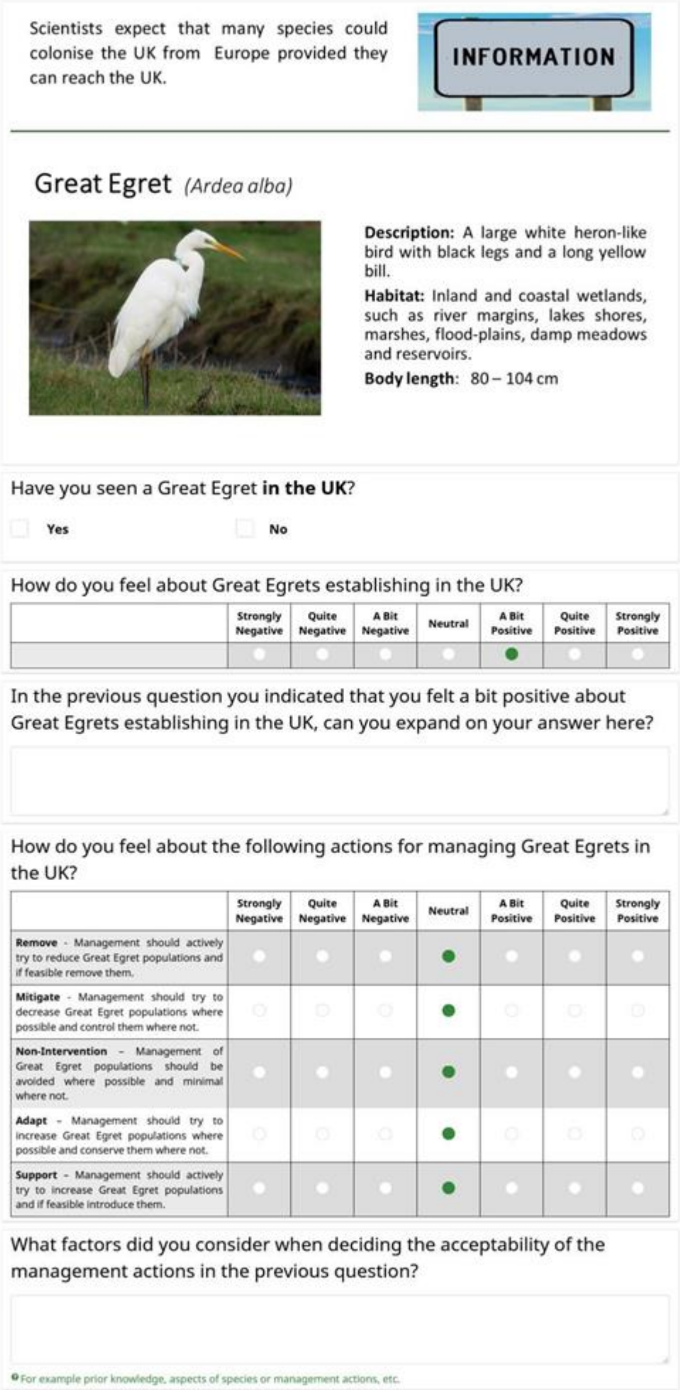
How do you feel about the following actions for managing Little Egrets in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Little Egret populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Little Egret populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention – Management of Little Egrets populations should be avoided where possible and minimal where not.	○	●	○	○	○	○	○
Adapt – Management should try to increase Little Egret populations where possible and conserve them where not.	○	○	○	○	●	○	○
Support – Management should actively try to increase Little Egret populations and if feasible introduce them.	○	○	○	○	○	●	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

7



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Great Egret *(Ardea alba)*

Description: A large white heron-like bird with black legs and a long yellow bill.

Habitat: Inland and coastal wetlands, such as river margins, lakes shores, marshes, flood-plains, damp meadows and reservoirs.

Body length: 80 – 104 cm

Have you seen a Great Egret **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Great Egrets establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	○	●	○	○

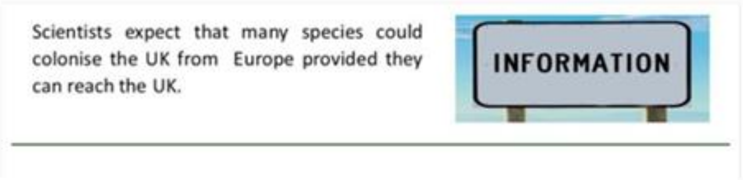
In the previous question you indicated that you felt a bit positive about Great Egrets establishing in the UK, can you expand on your answer here?

How do you feel about the following actions for managing Great Egrets in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Great Egret populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Great Egret populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention – Management of Great Egret populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt – Management should try to increase Great Egret populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Great Egret populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

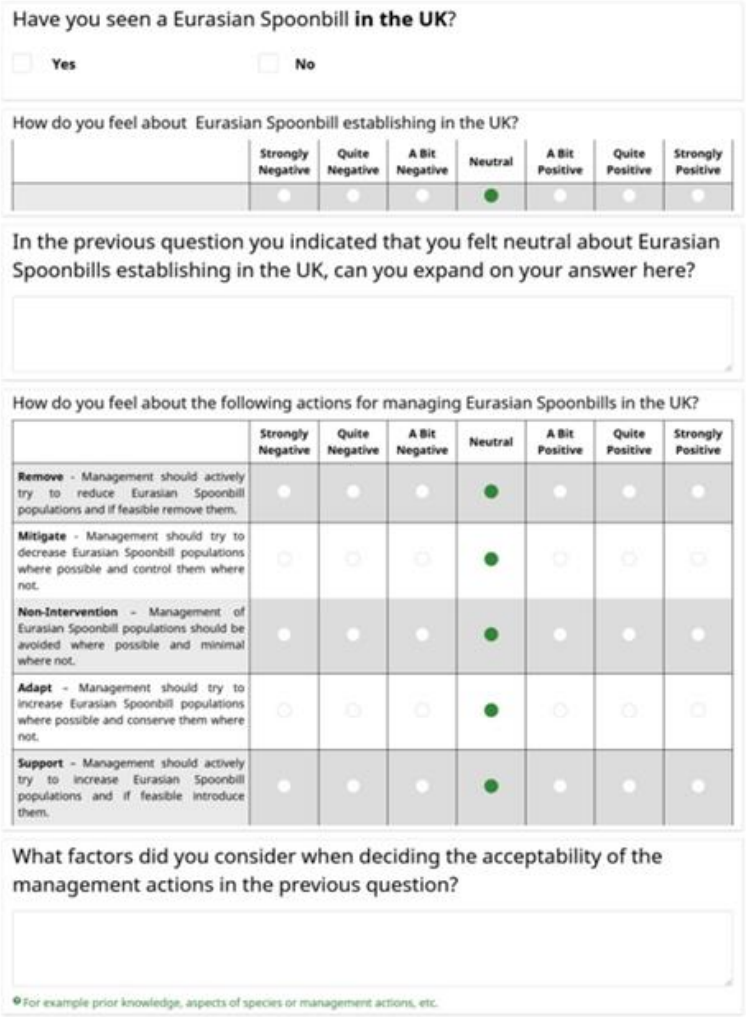
8

Eurasian Spoonbill *(Platalea leucorodia)*

Description: A large white wading bird with a wide spoon-like bill. Adults have a small crest and a yellow breast patch.

Habitat: Shallow wetlands with mud, clay or fine sand substrates including fresh, brackish or saline marshes, rivers, lakes and flooded areas.

Body length: 70 – 95 cm



Have you seen a Eurasian Spoonbill **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Eurasian Spoonbill establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Eurasian Spoonbills establishing in the UK, can you expand on your answer here?

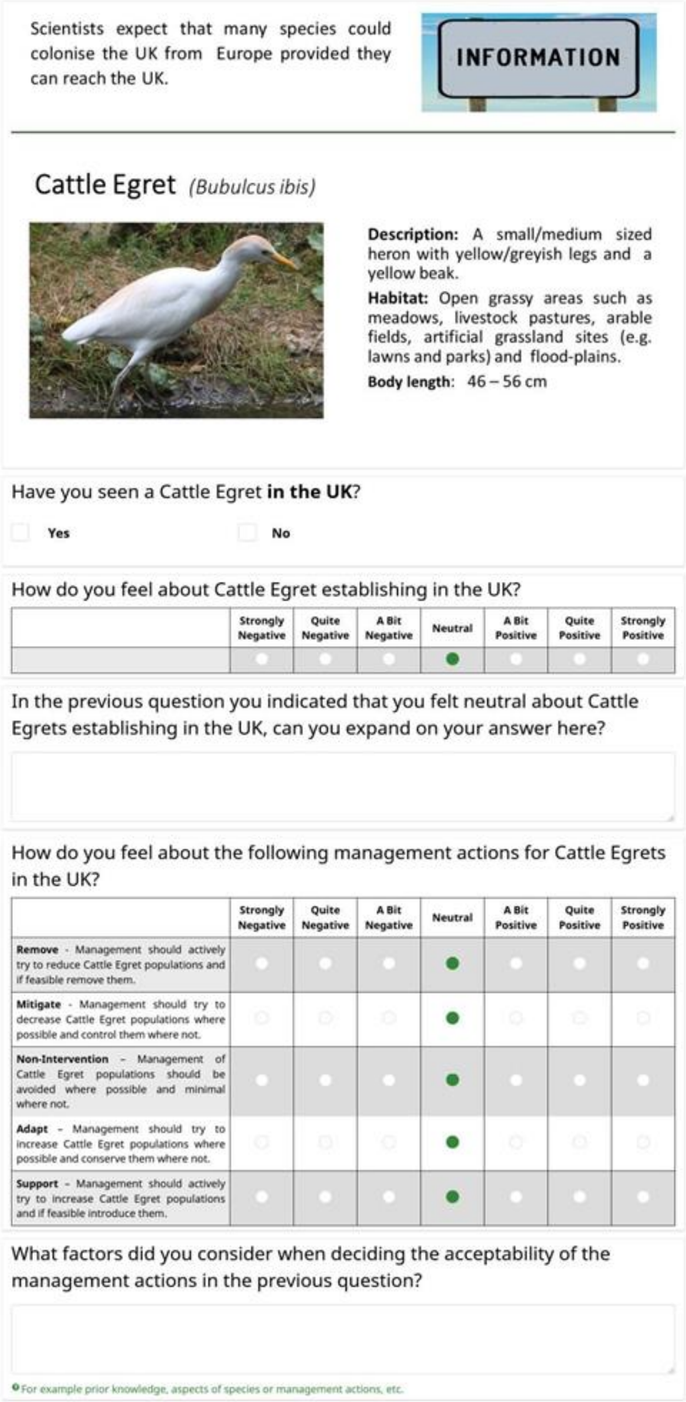
How do you feel about the following actions for managing Eurasian Spoonbills in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Eurasian Spoonbill populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Eurasian Spoonbill populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Eurasian Spoonbill populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Eurasian Spoonbill populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Eurasian Spoonbill populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

9



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Cattle Egret *(Bubulcus ibis)*

Description: A small/medium sized heron with yellow/greyish legs and a yellow beak.

Habitat: Open grassy areas such as meadows, livestock pastures, arable fields, artificial grassland sites (e.g. lawns and parks) and flood-plains.

Body length: 46 – 56 cm

Have you seen a Cattle Egret **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Cattle Egret establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Cattle Egrets establishing in the UK, can you expand on your answer here?

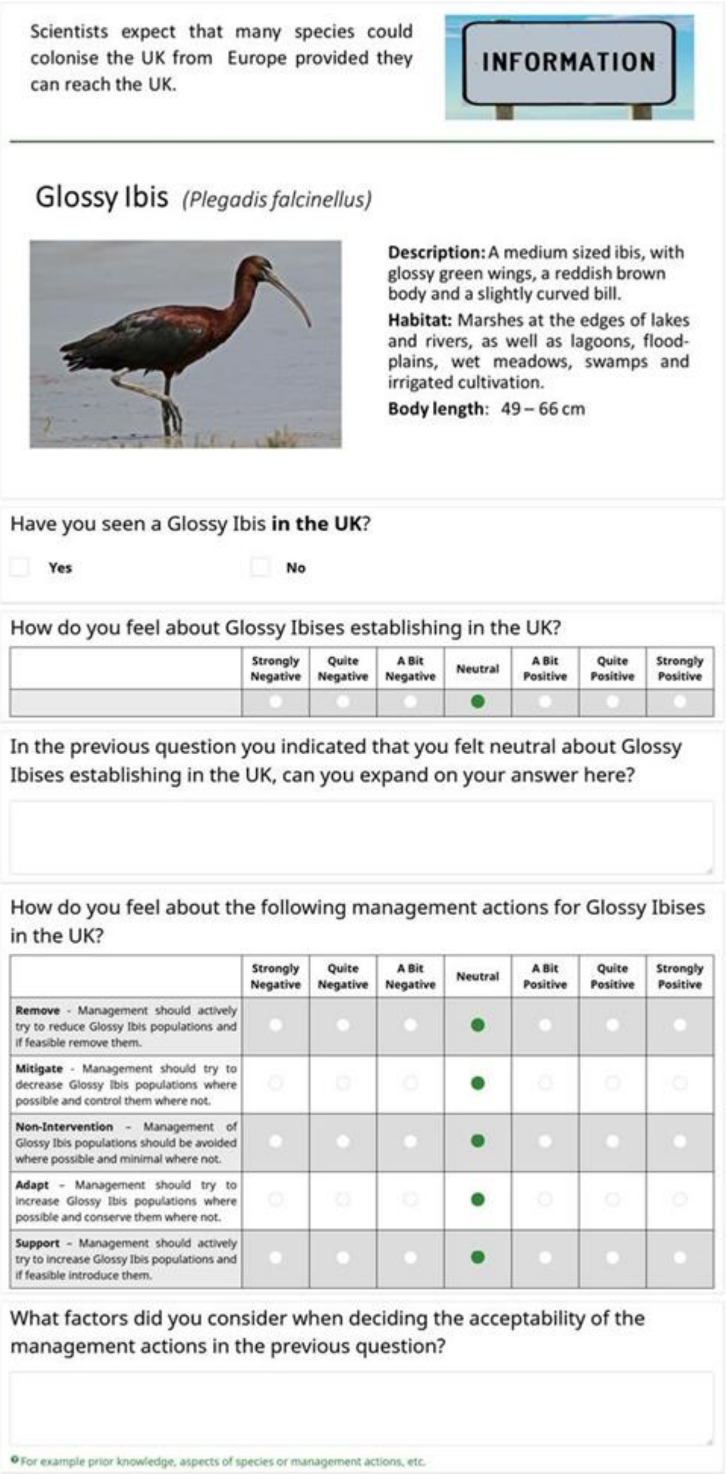
How do you feel about the following management actions for Cattle Egrets in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Cattle Egret populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Cattle Egret populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention – Management of Cattle Egret populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt – Management should try to increase Cattle Egret populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Cattle Egret populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

10



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Glossy Ibis *(Plegadis falcinellus)*

Description: A medium sized ibis, with glossy green wings, a reddish brown body and a slightly curved bill.

Habitat: Marshes at the edges of lakes and rivers, as well as lagoons, flood-plains, wet meadows, swamps and irrigated cultivation.

Body length: 49 – 66 cm

Have you seen a Glossy Ibis **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Glossy Ibises establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Glossy Ibises establishing in the UK, can you expand on your answer here?

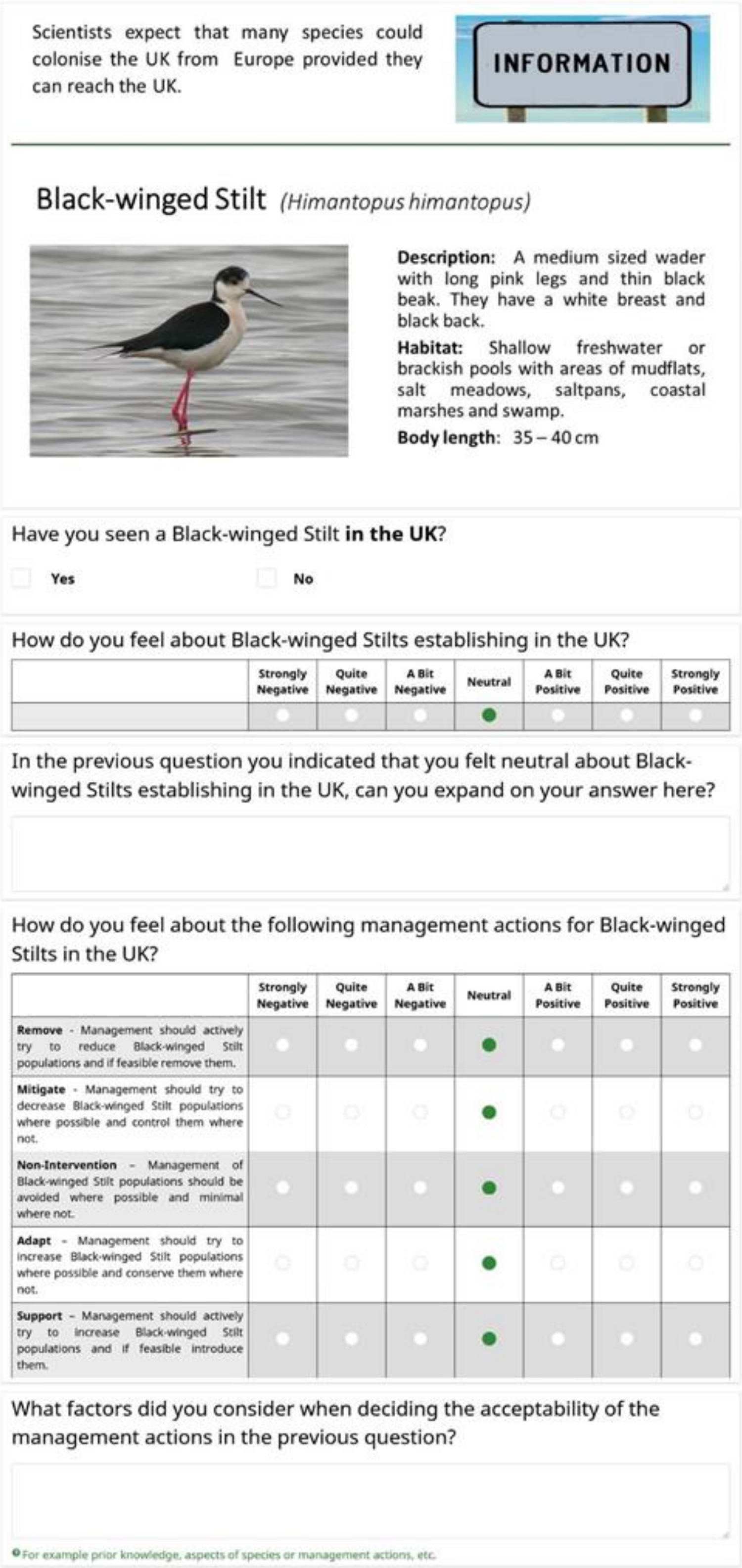
How do you feel about the following management actions for Glossy Ibises in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Glossy Ibis populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Glossy Ibis populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Glossy Ibis populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Glossy Ibis populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Glossy Ibis populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

11



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Black-winged Stilt *(Himantopus himantopus)*

Description: A medium sized wader with long pink legs and thin black beak. They have a white breast and black back.

Habitat: Shallow freshwater or brackish pools with areas of mudflats, salt meadows, saltpans, coastal marshes and swamp.

Body length: 35 – 40 cm

Have you seen a Black-winged Stilt **in the UK**?

☐ Yes ☐ No

How do you feel about Black-winged Stilts establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Black-winged Stilts establishing in the UK, can you expand on your answer here?

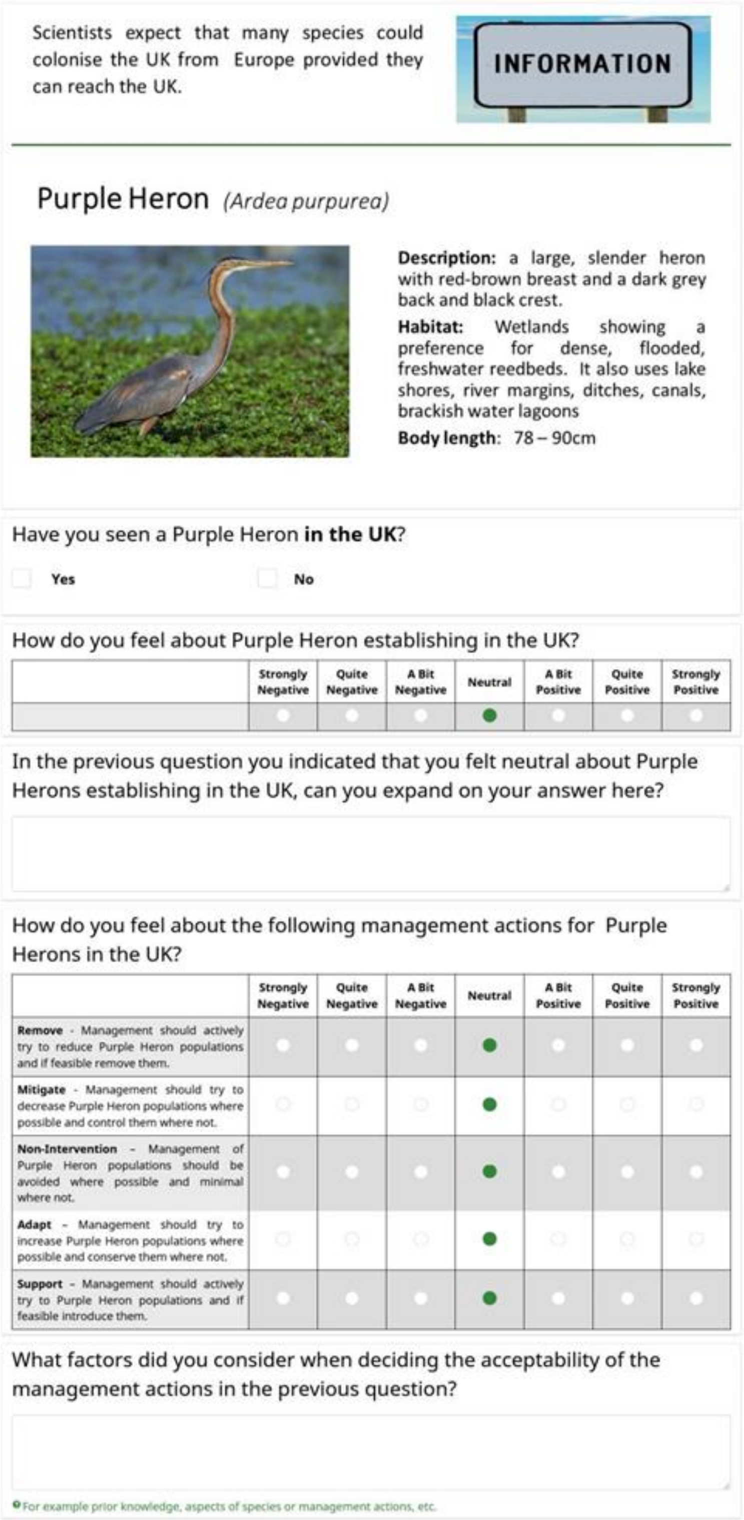
How do you feel about the following management actions for Black-winged Stilts in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Black-winged Stilt populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Black-winged Stilt populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Black-winged Stilt populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Black-winged Stilt populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Black-winged Stilt populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

12



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Purple Heron *(Ardea purpurea)*

Description: a large, slender heron with red-brown breast and a dark grey back and black crest.

Habitat: Wetlands showing a preference for dense, flooded, freshwater reedbeds. It also uses lake shores, river margins, ditches, canals, brackish water lagoons

Body length: 78 – 90cm

Have you seen a Purple Heron **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Purple Heron establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Purple Herons establishing in the UK, can you expand on your answer here?

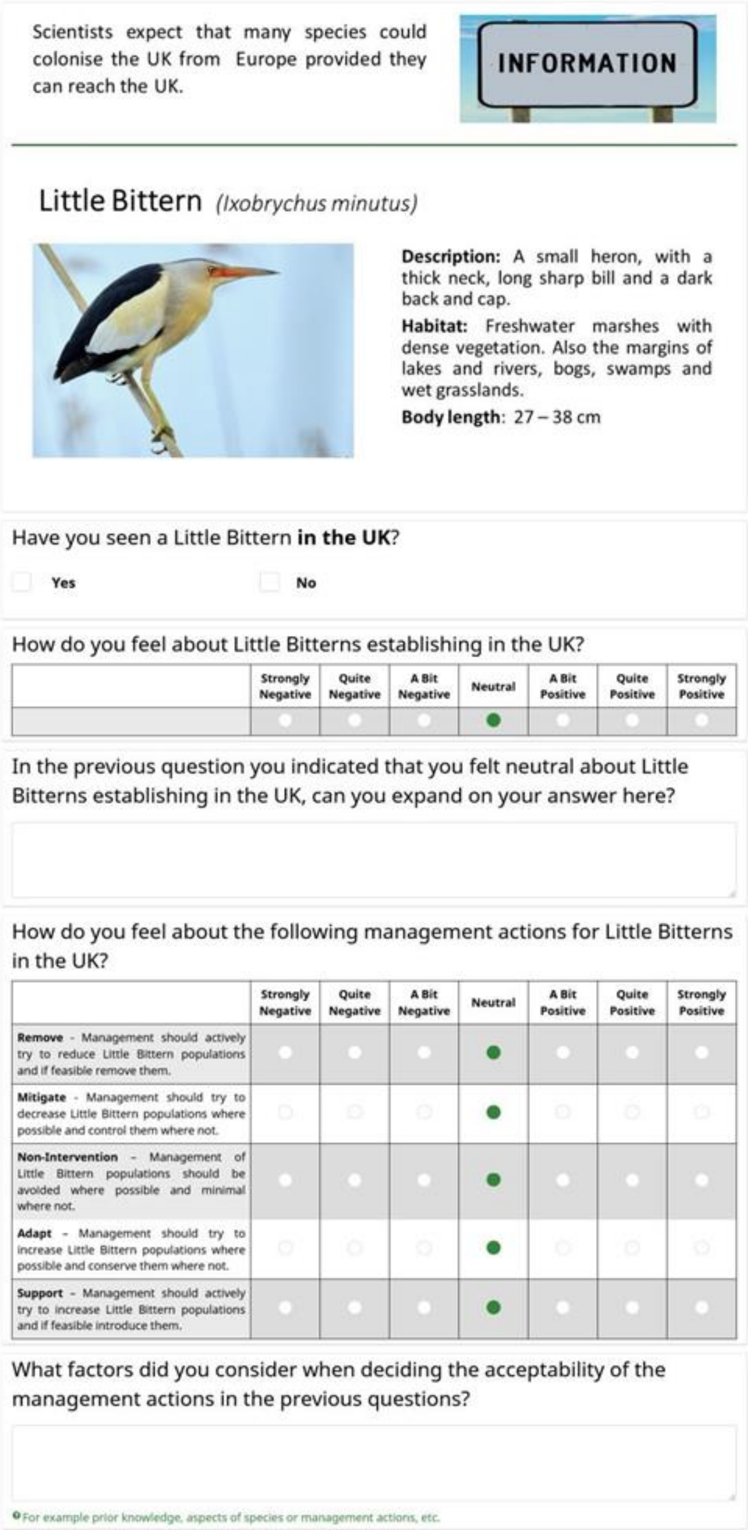
How do you feel about the following management actions for Purple Herons in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Purple Heron populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Purple Heron populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Purple Heron populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Purple Heron populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to Purple Heron populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous question?

For example prior knowledge, aspects of species or management actions, etc.

13



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Little Bittern *(Ixobrychus minutus)*

Description: A small heron, with a thick neck, long sharp bill and a dark back and cap.

Habitat: Freshwater marshes with dense vegetation. Also the margins of lakes and rivers, bogs, swamps and wet grasslands.

Body length: 27 – 38 cm

Have you seen a Little Bittern **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Little Bitterns establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Little Bitterns establishing in the UK, can you expand on your answer here?

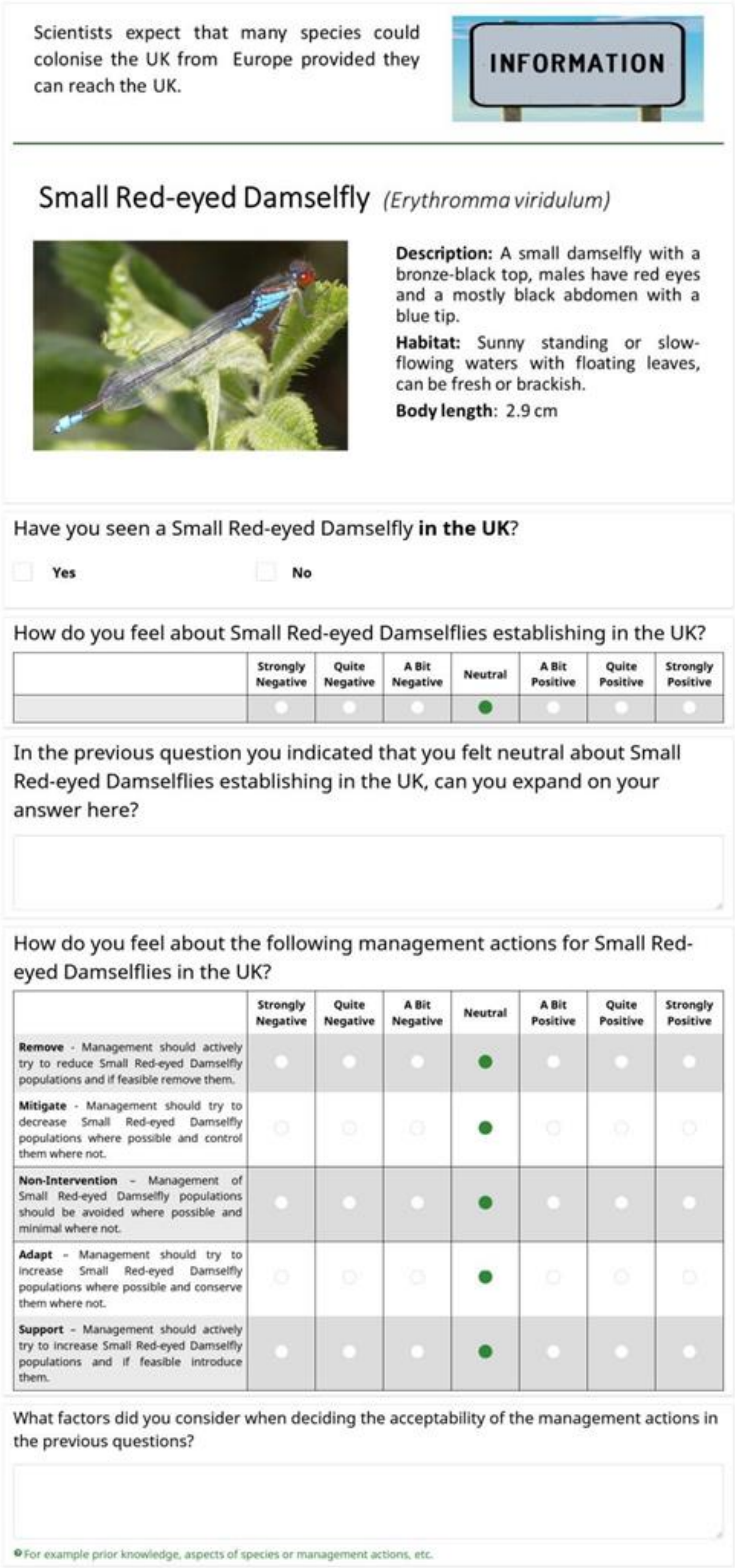
How do you feel about the following management actions for Little Bitterns in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Little Bittern populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Little Bittern populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Little Bittern populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Little Bittern populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Little Bittern populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

14



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Small Red-eyed Damselfly *(Erythromma viridulum)*

Description: A small damselfly with a bronze-black top, males have red eyes and a mostly black abdomen with a blue tip.

Habitat: Sunny standing or slow-flowing waters with floating leaves, can be fresh or brackish.

Body length: 2.9 cm

Have you seen a Small Red-eyed Damselfly **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Small Red-eyed Damselflies establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Small Red-eyed Damselflies establishing in the UK, can you expand on your answer here?

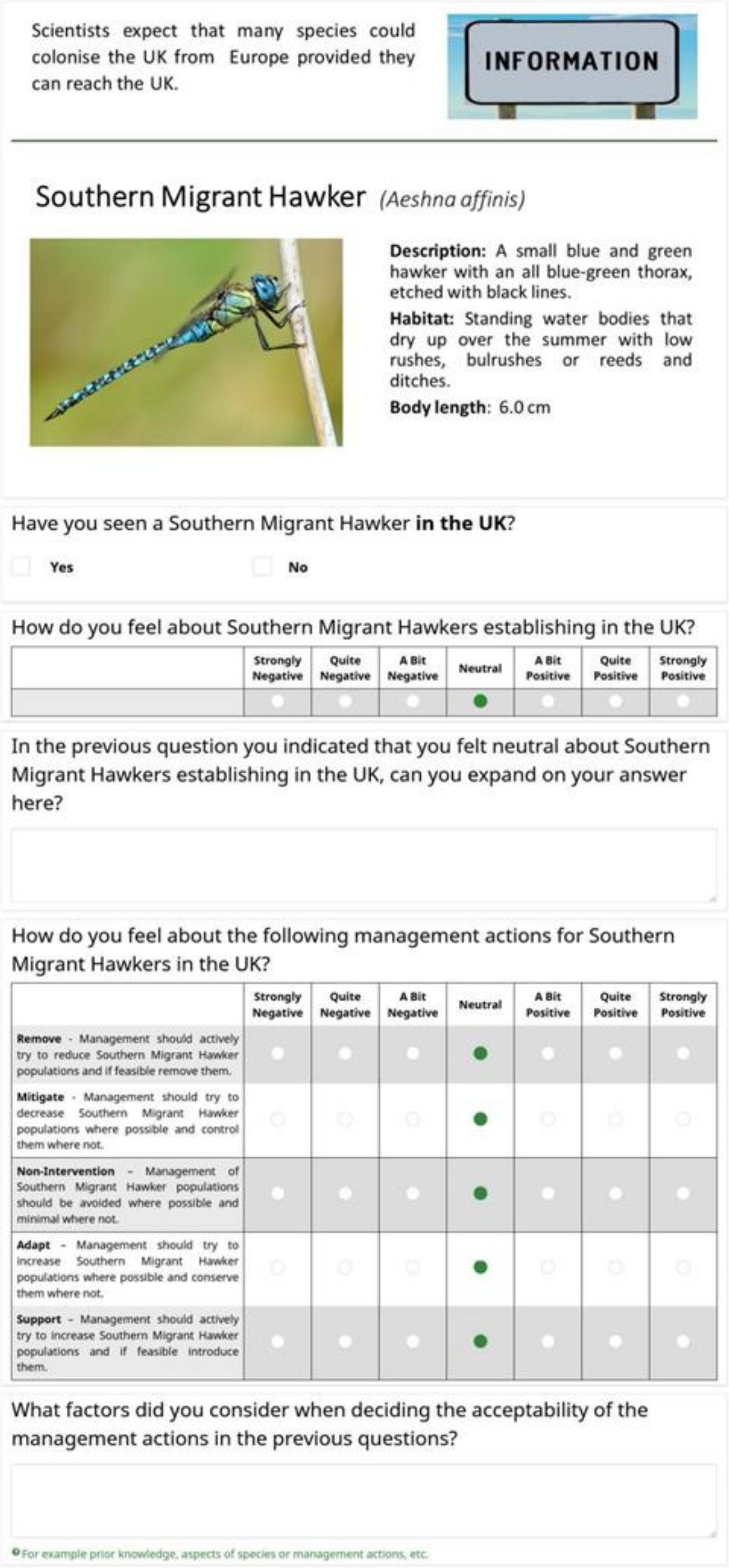
How do you feel about the following management actions for Small Red-eyed Damselflies in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Small Red-eyed Damselfly populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Small Red-eyed Damselfly populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Small Red-eyed Damselfly populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Small Red-eyed Damselfly populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Small Red-eyed Damselfly populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

15



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Southern Migrant Hawker *(Aeshna affinis)*

Description: A small blue and green hawker with an all blue-green thorax, etched with black lines.

Habitat: Standing water bodies that dry up over the summer with low rushes, bulrushes or reeds and ditches.

Body length: 6.0 cm

Have you seen a Southern Migrant Hawker **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Southern Migrant Hawkers establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Southern Migrant Hawkers establishing in the UK, can you expand on your answer here?

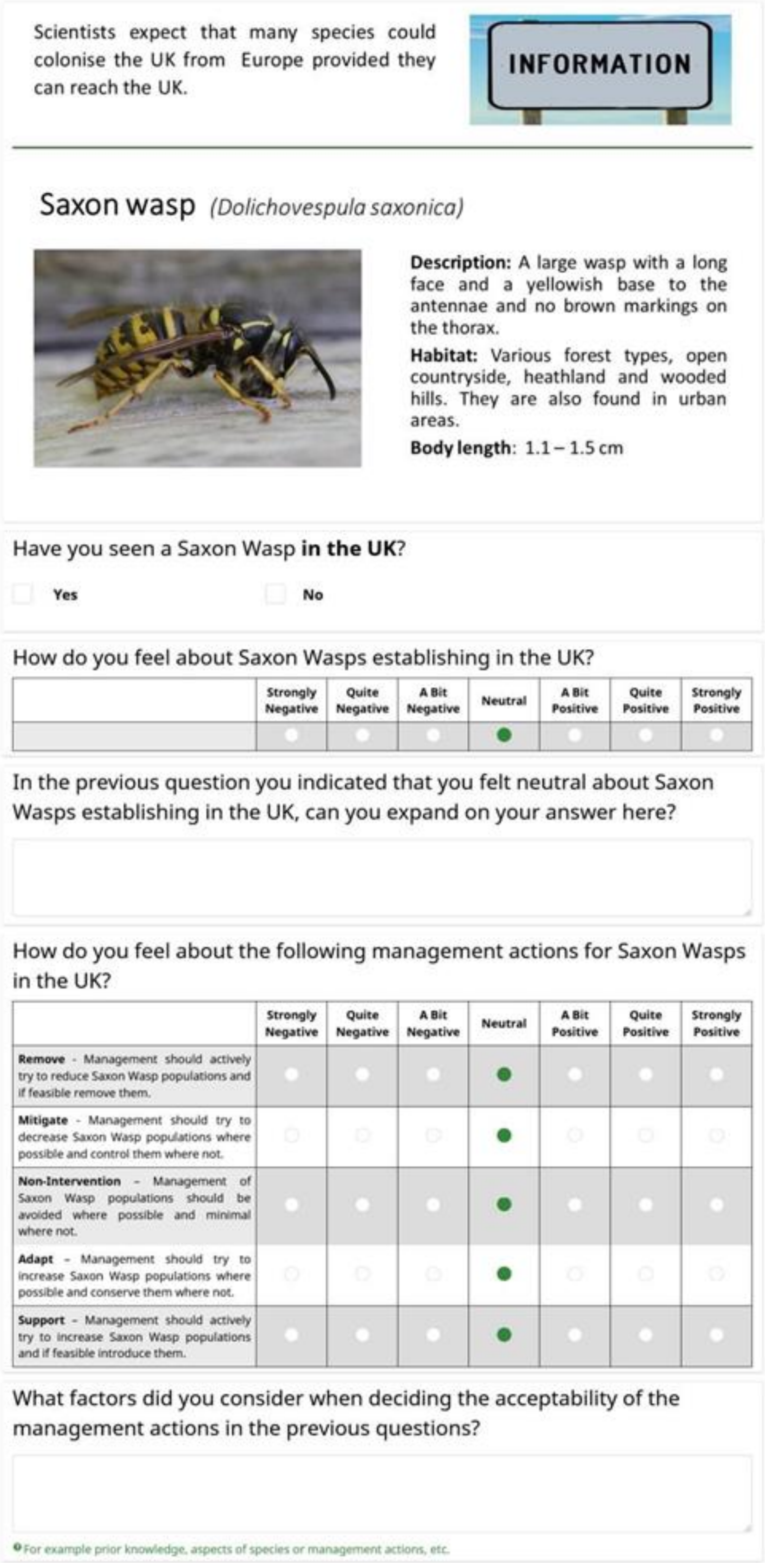
How do you feel about the following management actions for Southern Migrant Hawkers in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Southern Migrant Hawker populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Southern Migrant Hawker populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Southern Migrant Hawker populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Southern Migrant Hawker populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Southern Migrant Hawker populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

16



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Saxon wasp *(Dolichovespula saxonica)*

Description: A large wasp with a long face and a yellowish base to the antennae and no brown markings on the thorax.

Habitat: Various forest types, open countryside, heathland and wooded hills. They are also found in urban areas.

Body length: 1.1 – 1.5 cm

Have you seen a Saxon Wasp **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Saxon Wasps establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Saxon Wasps establishing in the UK, can you expand on your answer here?

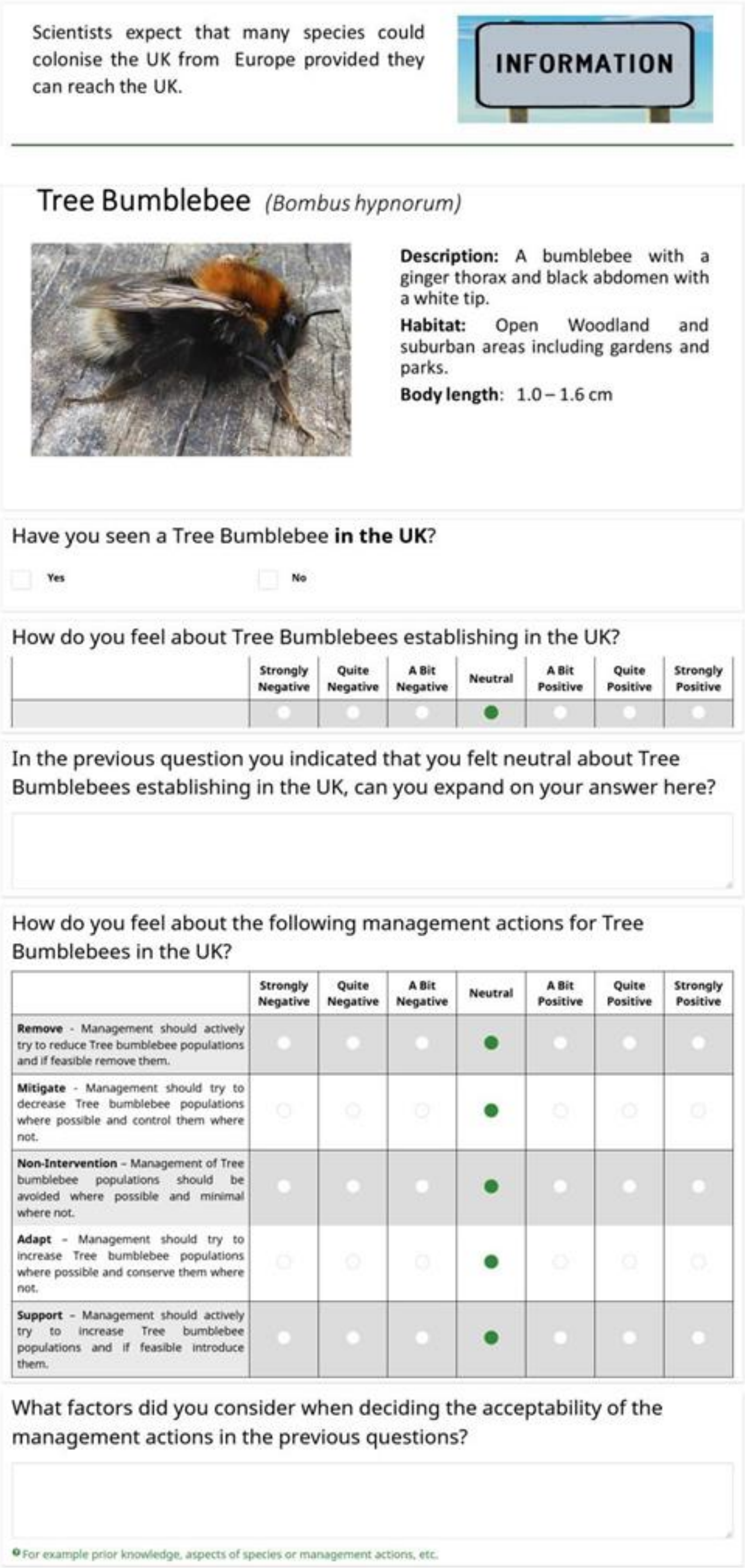
How do you feel about the following management actions for Saxon Wasps in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Saxon Wasp populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Saxon Wasp populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Saxon Wasp populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Saxon Wasp populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Saxon Wasp populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

17



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Tree Bumblebee *(Bombus hypnorum)*

Description: A bumblebee with a ginger thorax and black abdomen with a white tip.

Habitat: Open Woodland and suburban areas including gardens and parks.

Body length: 1.0 – 1.6 cm

Have you seen a Tree Bumblebee **in the UK**?

☐ Yes ☐ No

How do you feel about Tree Bumblebees establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Tree Bumblebees establishing in the UK, can you expand on your answer here?

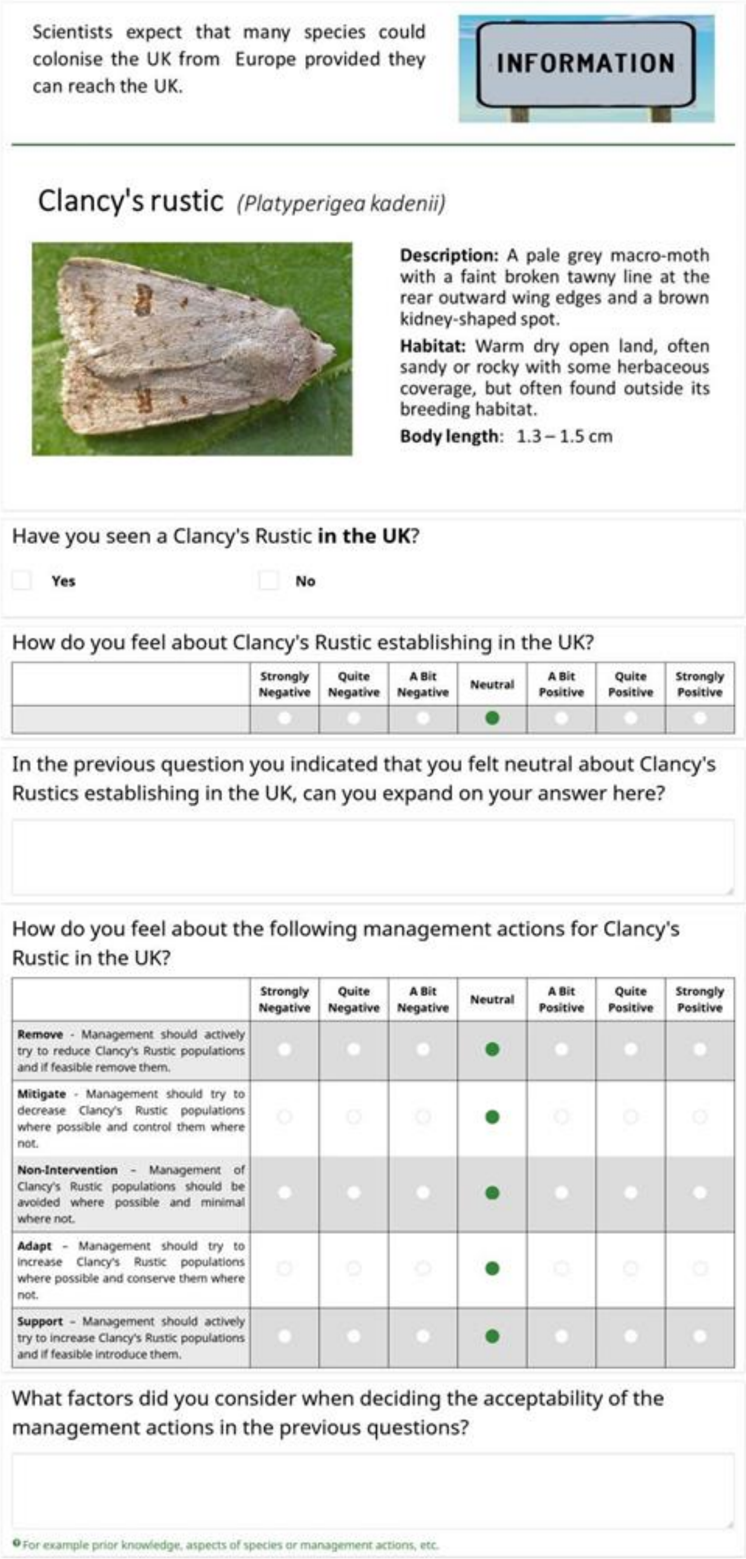
How do you feel about the following management actions for Tree Bumblebees in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Tree bumblebee populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Tree bumblebee populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention – Management of Tree bumblebee populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Tree bumblebee populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support – Management should actively try to increase Tree bumblebee populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

18



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Clancy's rustic *(Platyperigea kadenii)*

Description: A pale grey macro-moth with a faint broken tawny line at the rear outward wing edges and a brown kidney-shaped spot.

Habitat: Warm dry open land, often sandy or rocky with some herbaceous coverage, but often found outside its breeding habitat.

Body length: 1.3 – 1.5 cm

Have you seen a Clancy's Rustic **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Clancy's Rustic establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Clancy's Rustics establishing in the UK, can you expand on your answer here?

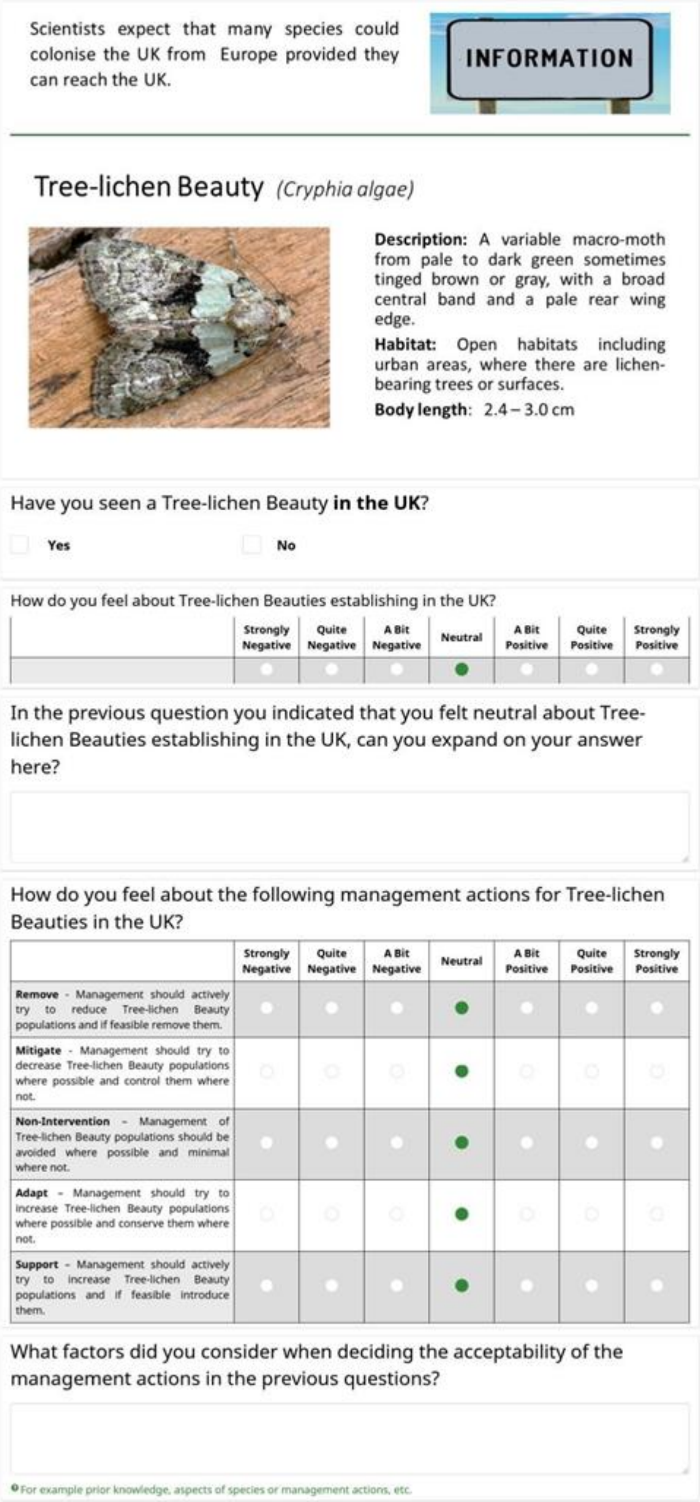
How do you feel about the following management actions for Clancy's Rustic in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Clancy's Rustic populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Clancy's Rustic populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Clancy's Rustic populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Clancy's Rustic populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Clancy's Rustic populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

19



Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Tree-lichen Beauty *(Cryphia algae)*

Description: A variable macro-moth from pale to dark green sometimes tinged brown or gray, with a broad central band and a pale rear wing edge.

Habitat: Open habitats including urban areas, where there are lichen-bearing trees or surfaces.

Body length: 2.4 – 3.0 cm

Have you seen a Tree-lichen Beauty **in the UK**?

☐ **Yes** ☐ **No**

How do you feel about Tree-lichen Beauties establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Tree-lichen Beauties establishing in the UK, can you expand on your answer here?

How do you feel about the following management actions for Tree-lichen Beauties in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Tree-lichen Beauty populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Tree-lichen Beauty populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Tree-lichen Beauty populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Tree-lichen Beauty populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Tree-lichen Beauty populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

21

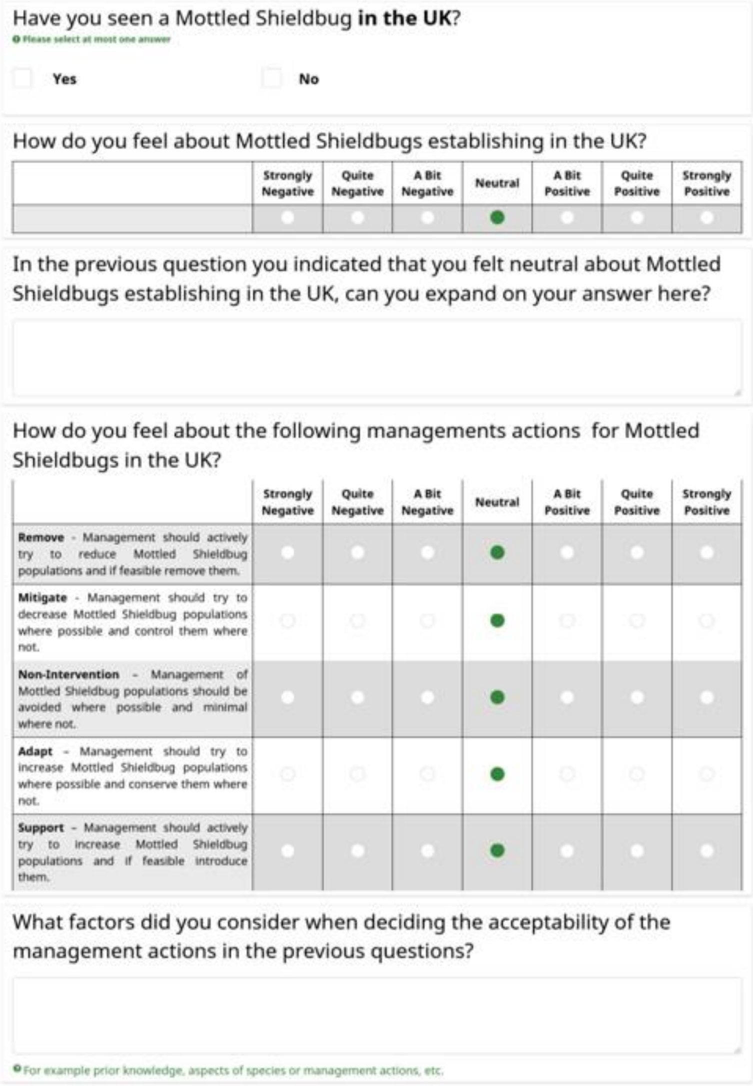
Scientists expect that many species could colonise the UK from Europe provided they can reach the UK.

Mottled Shieldbug *(Rhaphigaster nebulosa)*

Description: A large shield bug with yellow and black banded antennae and a dark mottled markings.

Habitat: Warm deciduous forest, fallow land, parks and gardens, where they can be found on deciduous trees.

Body length: 1.4 – 1.6 cm



Have you seen a Mottled Shieldbug **in the UK**?

Please select at most one answer

☐ Yes ☐ No

How do you feel about Mottled Shieldbugs establishing in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
	○	○	○	●	○	○	○

In the previous question you indicated that you felt neutral about Mottled Shieldbugs establishing in the UK, can you expand on your answer here?

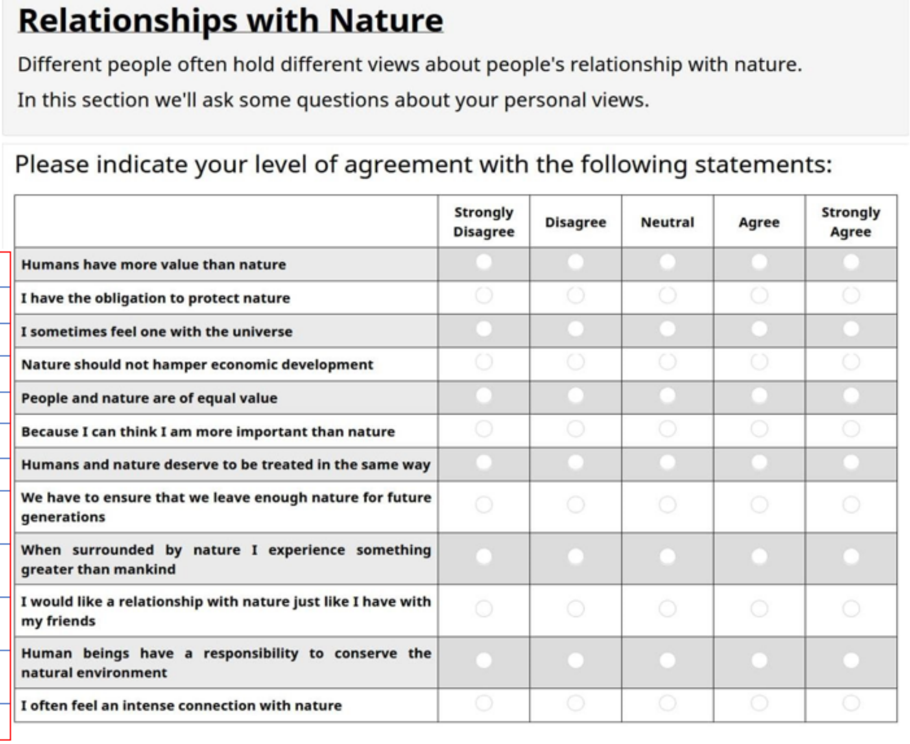
How do you feel about the following managements actions for Mottled Shieldbugs in the UK?

	Strongly Negative	Quite Negative	A Bit Negative	Neutral	A Bit Positive	Quite Positive	Strongly Positive
Remove - Management should actively try to reduce Mottled Shieldbug populations and if feasible remove them.	○	○	○	●	○	○	○
Mitigate - Management should try to decrease Mottled Shieldbug populations where possible and control them where not.	○	○	○	●	○	○	○
Non-Intervention - Management of Mottled Shieldbug populations should be avoided where possible and minimal where not.	○	○	○	●	○	○	○
Adapt - Management should try to increase Mottled Shieldbug populations where possible and conserve them where not.	○	○	○	●	○	○	○
Support - Management should actively try to increase Mottled Shieldbug populations and if feasible introduce them.	○	○	○	●	○	○	○

What factors did you consider when deciding the acceptability of the management actions in the previous questions?

For example prior knowledge, aspects of species or management actions, etc.

22



Relationships with Nature

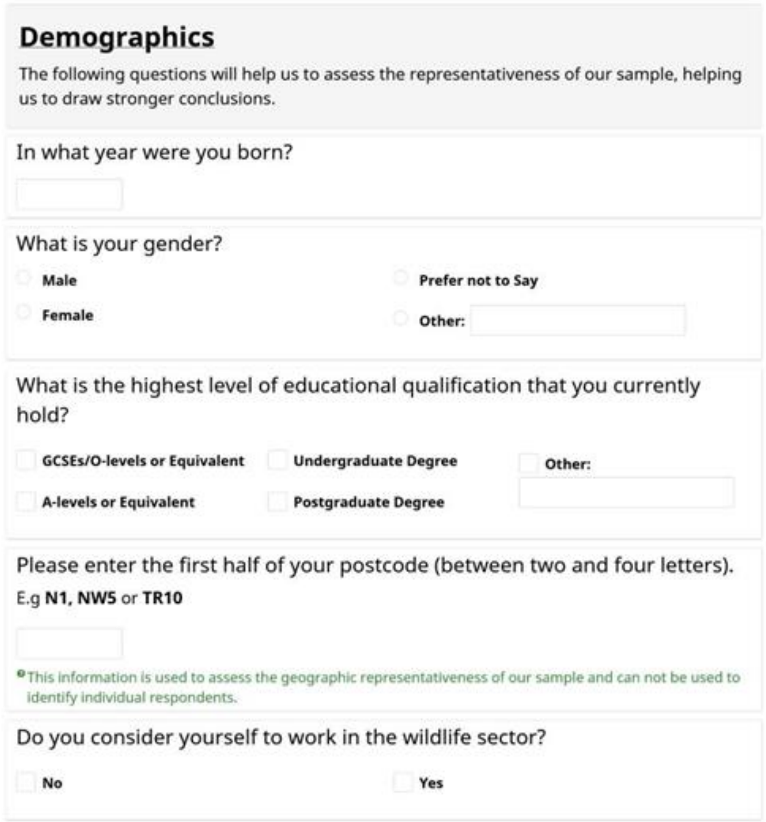
Different people often hold different views about people's relationship with nature.
In this section we'll ask some questions about your personal views.

Please indicate your level of agreement with the following statements:

		Strongly Disagree	Disagree	Neutral	Agree	Strongly Agree
Mastery	**Humans have more value than nature**	○	○	○	○	○
Stewardship	**I have the obligation to protect nature**	○	○	○	○	○
Participant	**I sometimes feel one with the universe**	○	○	○	○	○
Mastery	**Nature should not hamper economic development**	○	○	○	○	○
Partner	**People and nature are of equal value**	○	○	○	○	○
Mastery	**Because I can think I am more important than nature**	○	○	○	○	○
Partner	**Humans and nature deserve to be treated in the same way**	○	○	○	○	○
Stewardship	**We have to ensure that we leave enough nature for future generations**	○	○	○	○	○
Participant	**When surrounded by nature I experience something greater than mankind**	○	○	○	○	○
Partner	**I would like a relationship with nature just like I have with my friends**	○	○	○	○	○
Stewardship	**Human beings have a responsibility to conserve the natural environment**	○	○	○	○	○
Participant	**I often feel an intense connection with nature**	○	○	○	○	○

Next Page -> Pg 23

23



Demographics

The following questions will help us to assess the representativeness of our sample, helping us to draw stronger conclusions.

In what year were you born?

What is your gender?

○ **Male** ○ **Prefer not to Say**

○ **Female** ○ **Other:**

What is the highest level of educational qualification that you currently hold?

☐ **GCSEs/O-levels or Equivalent** ☐ **Undergraduate Degree** ☐ **Other:**

☐ **A-levels or Equivalent** ☐ **Postgraduate Degree**

Please enter the first half of your postcode (between two and four letters).

E.g **N1, NW5** or **TR10**

This information is used to assess the geographic representativeness of our sample and can not be used to identify individual respondents.

Do you consider yourself to work in the wildlife sector?

☐ **No** ☐ **Yes**

Next Page -> Pg 24

24

Thank you for your responses so far! (Final Page)

The next questions give you more of a chance to share your own views and will let us contextualise your previous responses.

So if you are willing to spare another few minutes, please fill out these further questions.

If you are finished with the survey please press submit at the bottom of the page. Thanks!

Are you aware of any other species that are establishing **in the UK**, after arriving through natural dispersal (i.e. not introduced), which you think may...

Require special protection / conservation	
Be an ecological / economic risk (i.e. invasive)	

What actions/strategies do you think would **or** would not work well for the achieving the following three conservation goals?

1. **Monitoring** the effects of newly establishing species on biodiversity and humans
2. **Protecting** newly establishing species from potential threats
3. **Minimising** the potential negative impacts of newly establishing species

	What Would Work Well?	What Would Not Work Well?
1. Monitoring...		
2. Protecting...		
3. Minimising...		

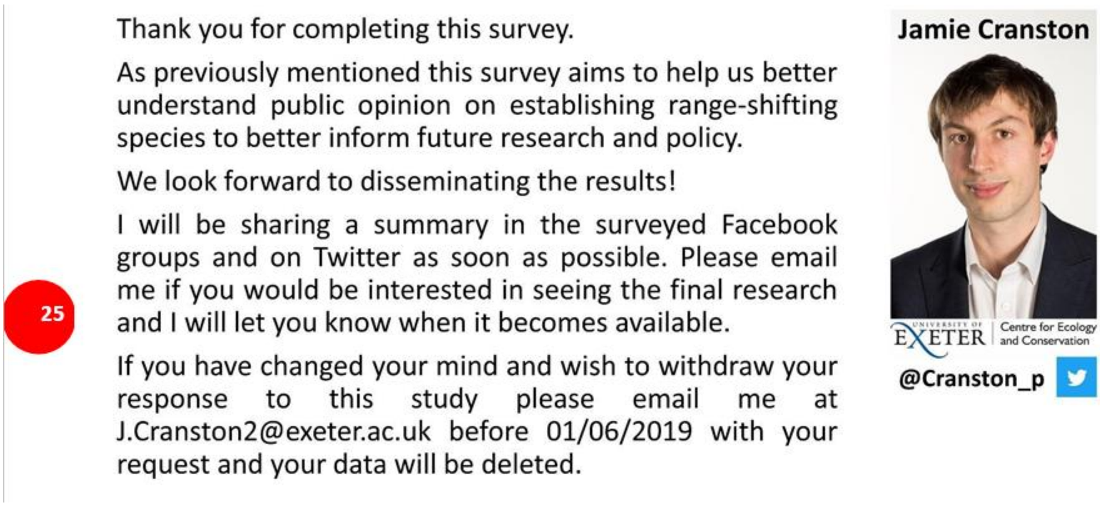
Some species are establishing because of **climate change** and others for **different reasons.**

In your opinion, what implications (if any) are there for responding to species that are establishing specifically due to **climate change**?

For example any practical or ethical considerations.

Do you have any other thoughts around the topic of **naturally establishing species** or **this survey** that you would like to share with us?

Next Page -> Pg 25 (Final Page) |



25

Thank you for completing this survey.

As previously mentioned this survey aims to help us better understand public opinion on establishing range-shifting species to better inform future research and policy.

We look forward to disseminating the results!

I will be sharing a summary in the surveyed Facebook groups and on Twitter as soon as possible. Please email me if you would be interested in seeing the final research and I will let you know when it becomes available.

If you have changed your mind and wish to withdraw your response to this study please email me at J.Cranston2@exeter.ac.uk before 01/06/2019 with your request and your data will be deleted.

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CHAPTER 1

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CHAPTER 3

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CHAPTER 5

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