Can ecological models be transferred in time and space? An investigation using a range of contrasting taxa

Joshua Copping

Supervised by Dr Katherine Yates & Dr Stephen Parnell

This thesis is submitted to the University of Salford,

School of Science, Engineering & Environment

In fulfilment of the requirements for the degree of Doctor of Philosophy (PhD)

November 2020

Table of Contents

List of Tables

List of Figures

Acknowledgements

Undertaking this PhD has been an immensely rewarding experience and would not have been possible without the inspiration, guidance, and support that have I received from my family, friends, and peers, to whom I will always be grateful.

I would like to start by expressing my gratitude to my supervisors, Dr Katherine Yates and Dr Stephen Parnell, without whom, this PhD would not have been possible. So, thank you for all the motivation, guidance and opportunities you have given me, along with the innumerable coffee breaks. You have helped me to grow as a researcher and your advice has been invaluable.

I'd like to thank my peers, in and out of the university, who provided me with opportunities to talk about my research and helped solve problems, whether that be during our meetings or visits to the pub. You help has been much appreciated.

I want to express my appreciation to my friends, both old and new, who have provided me with numerous ways to escape and take my mind off my research, even just for short periods of time. Your friendship and support, even from afar really helped. So, thank you.

I'm especially thankful to my family for the support and inspiration you've given me, not only during these past 3 years, but throughout my life. You have allowed me to explore my aspirations and helped me achieve goals. Dad, thank you for setting the best possible example of someone that works hard and cares about their work, it is one I have endeavoured to follow.

Finally, I would like to honour the memory of my beloved grandparents Patricia and Phillip who passed away in August 2017 and July 2019, respectively. I am deeply grateful for their love and support, and for their role in me finding a love for the natural world. I dedicate this thesis to you.

Abstract

Investigating the relationship between organisms and the environment has long been a focus of study in the conservation and ecology fields. Central to this research is the use of ecological models to explain, predict and project species distributions. Transferring ecological models into novel environments, both spatially and temporally, can prove vitally important when there is insufficient response data to create a model in the target area. However, there remain gaps in the knowledge and unanswered questions surrounding the concept and practice of transferring models. Therefore, in this thesis, I investigate how the performance and transferability of correlative SDMs are influenced by 1) the number of points a model is trained with, 2) the spatial resolution of predictor data, and 3) the choice of algorithm used. This research focuses on twenty amphibian, bird, insect, mammal, plant, and reptile species and utilises three popular correlative modelling algorithms; boosted regression trees (BRTs), generalised linear models (GLMs) and Maxent, before I investigate the transferability of a further five algorithms and an ensemble approach. Furthermore, I investigate the transferability of a simple and potentially generic mechanistic risk model for an emerging plant pathogen. In general, the correlative models, particularly the machine learning methods performed well and were transferable, though to what degree varied by the algorithm chosen and species modelled. However, in all chapters, perhaps the greatest influences on model transferability were data quality and differences in data between the area in which models were trained and transferred to. Nevertheless, this research demonstrates model transferability is achievable and can be improved through testing and selecting the most appropriate modelling approach, resolution, and complexity for both the correlative and mechanistic models.

Chapter 1 - Introduction and Background

1.1 Ecological models

For centuries, humans have recorded relationships determining the distribution of species. Arguably, the simplistic predator-prey population interaction equations, developed by Lotka (1925) and Volterra (1926) are thought to be the first true ecological models. The equations are now known as the Lotka-Volterra model and this has subsequently been used in innumerable variations and adapted to fit specific situations (Bahar & Mao, 2004; Reichenbach *et al.*, 2006; Zhu & Yin, 2009). The original published works of Lotka and Volterra are still amongst the most frequently cited ecological modelling papers (Jopp *et al.*, 2011).

In the 90 years or so that have passed since these models were developed, ecological modelling has become a well-established discipline and has advanced considerably (Zimmermann *et al.*, 2010; Zurell *et al.*, 2016), with more techniques and data available to use in a variety of ways depending upon the questions being answered. Nowadays, the more common approach to ecological modelling is quantitative, rather than the descriptive or qualitative approach that was prominent decades ago (Grinnell, 1904; Jopp *et al.*, 2011). This has allowed researchers to unveil complex biological systems and the environmental interactions happening within (Jorgensen, 2017).

Ecology is a broad field, therefore models have many different applications, all with varying degrees of complexity, dependent on their intended use (Refsgaard & Henriksen, 2004). There is an ever increasing number of methods for ecological modelling, with new techniques and approaches regularly becoming established and widely used (Candela *et al.*, 2010; Booth *et al.*, 2014; Zurell *et al.*, 2016). Despite the differences in the way models work and their differing purposes, such as modelling distribution, range shift or spread and so on, they all have the same overarching goal; to provide quantitative information about the environment they are representing, or a species' response to certain predictors (Jackson *et al.*, 2000). Therefore, to ensure this goal is met, and that a model can represent a given system as accurately as possible, the most suitable model for a specific situation should be selected based on the research aims (Aho *et al.*, 2014; Hjorth, 2017).

In the past 25 years, the traditional correlative or statistical approach mainly used for species distribution models (SDMs, also known as ecological niche models) has rapidly developed (Kearney *et al.*, 2010; Guillera-Arroita, 2017). This method uses observations of species occurrence or abundance at known locations and relates them to information on a range of environmental characteristics at those locations (Elith & Leathwick, 2009). This is used to gain ecological insights about the species' environmental tolerances or requirements and is often used to predict spatial distributions into areas with similar environmental conditions (Jarnevich *et al.*, 2015). The now widespread use of correlative models in the conservation field can be owed to their ease of use, simplicity and flexibility with data requirements and the range of biotic and abiotic interactions they can detect and subsequently characterise (Kearney & Porter, 2009; Elith *et al.*, 2011).

1.1.1 Niche theory

Underpinning all ecological models is niche theory; simply, the concept of a species' relationship to its environment and how said species responds to the distribution of resources and competitors (Polechova & Storch, 2019). This century-old concept was first described by Grinnell (1917), who saw a niche as a section of habitat that contains the correct abiotic conditions to allow a species to survive. These conditions govern where a species will occur, its distribution and its abundance. Move forward ten years and Elton (1927) expanded on this idea, placing the emphasis on the functional role of a species within a community, shifting the focus towards interactions with other species. Decades later and using Elton's theory as a foundation, Hutchinson (1957) and MacArthur (1972) focused mainly on resource utilisation and interspecific competition, pushing Grinnell's niche theory firmly into the background. When ecological modelling grew in prominence, particularly the modelling of range shifts due to environmental change, Grinnell's original niche theory once again grew in popularity (Wiens, 1977; Holt, 1990; Thuiller *et al.*, 2005a). Grinnell's work, combined with that by Elton and Hutchinson led the way in distinguishing between the fundamental and realised niches, and became niche theory as we know it today (Figure 1.1).

In essence, the fundamental niche is determined by the set of resources, both biotic and abiotic that a species can use to maintain a viable population (Soberón, 2007; Sillero, 2011). Therefore, the fundamental niche is defined by the intrinsic properties of a species, i.e. how it responds to abiotic aspects of the environment such as temperature, rainfall and altitude (Hirzel & Lay, 2008). The realised niche is a subset of the fundamental niche, using the same biotic and abiotic factors determining a species' range, but also considers constraints from interactions with other species. Factors include predation and competition, parasitism, human disturbance and the ability of a species to disperse to such areas, which is why the realised niche overlaps with the fundamental niche, but is typically smaller (Wiens *et al.*, 2009; Khatibi & Sheikholeslami, 2016).

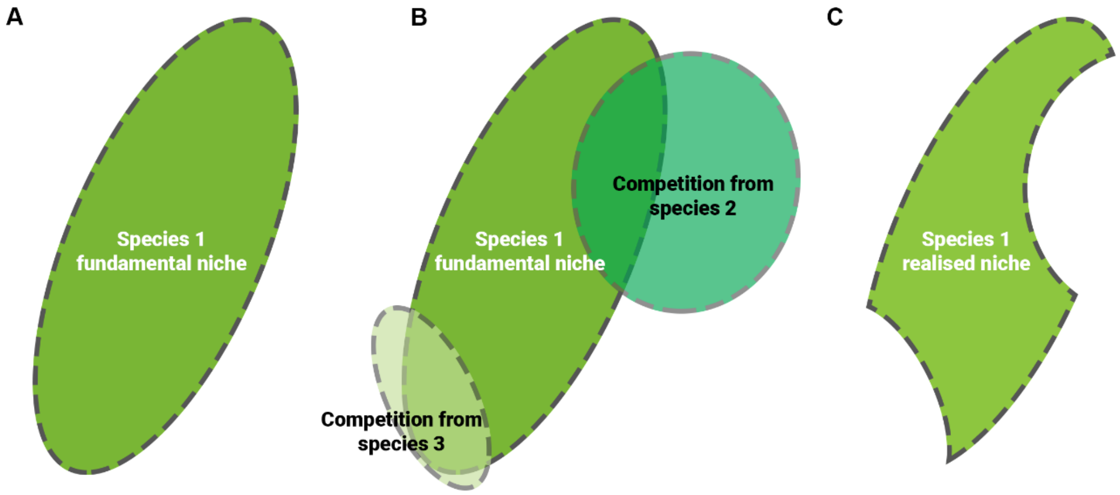


Figure 1.1 Simple representation of niche theory. (A) The fundamental niche, where a species can survive based on available environmental conditions. (B) The fundamental niche of a species, but also showing interspecific competition and competitive exclusion. (C) The realised niche, where the species can survive when limiting biotic factors are also taken into account. Competition is one of many factors determining a species' realised niche, and others include predation, parasitism, and human disturbance.

Another way of looking at a niche is with the theory by Soberón & Peterson (2005), describing biotic, abiotic and movement factors (BAM) and the subsequent diagrams created (Figure 1.2). These simple visualisations of BAM show the niche of a species based on three factors: 1) Abiotic variables which set physiological limits on the ability of a species to survive within an area, such as climate and the physical environment. 2) Biotic factors or interactions with other species, which determine a species' ability to maintain a population either through mutualism, such as pollination and seed dispersal or through predation and competition. 3) Movement factors such as the regions that are accessible to the species through dispersal from the original area, which is an important variable for distinguishing between the actual distribution and potential distribution of a species, as described by Václavík *et al.* (2010).

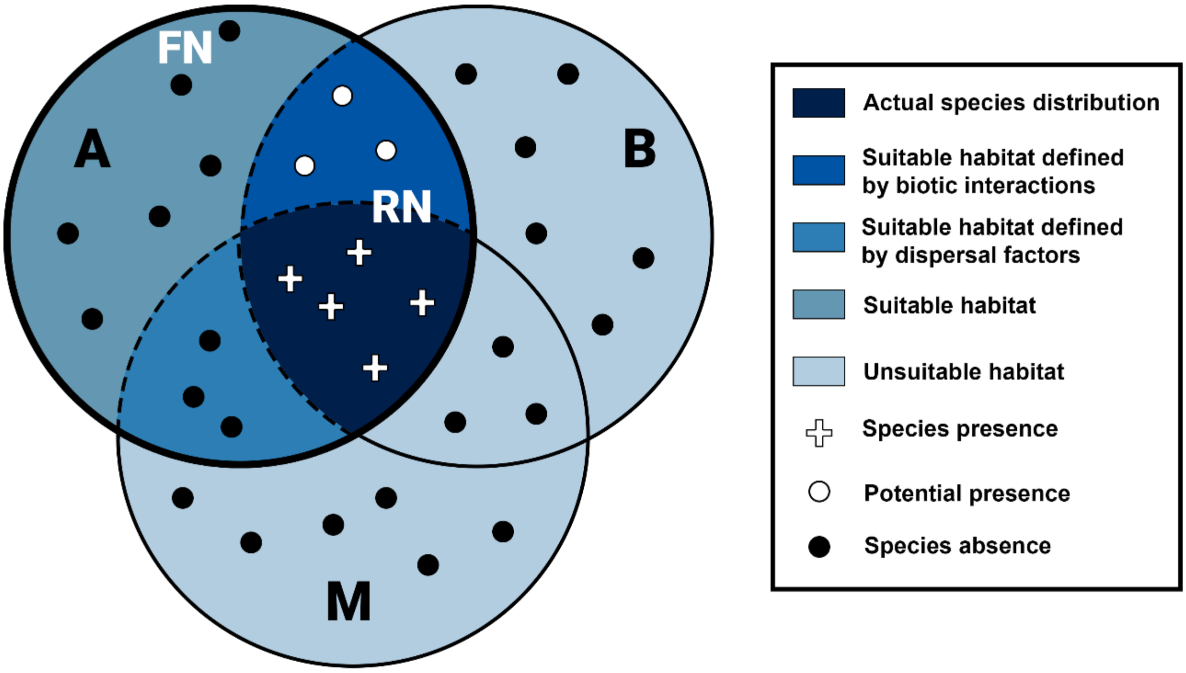


Figure 1.2 An abstract representation of a species' niche, determined by, biotic, abiotic and movement (BAM) factors as described by (Hutchinson, 1978; Soberón & Peterson, 2005; Soberón, 2007; Sillero, 2011). The diagram is divided into three key areas determined by, (A) abiotic, (B) biotic and (M) dispersal/movement factors, limiting a species' distribution. A species can only be present inside the area common to the three factors (indicated by the pluses) due to the unsuitability of one of more of the BAM aspects outside this shared region. The area shared between A and B, and A, B and M represent the region where the realised niche (RN) occurs. The region represented by A is where the fundamental niche (FN) occurs. Adapted from: Soberón & Peterson, 2005 and Sillero, 2011.

1.1.2 Modelling methods: Correlative

With the aim of ecological modelling to capture or quantify aspects of a species' niche, there are innumerable modelling approaches and techniques that can be used and adapted for each unique situation. Traditional species distribution or correlative models use observations of properties in the environment, independent of the species to predict distribution (Figure 1.3). These types of model can be typically classified into three categories: presence-only, presence-absence, and presence pseudo-absence/presence-background models. The choice of which to use is determined by the intended aim of the research and type of data available (Sillero, 2011; Guillera-Arroita *et al.*, 2015).

A widely used modelling approach in SDM studies is with presence-only data (Elith *et al.*, 2006; Kearney *et al.*, 2010; Guillera-Arroita *et al.*, 2015). These types of model use data which only contain locations where target organisms have been observed to occur, but they cannot be used to show areas that the organisms do not occur (Dettmers & Bart, 1999). Therefore presence-only data isn't as susceptible to some of the issues of imperfect detectability such as variability in abundance and variability in behaviour (Tsoar *et al.*, 2007; Elith & Leathwick, 2009). Presence-only data is used due to the ease, and time and costs associated with its collection. Presence-only models such as those within the envelope and profile modelling families, i.e. Bioclim and Domain required only presences, unlike Maxent, which is often mislabelled and is in fact a presence-background model, discussed in more detail in subsequent sections.

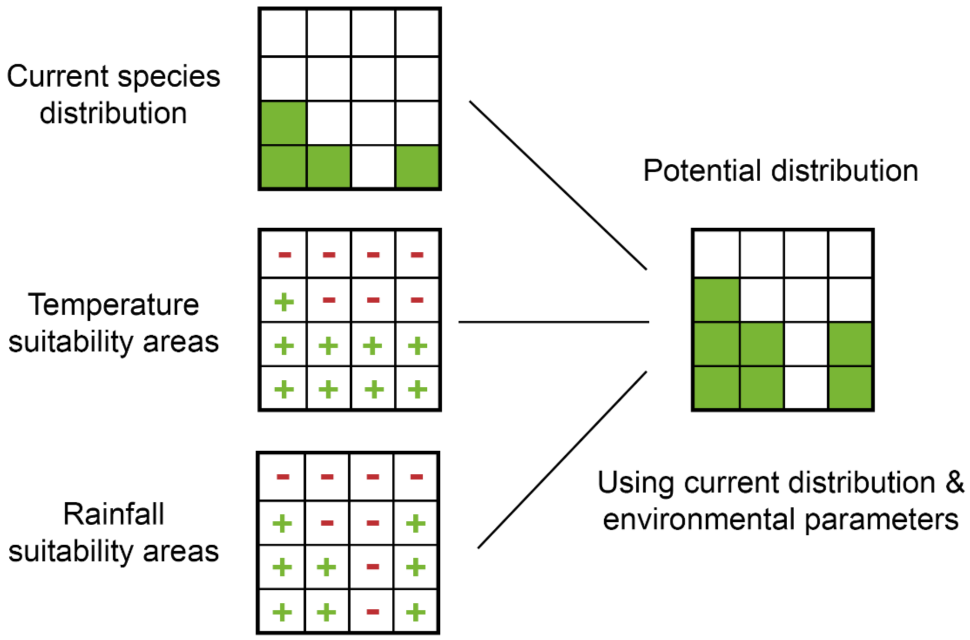


Figure 1.3 A simple representation of how a correlative species distribution or ecological niche model works, showing areas with suitable abiotic factors (temperature and rainfall) and the current species distribution. Potential distribution is the projection based on observations of abiotic factors in the species' current range. + indicates factor suitability, - indicates unsuitability, coloured sections indicate species distribution.

However, there are many misconceptions and many underlying issues surrounding the use of presence-only models. When modelled, imperfect detection data i.e. errors of omission (false negative) and commission (false positive), can seriously bias model estimates and predictions, subsequently distorting conclusions derived from SDMs using such data (Hefley *et al.*, 2013; Gomes *et al.*, 2018). This is also the case with prevalence; presence-only data lacks information on the prevalence of a species, or the proportion of occupied sites within a landscape (Tsoar *et al.*, 2007; Yackulic *et al.*, 2013).

For some analysis, prevalence data is needed, and this can be obtained when collecting presence-absence data. As the name suggests, presence-absence data also contains recorded absences of a species. In contrast to presence data, reliable absence data is rare due to the time and financial costs associated with its collection, therefore making it harder to obtain (Gu & Swihart, 2004; Guillera-Arroita, 2017). In addition, assuring collected data contains true absences is a difficult task and becomes unaffordable over large areas or in the many studies using coarse resolution data (Brotons *et al.*, 2004). This problem escalates further when the species studied is mobile or cryptic, requiring more effort in collecting data and confirming true absences (Manel *et al.*, 2001; Yee & Dirnböck, 2009). A fundamental issue facing both presence-only and presence-absence models is the inherent sampling bias that occurs when certain parts of a landscape are inevitably sampled more intensively than others (Byrt *et al.*, 1993; Syfert *et al.*, 2013). For example, species may be reported at higher rates near roads or easily accessible areas and sampling may not be carried out in a systematic manner, particularly when citizen science data is used (Bird *et al.*, 2014; Varela *et al.*, 2014).

Like presence-only models, presence-absence models relate a species' presence to the predictor variables (usually environmental) at the occurrence locations. However, the difference comes with the absence points; by knowing where a species does not occur and the environmental conditions there, allows areas to be excluded when the species' range is predicted (Brotons *et al.*, 2004; Jiménez-Valverde *et al.*, 2008; Liu *et al.*, 2011). Whilst this may provide more accurate predictions, many researchers note a recorded absence of a species may not be solely down to environmental conditions (Lobo *et al.*, 2006; Soberón, 2007) and therefore suggest it is necessary to include other factors that may restrict a species' distribution.

Due to the constraints often associated with collecting presence-absence data, there is another option; pseudo-absence data. Pseudo-absences can be generated by the modeller and used in place of real absences in order to infer a species' absence and to obtain a complete sample of the environment (Iturbide *et al.*, 2015). This is to develop a clear understanding of the factors influencing the spatial distribution of occurrence or abundance records (Phillips *et al.*, 2009). However, there is some criticism of their use, particularly how they are generated, without explicit knowledge of a species' absence (Guisan & Thuiller, 2005; Hastie & Fithian, 2013). Additionally, pseudo-absences are regularly confused with background points; again, user-generated points within the landscape of interest, but generated randomly with no assumptions or knowledge of sampling effort (used in pseudo-absence generation to ensure that points mimic "true" but unobserved absences). The sole use of background points is to provide a sample set of environmental conditions available to a species in a landscape, aiding in the characterisation of species' occurrence requirements (Engler *et al.*, 2004).

The decades of correlative species distribution modelling which have provided a wealth of literature and developments to the available methods have naturally advanced this subject area. However, one key question continually re-occurs: which models are best? Despite there being a suite of algorithms available to model distributions, whether that be profile and regression-based methods or machine learning (Elith *et al.*, 2006; Shabani *et al.*, 2016; Norberg *et al.*, 2019),the extrinsic nature of correlative models, requiring observation data, make them less suitable for certain situations and applications (Robertson *et al.*, 2003). This is where the use of mechanistic models has advantages and why their use has been increasing in popularity in the fields of conservation and biology in recent years (Peterson *et al.*, 2015).

1.1.3 Modelling methods: Mechanistic

In contrast to correlative models, mechanistic models are process based and use data on the intrinsic properties of species that determine their sensitivity to features of the environment (Leibold *et al.*, 1995; Elith & Leathwick, 2009). These tend to be based on their physiology, life-history and behavioural plasticity to map current or future locations which are within a species' tolerance limits (Kearney *et al.*, 2010). A simple example of a mechanistic species distribution model would be the prediction of distribution using the species' intrinsic values such as maximum and minimum temperature tolerance for survival. The species' tolerances would need to be found through lab-based research and the resulting temperature range for survival would be delineated on a map of spatial temperature values. This approach differs from a correlative model which would project the species' distribution based on observations of occurrence. However, whilst mechanistic models are largely intrinsic, there is an extrinsic aspect, in that they require large volumes of empirical data for calibration and parametrisation (Bouchet *et al*., 2019).

Mechanistic models have become increasingly common in the ecology field due to their ability to replicate complex systems by reviewing underlying processes and interactions (Leibold *et al.*, 1995; Robertson *et al.*, 2003). When considering niche theory, the consensus amongst researchers suggests correlative SDMs represent the realised niche, whereas mechanistic models represent the fundamental niche (Figure 1.4), due to the intrinsic nature of these models (Soberón, 2007; Kearney & Porter, 2009; Sillero, 2011). Because of this, mechanistic models tend to overpredict a species' range, whereas correlative models typically underpredict (Robertson *et al.*, 2003; Kearney & Porter, 2009).

The strength of mechanistic models is that they can be extensively customised and developed for each situation, and prove particularly useful for monitoring spread and distribution of invasive species (Kearney *et al.*, 2010; Fordham *et al.*, 2018). This is because of the many different invasion pathways, dispersal and spread patterns and traits or characteristics of a species which may not be able to be effectively modelled using a correlative approach (Guisan & Thuiller, 2005). A key feature of mechanistic models in invasive species modelling is their ability to model non-uniform spread such as the spread of species along a road network in addition to outward dispersal from a singular point (Brooks-Pollock *et al.*, 2014). Correlative models struggle to represent species with patchy dispersal, whereas mechanistic models can take into account these subpopulations within the metapopulation by programming these characteristics into the model (Jesse *et al.*, 2008). This is due to the process-based nature of mechanistic models, which do not work on the same assumptions and observations as correlative models (Jopp *et al.*, 2011).

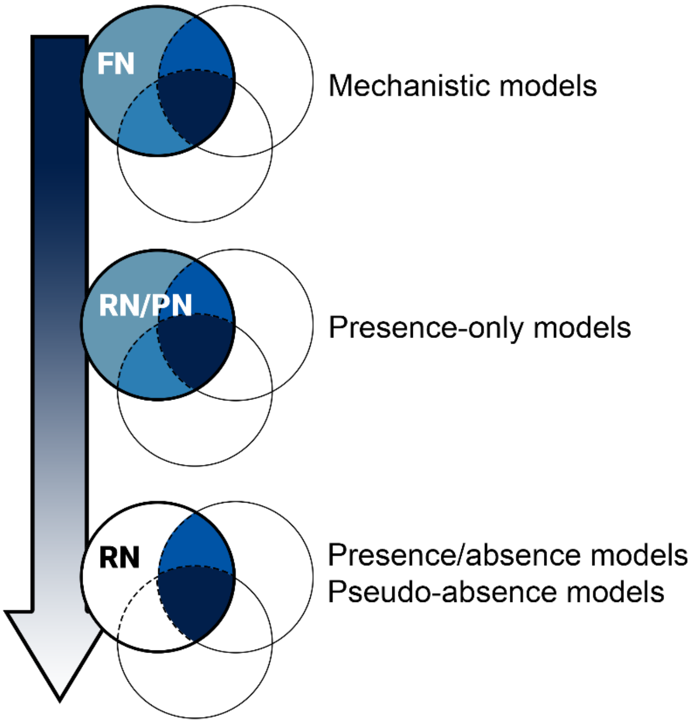


Figure 1.4 Representation of the BAM diagram, Figure 1.2, with a gradient of niche type calculation ability based on the type of model being used: Mechanistic models calculate the fundamental niche (FN). Presence-only models calculate the realised nice (RN) in combination with a portion of FN, forming the potential niche (PN). Presence/absence and presence/pseudo-absence are the only models with the ability to calculate RN. Adapted from: Sillero, 2011

An array of studies illustrate correlative models are easier to use and develop compared to mechanistic models, but this often comes at the cost of predictive accuracy (Yates *et al.*, 2000; Lawler *et al.*, 2006; Buckley *et al.*, 2010; Oppel *et al.*, 2012). By integrating biological interactions, dispersal ability, adaptation and even thermodynamics through an organism's energy requirements, mechanistic models are particularly efficient at predicting changes in behaviour and range caused by habitat loss or climate change (Fulford *et al.*, 2013). Bogosian *et al.* (2012) highlight that correlative models accurately describe niches over small spatial scales with high precision, but over large areas, mechanistic models offer greater predictive accuracy but less precisely. Research has shown that both correlative and mechanistic models can perform well in characterising the distributions of species within their current range, particularly when relevant predictors are analysed using an appropriate model (Guillera-Arroita *et al.*, 2015). In this scenario, models can provide valuable insights and robust predictive ability. However, models that extrapolate spatially or temporally, or those that use poor quality data tend to provide more ambiguous results (Randin *et al.*, 2006; Wenger & Olden, 2012).

When modelling future distributions such as potential invasions or range shifts due to climate change mechanistic models have generally been shown to be more robust than correlative models due to their intrinsic nature (Robertson *et al.*, 2003; Bogosian *et al.*, 2012). In such cases, the reliability of predictions with correlative models is often questioned because correlative models often lack a mechanistic foundation and heavily rely on assumptions about climates which are still largely unknown (Kearney *et al*., 2010; Bouchet *et al*., 2019). Whilst mechanistic models also rely upon climate assumptions, the difference is that mechanistic models are based on processes that are arguably more likely to hold truth in new contexts. The increased predictive accuracy and robustness, along with efficiency in modelling change and adapting to new situations make mechanistic models particularly useful when extending their use into novel environments (Randin *et al.*, 2006; Werkowska *et al.*, 2017). However, with this comes a range of issues such as non-stationary processes, novel biotic interactions, and the often, untested predictive accuracy of models, leading to uncertainties in the results (Sequeira *et al.*, 2018b; Yates *et al.*, 2018). The area of research focusing on extending a model’s use and spatial and/or temporal extrapolation is gaining in popularity and in recent years has become known as transferability.

1.2 Model Transferability

Whilst not a particularly new idea, transferability has gained attention in the past decade (Figure 1.5). It is the concept of spatial or temporal cross-applicability of a model (Guisan & Thuiller, 2005; Wenger & Olden, 2012), previously referred to as generality (Fielding & Haworth, 1995), but more recently termed transferability. It is essentially the projection of an existing model in time and/or space to extend its use from the system it was created (reference area) into a system the model was not developed in (target area, Elith & Leathwick, 2009; Sequeira *et al.*, 2018b). Such transfers tend to be driven by limited research funding, data deficiencies and accelerating changes to biodiversity and the environment.

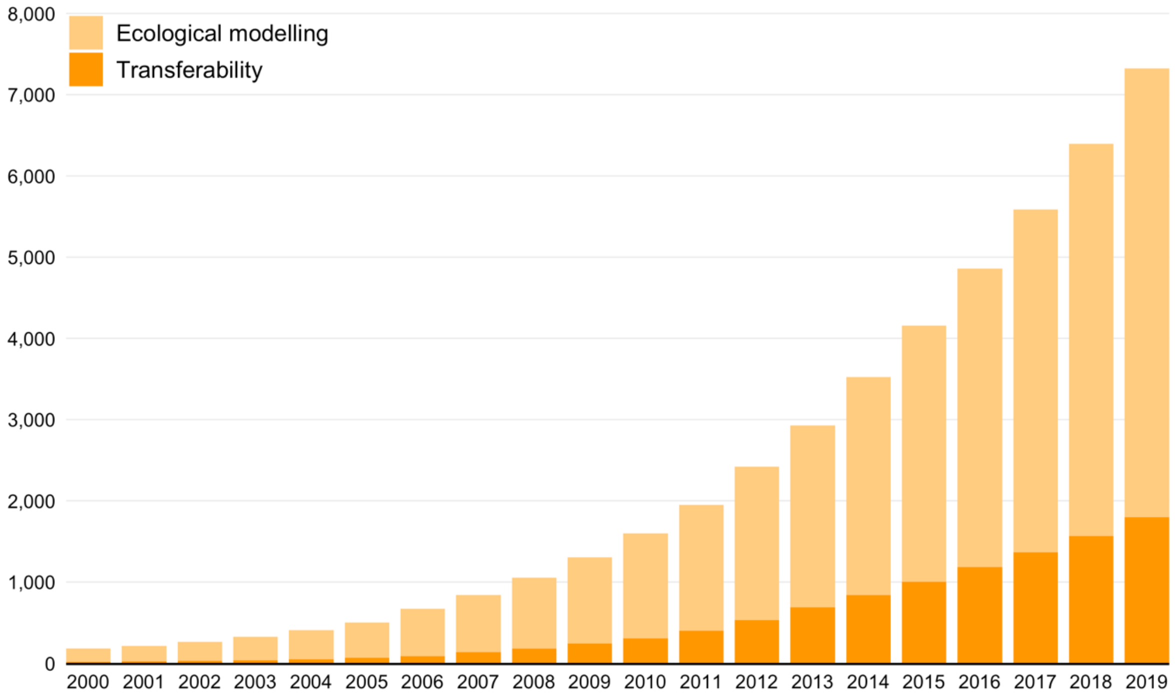


Figure 1.5 Temporal trends in published papers related to ecological modelling (light bars) and model transferability (dark bars) between the years 2000 and 2019. Bars indicate the cumulative number of peer-reviewed journal articles listed on the Web of Science (webofknowledge.com). Data shown are valid as of 3rd of August 2020. Search details are outlined in Appendix I. Adapted from Sequeira *et al*. (2018b).

Model transfers have been applied to single species, communities and ecosystems and there are a range of applications for transferable models; spatial transfers can be used to inform on suitable areas for the reintroduction of species (Schadt *et al.*, 2002), assist in the regulation of potentially disruptive and damaging human activities (Mannocci *et al.*, 2017) and to aid in the creation and management of protected areas (Fernández *et al.*, 2015). But perhaps the most common use of spatial transfers is to highlight areas vulnerable to invasion by pest organisms (Hudgins *et* *al.*, 2017; Fan *et al.*, 2018). For example, Peterson and Robins (2003) transfer a distribution model of the barred owl (*Strix varia*) from the northeast coast of the USA to the Pacific northwest, highlighting its potential invadable range and niche overlap with the endangered spotted owl (*Strix occidentalis*), which is threatened by habitat loss and fragmentation. In the fragmented areas of forest habitat *S. varia* would outcompete *S. occidentalis*, causing further population decline, however, with improved management such as corridors to increase connectivity between the areas of fragmented habitat, the impacts on *S. varia* could be less severe.

Similarly, there are multiple uses for temporal transfers, such as quantifying the impacts of past urbanisation on habitats and species (Fernández *et al.*, 2012), outlining the historic range of species and their evolution (Wogan, 2016) and predicting future ecosystem dynamics (Stewart *et al.*, 2015). However, the majority of temporal transfers tend to focus on projecting the impacts of climate change on a species' range or habitat suitability, as highlighted by Nabout *et al.* (2012) who predict the future productivity of an important maize crop in Brazil under projected climate change to ensure the security of this food crop. Moreover, a vital and increasingly common area of work with temporal transfers is the investigation of invasive species spread. Verbruggen *et al.* (2013) show the potential range of the highly invasive seaweed, *Caulerpa cylindracea*, increasing throughout Australia and Europe with projected climate change. Likewise, Fan *et al.* (2018) show the range of the invasive herb, *Flaveria bidentis*, expanding throughout China, posing serious threats to the agriculture industry. Studies such as these, highlighting the potential range shifts and invadable areas can aid in early detection of invasive organisms, which will result in lower economic costs associated with the subsequent control and management (Keller *et al.*, 2008; Ervin & Holly, 2011).

However, in contrast and quite often the case, there are many examples of poor model transfers (e.g. Huang & Frimpong, 2016; Roach *et al.*, 2017). For example Torres *et al.* (2015) transfer SDMs between three populations of the grey petrel (*Procellaria cinereal*) in the Southern Hemisphere. The transferred models exhibited poor predictive performance, indicating separate realised niches and contrasting habitat choices for each population. Ultimately, poor transfers show developing a transferable model is not a straightforward task and there are often a range of challenges encountered (Werkowska *et al.*, 2017; Sequeira *et al.*, 2018b; a; Yates *et al.*, 2018). In many situations, data deficiencies and a limited understanding of the performance of transferred models undermines confidence in their predictions. And although the volume of research surrounding model transferability is increasing (Figure 1.5), there remain several important questions in both the theory and application of transferring models. These include challenges with the theory, data use, modelling and result interpretation of transferability, which are described below.

1.2.1 Challenges with transferability: Theoretical

Some of the greatest challenges facing model transferability are theoretical, namely whether the quality of a transfer is taxon or trait specific. By knowing whether models are more transferable for certain taxonomic groups or species with specific traits, confidence in predictions would be increased. There have been a large number of studies working to investigate this issue, with Dobrowski *et al.* (2011) demonstrating that the biggest driver of variability in model performance was caused by differences in species and their traits, not by model algorithms, which can be seen in Figure 1.6, showing the differing levels of transferability amongst taxa.

This is further emphasised by Thuiller *et al.* (2005) using SDMs to predict the risk of alien plant invasions from 96 South African plant species based on climate variables and transferring models to new areas. When testing predictive accuracy, not all models behaved the same and it was thought to be due to the specific traits of a species, i.e. phenotypic plasticity and ability to adapt to new climate conditions quicker than other species, therefore the models underpredict the potential range of species with high plasticity (Pan *et al.*, 2006). Similarly, Wogan (2016) highlights the increased difficulty in developing transferable models for generalist species with a broad niche and those with greater movement dynamics. For example, of the 77 butterfly species modelled by Eskildsen *et al.* (2013), those that were highly mobile, had a large range, or with long flight seasons produced poor predictions when models were transferred.

Another issue is calculating and understanding the limits to model transfers. Whilst Houlahan *et al.* (2017) suggest increases in spatial and temporal distance from the reference conditions is likely to increase prediction error, there have been a number of successful long distance (spatial and temporal) transfers (Figure 1.6, Kharouba *et al.*, 2009; Medley, 2010; Dobrowski *et al.*, 2011) and increasing distance does not appear to be necessarily detrimental to transferability. In reality, similarity in abiotic conditions between the reference and target areas seems to determine transfer quality more than distance (Dormann, 2007; Roach *et al.*, 2017; Fan *et al.*, 2018). However, the minimum level of similarity required to enable high quality transfers remains unknown.

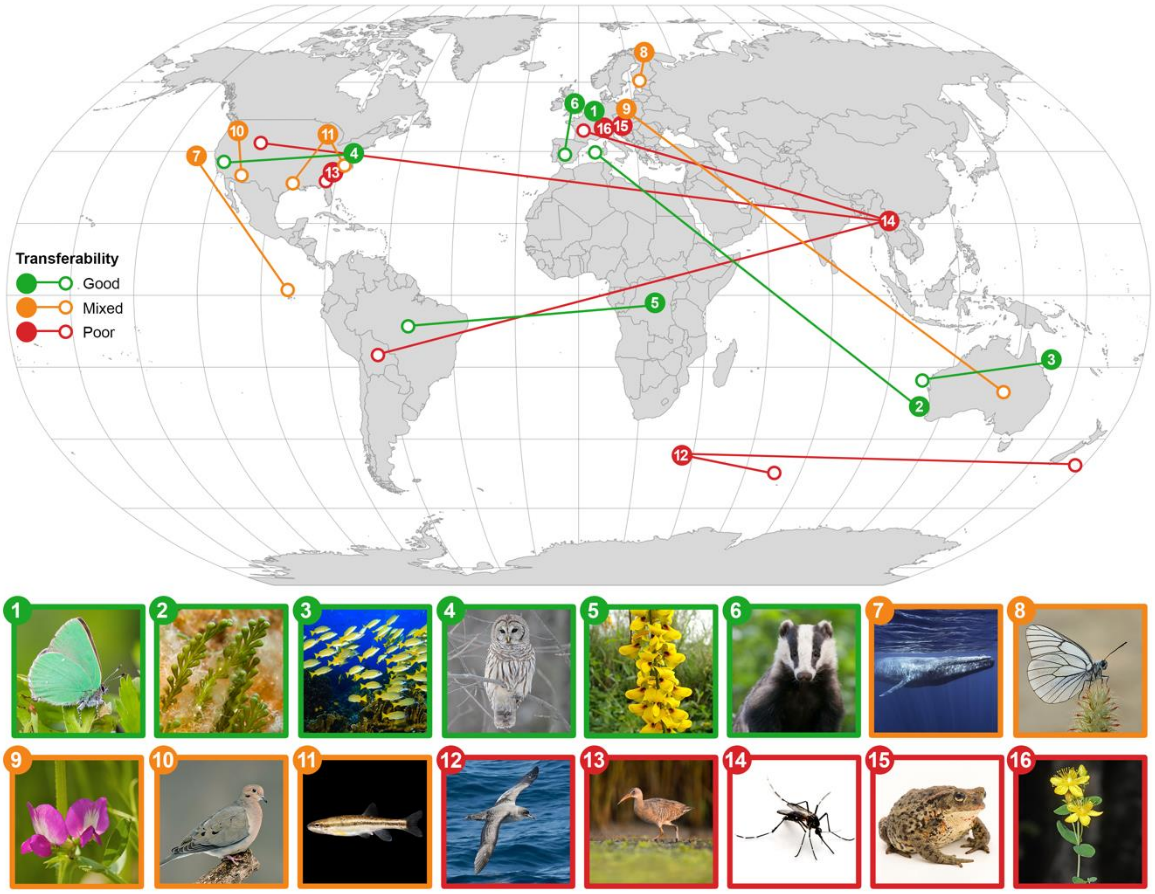


Figure 1.6 Diagram of 16 predictive model transfers, showing that transfer quality varies per taxon and distance transferred. These studies have been chosen to highlight a wide range of taxa (birds, fish, insects, mammals, and plants), and transfer distances (tens to thousands of km). Colours indicate the transferability of the model, with good-quality transfers shown in green using examples 1-6, mixed results using orange and demonstrated by 7-11 and poor-quality transfers using red, for examples 12-16. Reference and target range are shown as filled and open circles, respectively, with numbers referring to the taxa being transferred. Photographs represent the taxa modelled and include: (1) green hairstreak, *Callophrys rubi*; (2) invasive seaweed, *Caulerpa cylindrace*; (3) bluestripe snapper, *Lutjanus kasmira*; (4) barred owl, *Strix varia*; (5) smooth crotalaria, *Crotalaria pallida*; (6) Eurasian badger, *Meles meles*; (7) blue whale, *Balaenoptera musculus*; (8) black-

veined white, *Aporia crataegi*; (9) common vetch, *Vicia sativa*; (10) mourning dove, *Zenaida macroura*; (11) blacknose dace, *Rhinichthys atratulus*; (12) grey petrel*,* *Procellaria cinereal*; (13) clapper rail, *Rallus crepitans*; (14) Asian tiger mosquito, *Stegomyia albopicta*; (15) common toad, *Bufo bufo*; (16) spotted St. John's-wort, *Hypericum maculatum*. Additional details about these studies, the ranking of transferability and references are given in Appendix II. Reproduced and adapted from Yates *et al.*, 2018.

A greater challenge, little understood, is how to account for non-analogue conditions in transfers. Or simply put, how to account for the novel conditions not currently experienced by the species being modelled, for example the climatic conditions under future scenarios (Kearney & Porter, 2009). When transferring into these non-analogous environments, predictive performance in these novel conditions is rarely explicitly tested, despite a wide array of well documented issues (Perrin, 1904; Webber *et al.*, 2011). To account for such conditions, a range of different methods will be needed, dependent upon environmental dissimilarity, species modelled and type of algorithm used (Evans *et al.*, 2012). Zurell *et al.* (2012) propose two methods to visualise non-analogue conditions: First, through extending multivariate environmental similarity surface maps to identify parts of the environmental space that are within the sampled, univariate range of the predictors but represent novel multivariate combinations. Second, by using inflated response curves to visualise the full range of values for each predictor, whilst also plotting the available data in that space. Unfortunately, whilst both of these methods aid in the visualisation of non-analogous conditions, they cannot predict a species' response to these conditions, therefore further development is needed (Zurell *et al.*, 2016).

1.2.2 Challenges with transferability: Data

The quality of data plays an important role in any ecological study and high-quality data is much sought after but can be expensive. "Big data" or the vast volumes of data collected over numerous years can be extremely useful to ecologists (Hampton *et al.*, 2013) and their use is increasing. It has been argued that when a model is developed with greater volumes of data, capturing more of the environment a species is in, the predictive accuracy is increased (Jiménez-Valverde *et al.*, 2008). Numerous ecological studies have shown the impact of limited vs expansive quantities of data on model predictive accuracy (e.g. Chen *et al.*, 2003; Vaughan & Ormerod, 2003; Pearce & Boyce, 2006). However, when transferring a model, there have been few studies investigating this area. Aubry *et al.* (2017) show that data with high accuracy and/or precision can be more important to transferability than the volume of data and spatial extent, therefore it is suggested that unreliable data such as easily misidentified species, anecdotal reports and some potentially citizen science data should not be used.

Another key point about the data used in transferable models has been outlined by Scales *et al.* (2017), who highlight the importance of resolution and its influence on model fit, prediction and subsequent transferability. Often, there are differing resolutions between the species record data and predictor variables. If predictor data is at a lower resolution, this may not fully capture the important aspects of a species' ecology and the surrounding environment, therefore wrongly characterising aspects of the environment thought to be of use to the species (Dale *et al.*, 1989). This is particularly relevant when using models such as resource selection function and mapped habitats as a predictor; if resolution is low, the perceived habitat preference may be falsely recorded (Boyce, 2006). In such cases, models are sensitive to the extent of the study area, particularly with fragmented habitats (Paton & Matthiopoulos, 2015). To overcome this and increase transferability, Bamford *et al.* (2009) recommend combining distinct geographic regions and environments, therefore capturing more of the niche to truly represent a species' requirements.

When planning a transfer, it is advised that data be obtained at the highest resolution possible, despite no clear answers as to what is the correct approach to collecting data and the proper use of data for model transfers. What is clear is that poor-quality data will almost certainly result in a poor-quality transfer. So even if only limited high-quality data is available, this should be the preference over larger volumes of lower quality data (García-Callejas & Araújo, 2016; Aubry *et al.*, 2017).

1.2.3 Challenges with transferability: Modelling

When it comes to modelling there are several aspects to be considered. One of the key challenges is determining the effect of model complexity on transferability. Whilst developing an algorithmically complex model (i.e. the degree of flexibility) may produce accurate results in the region it was created, the complexity may result in overfitting and subsequently biased predictions when transferred therefore, simple models are expected to have greater transferability (Merow *et al.*, 2014; Moreno-amat *et al.*, 2015). However, this is not always the case, as simple models have also been shown to produce ambiguous predictions when transferred, which implies that simplicity is not always the best choice (Thuiller *et al.*, 2004; Evans *et al.*, 2013). Every model serves a different purpose, and certain situations may call for accurate and precise predictions over transferability. Ultimately, complexity should be determined by the situation the model is developed for and intended to be used in (Merow *et al.*, 2014).

Similarly, an issue defined by the model user is the trade-off between model transferability and predictive performance, i.e. internal vs external validation (Sequeira *et al*., 2018b). Pearson & Dawson (2003) show that more accurate simulations of range shifts caused by climate change require a greater understanding of the interactions between species and the underlying factors affecting distributions. Furthermore, Verbruggen *et al.* (2013) show transferability can be improved considerably by appropriate predictor selection; only those that explicitly describe a species' distribution. To find the balance of an accurate, precise model with good transferability, the user needs to understand the parameters defining a species' range and only include those essential to the model. As previously outlined, the final decision of what to model and which techniques to use should be based on the situation, degree of accuracy and the overall need for transferability (Guillera-Arroita *et al.*, 2015; Aubry *et al.*, 2017).

Another question commonly highlighted in the literature is how the performance of correlative and mechanistic models compare when transferred (Meineri *et al.*, 2015; Rougier *et al.*, 2015; Fordham *et al.*, 2018). These two contrasting techniques have the same aim but use very different methods to achieve it, therefore influencing transferability. Studies suggest that mechanistic models should be more transferable due to the underlying independence from empirically derived relationships, but these models will have low precision (Fulford *et al.*, 2013). Whereas in contrast, correlative models typically have high local accuracy and precision, however this decreases with distance and size of area being modelled, therefore indicating poor transferability (Webber *et al.*, 2011; Fischer *et al.*, 2014). Despite this, a handful of studies have shown correlative models to perform as well as mechanistic models when transferred (Robertson *et al.*, 2003; Kearney *et al.*, 2010; Rougier *et al.*, 2015). And, it is thought the majority of transfers will be correlative, due to the relatively easy to use modelling approaches such as Maxent, in contrast to mechanistic models which have the extra cost of increased data and computational requirements. In practice, the type of model chosen to be transferred will most likely be selected based on the context of the study, and the available data and predictors.

Whilst the above is quite a generalisation, there has been an array of studies examining this question in further detail by comparing specific algorithms. Amongst the most popular methods are Maxent, general linear models (GLMs) and generalised additive models (GAMs) which have all been considered as some of the most transferable methods (Heikkinen *et al.*, 2012; Duque-lazo *et al.*, 2016). However, the quality of a transfer is largely case-specific, dependent upon predictor variables chosen, data treatment and model tuning, all of which cause differences in model performance (Werkowska *et al.*, 2017; Iturbide *et al.*, 2018b). And whilst a ‘silver-bullet’ model with high performance and transferability is much sought after, it is highly unlikely that one could be developed due to issues such as overfitting whilst remaining general enough to be transferable (Guisan *et al.*, 2007a; Qiao *et al.*, 2015).

A further area of research needing more development, is the incorporation of non-stationary interactions into model transfers. These are changing relationships between variables, model parameters and species through space and time, often caused by shifts in population density, resource availability, predation and competition (McLoughlin *et al.*, 2010; Mellin *et al.*, 2014). Such changes in relationships may inhibit model transferability, as successful transfers rely on the underlying idea of consistent relationships between species and their environments at the model's calibration site and remain consistent once transferred (Godsoe *et al.*, 2014, Mannocci *et al*., 2020). One such work around appearing to gain traction is the inclusion of a species' functional response from different regions, training the model with more information as to a species' tolerances or needs, combined with the use of nonstationary model coefficients (Matthiopoulos *et al.*, 2011; Paton & Matthiopoulos, 2015). Both these aspects together will allow for enhanced model transfers in the face of non-stationary processes.

1.2.4 Challenges with transferability: Result interpretation

There are no standardised methods to assess transferability and no consensus on how to quantify the uncertainty in results that arises from transferring a model to a new system. Uncertainty will always be present in modelling studies, it is common and can arise from a variety of sources throughout the study, such as the species' identification, the sampling methodology, quality of data, choice of predictors, algorithm selection, and parameter estimation (Beale & Lennon, 2012; Evans, 2012; Heikkinen *et al.*, 2012). However, uncertainty can vary spatially, and its magnitude is often unknown (Wiens *et al.*, 2009). This variation in uncertainty, particularly in transferred models, can present significant challenges and lead to unreliable results. Therefore, clear procedures for quantifying and reporting on such uncertainty are needed to enable transparent results and an increased trust in what is being presented (Dormann *et al.*, 2008; Beale & Lennon, 2012).

The lack of a standardised assessment method for results can lead to different interpretations of transfer quality which in turn will impede comparisons of performance between model transfers (Wenger & Olden, 2012). Therefore, to increase reliability of results, appropriate diagnostic metrics of accuracy and precision should be used (Randin *et al.*, 2006). However, assessment of transferability can be difficult as true validation is often not possible as an independent dataset is required, for example, if looking at the spread of an invasive species, the potential invaded range is often lacking data (Jiménez-Valverde *et al.*, 2011). In such scenarios, transferability can only be estimated, but where feasible, one option to increase knowledge of transfer quality is to project the model into an alternative data-rich area and test performance of this transfer (Sequeira *et al.*, 2018b). Ultimately, to provide an increase in transferability knowledge, assessment of performance needs to be consistent using the same metric across model types, taxa, and studies to enable comparison. For this to happen, a novel approach to model evaluation and validation needs to be found for use in areas lacking available data (Fieberg *et al.*, 2018).

1.2.5 Best practice with transferring models

As with all research, there are methods, techniques and rules of thumb that will yield the best results or allow greater comparison with studies to enable increased transparency and improved understanding within this research area. Sequeira *et al.* (2018b) summarise the key findings from transferability literature to highlight the positive and negative impacts of key features on transferability. Outlined below are a selection of the priority best practice recommendations to be used to improve predictive performance, transferability, and allow greater transparency when publishing work, through comparison and reproducibility.

There are several suggestions in the literature to ensure best practice with transferability from the beginning of the study, even before modelling begins. Preferably, the data should be unbiased, cover as great a range of predictor gradients where the species is found, and if possible, long-term, and high frequency. However, this will be difficult in most situations, particularly when dealing with future temporal transfers as seen in a large number of transfer studies (see Lawler *et al.*, 2006; Kharouba *et al.*, 2009; Varela *et al.*, 2009; Tuanmu *et al.*, 2011; Rapacciuolo *et al.*, 2012). In temporal transfer situations such as these, a best practice suggestion by Kharouba *et al.* (2009) is to only compare forecasts for species for which hind-casting has shown high predictive performance. Alternatively, transfers could be carried out prospectively, and evaluated once data becomes available (Yates *et al.*, 2018). When reporting on the data used in transferability studies, descriptions should include a summary of the relationships between predictor and response variables in both the target and reference areas, again to increase transparency and subsequent confidence (Werkowska *et al.*, 2017).

When it comes to modelling and the successive transfer, best practice guidelines are quite simple. The modelling method should be selected based on the most suitable approach for the study, in terms of data type and result output. It has been suggested by Sequeira *et al.* (2018b) that a range of model algorithms should be tested in the reference area, and the best performing selected for the transfer to the target area. This has the potential to reduce uncertainty, however it must always be acknowledged that whilst models may have good predictive performance in the reference area, they may not always transfer well. Another point is to investigate and report the effects of model complexity. This can be performed by removing predictors through processes such as stepwise reduction, as the effects of complexity vary considerably between data, model type, taxa, and geographic location (Bell & Schlaepfer, 2016). And finally, whilst this should be common practice for all ecological modelling studies, with transfers it is important to carefully check the model assumptions and report the residuals to allow better interpretation of results, thus increasing confidence in model outputs (Werkowska *et al.*, 2017).

Best practice guidelines for results of transferability studies aim to increase the standardisation of assessment and reporting. These include providing details on the type of models and algorithms used and the assumptions made during the transfer, for example equilibrium, stationarity, and environment vs human drivers. Additionally, details on the type of data being used, such as data-rich, data-sparse, presence only or abundance data and summaries of the predictors should be included, perhaps as a boxplot, demonstrating the degree of similarity between target and reference areas (Peterson *et al.*, 2007; Sequeira *et al.*, 2018b). The model fit and performance should also be reported, focusing on the basic statistics, such as comparisons of true and false positives and negatives by using ROC and AUC or similar methods (Wenger & Olden, 2012). But most importantly, results of extrapolation should be explicitly indicated so the reader is under no illusion of which set of results are from the reference and target areas.

As the field of model transferability progresses, and the pressure for cheaper research delivered at a faster rate continues due to our rapidly changing ecosystems, the necessity for powerful predictions from transferable models will become more apparent. Whilst this review has highlighted a number of successful transfers with high predictive performance (Figure 1.6; e.g. Peterson & Robins, 2003; Vanreusel *et al.*, 2007; Sequeira *et al.*, 2016), this is not the norm and transfer success is variable per study. Clearly ecological model transferability is a complex field with many unanswered questions and in need of more research. However, the benefits of transferable models are increasingly obvious, and the large number of researchers carrying out studies are rapidly increasing the knowledge and understanding surrounding this area.

1.3 Aims of this PhD Thesis

As outlined in the previous sections, transferable ecological models have many applications and benefits, however, there is still uncertainty as to what causes the success of model transfer, with many questions remaining unanswered (Yates *et al*., 2018). There have been numerous studies investigating key questions such as whether transferability is determined by the taxon modelled or the taxon’s traits, (e.g. Eskildsen *et al*., 2013; Moran-ordonez *et al*., 2017), how data quality impacts transferability (see Sequeira *et al*., 2016; Aubry *et al*., 2017), and if there spatial or temporal limits to transferring models (e.g. Dormann *et al*., 2007; Houlahan *et al*., 2017). However, there is less research into the fundamental aspects of modelling which when combined with the above challenges, will no doubt have a compounding effect on performance and transferability.

One of the central aspects, the choice of model algorithm, has received much attention in regard to transferability, however research shows little consensus, with the best performing algorithm determined by the species and predictor data used, the quality of data and scale of the research in question (Elith & Leathwick, 2009; Sequeira *et al.*, 2018b). This seemingly suggests that the best algorithm will vary per scenario and research question being answered, but as new algorithms and methods are in constant development, this question will always need updating to take into account the newer modelling methods such as the increase in popularity of machine learning methods or ensemble approaches. In addition, mechanistic modelling approaches have increased in popularity in the conservation and ecology fields in recent years (see Fischer *et al*., 2014; Fordham *et al*., 2018), most notably used in invasion science. However, whilst mechanistic models are thought to be more transferable due to their process-based nature (Kearney & Porter, 2009; Kearney *et al*., 2010), it is unclear if this is the case, particularly with models transferred to predict invasion pathways or risk of spread. Finally, the majority of modelling algorithm comparison studies have been performed at a large or global scale (e.g. Elith *et al*., 2006; Shabani *et al*., 2016), therefore results may not be applicable to regional or local studies.

The question of scale is another challenge with transferability, namely how resolution impacts model performance. Again, there has been much research into this, but not with transferable models, rather, predictions in the system the models were trained. The research that has been undertaken shows little consensus; Seo *et al.* (2009) suggest better model performance comes from higher resolution predictor data, whereas Tobalske (2002) found models performed better when using a coarse resolution. In contrast, Guisan *et al.* (2007a) show changing resolution did not severely impact model performance, however if and how this applies to transferrable models is not known. A core use of transferable models is the ability to make predictions in data poor areas, however if the only predictor data available is of a different resolution to that the model was trained with, which is highly likely in different geographic regions, it is unknown how performance will be affected or if the transfer will be reliable.

Similarly, a fundamental decision when modelling with background or pseudo-absence points is what quantity to use. Whilst there have been numerous studies looking at the best ways to generate such points (i.e. Wisz & Guisan, 2009; Iturbide *et al.*, 2015), there have been fewer investigating the impact of prevalence (see Sor *et* al., 2017; Liu *et al*., 2019), and a lack of published work examining this in regard to model transferability. It has been shown that prevalence can influence model performance, but whether this applies to model transfers is unknown and therefore needs answering to enable the most suitable methods to be chosen. Furthermore, in research investigating these three fundamental areas of modelling, it is common to see virtual species used, rather than real occurrence observations. Virtual species are typically used to minimise bias and not contain any idiosyncrasies in the data, often observed with real species. However, idiosyncrasies and bias will always be present when modelling real species (Jarnevich *et al.*, 2015), therefore testing the validity of recommendations made using virtual species is required.

Therefore, this research aims to answer these questions and provide insight into model transferability and how to improve predictions. As the literature shows, there are a breadth of challenges and questions that require addressing, however the questions answered in this thesis were chosen due to their fundamental foundations within the modelling process. If a poor choice of algorithm, predictor resolution and prevalence value are selected, no matter the other choices when training the model, performance would most likely always be poor. Therefore, to address these important knowledge gaps and ensure the presented results are not solely applicable to one species or situation, this research uses twenty species from a range of different taxonomic groups (amphibians, birds, insects, mammals, plants, and reptiles). Rather than selecting species to answer questions such as where are areas suitable for reintroductions, the species were selected based on a range of criteria including data quality and number of data points, in order to allow the main research questions to be answered effectively.

1.3.1 Research questions

As previously outlined, transferring models is an important method for answering questions within the conservation and ecology fields. Literature shows the numerous outstanding challenges in this field, with the important aspects of modelling highlighted in the preceding section and their influence on model transferability, still relatively unknown. Therefore, to address these gaps in the model transferability literature, the following four questions will be answered:

I. Does the number of pseudo-absences or background points a model is trained with impact performance and transferability into novel environments and is there an optimum number?
II. Does the spatial scale of environmental predictor data influence model performance and transferability? If so, how should the resolution be chosen?
III. Is there a single best correlative modelling algorithm for transferring species distribution models into novel environments?
IV. Is a generic mechanistic plant disease risk model able to be transferred to a newly emerged foci of citrus greening disease (Huanglongbing), in a novel spatial region, and can this be used to accurately predict future disease spread?

Chapter 2 - Does the number of background points impact species distribution model performance and transferability?

2.1 Introduction

Species distribution models (SDMs), also known as ecological niche models, are a common tool in the fields of conservation biology and ecology (Guisan & Thuiller, 2005). Their fundamental use is to explore the relationship between the spatial distribution of a species and the environment (Elith & Leathwick, 2009). They have been used in a range of applications: from supporting conservation planning (Le Roux *et al.*, 2017), and providing insights into complex seasonal species-habitat associations (Zuckerberg *et al.*, 2016) to identifying key sites likely to hold unknown populations of a species, providing a focus for sampling efforts (Fois *et al.*, 2015). In addition, SDMs often have their use extended beyond the time or geographic range they were developed for, to predict species occurrences in novel environments. This process is known as temporal or spatial transferability (Peterson *et al.*, 2007). For example, they have been used to predict the future range of species in response to climate change (Lawler *et al.*, 2006; Dobrowski *et al.*, 2011) or estimate areas most susceptible to species' invasions (Gallien *et al.*, 2010).

When modelling a species distribution, there are a whole suite of algorithms available for use, however performance is not equal across modelling approaches. Several studies have compared model performance, suggesting that boosted regression trees (BRTs), generalised linear models (GLMs), and Maxent are amongst the best performing methods (Elith *et al.*, 2006; Randin *et al.*, 2006; Peterson *et al.*, 2007; Zurell *et al.*, 2009). Additionally, these three methods are also arguably some of the most popular model algorithms in species distribution modelling (Aguirre-Gutiérrez *et al.*, 2013; Merow *et al.*, 2013). Their popularity may be in part due to their ease of use, but also because presence data does not suffer with data collection issues to the same degree as when recording absences. Common issues encountered are typically the time and cost associated with data collection, the potential bias in sampling techniques and the fact that it is almost impossible to be certain of a species' absence, particularly with mobile and cryptic species (Guillera-Arroita, 2017). Instead, the previously listed algorithms can use pseudo-absence or background points.

Both pseudo-absence and background points are user-generated, and the names often used interchangeably, however, there are subtle differences. Pseudo-absences are generated in areas that have not been surveyed, but with the presumption that the species is absent from this sampled area. Therefore, pseudo-absences tend to be generated at a given distance from presences, meaning the greater the distance, the greater the likelihood of them being true absences (Barbet-Massin *et al.*, 2012; Senay *et al.*, 2013). In contrast, background points require fewer assumptions so tend to be generated randomly across the whole study area with the purpose of them not to inform a model of a species' absence, but to simply provide points to characterise explanatory background data (Phillips *et al.*, 2009).

Mathematically there are no differences between pseudo-absences and background points, both represented by 0's and representing an area with no species presence records. Therefore, modelling algorithms treat them the same, along with true recorded absence points (Phillips *et al.*, 2009; Lobo *et al.*, 2010). However, these three data types do represent different things and certain algorithms are less robust at handling them than others (Guillera-Arroita *et al.*, 2015). An example of this is Maxent, which should be used with background points not pseudo-absences (Guillera-Arroita *et al.*, 2014). This is because the algorithm calculates habitat suitability by comparing the predictor variable values at species presence locations, with the predictor values across the whole study area, hence needing random unbiased background points (Phillips *et al.*, 2004; Elith *et al.*, 2011).

Much has been studied on the best approach to generate background and pseudo-absence points, with the literature showing three commonly used methods: 1) Random generation in the area of study; 2) Random generation in the area of study but within a delimited distance from presence points; and 3) Random generation in areas with dissimilar environmental conditions from areas where presences were recorded, based on the assumption that environmental dissimilarities will ensure the species is not be present (Chefaoui & Lobo, 2008; Wisz & Guisan, 2009; Senay *et al.*, 2013; Iturbide *et al.*, 2015). Of the above methods, the latter two refer to pseudo-absence generation, not background points.

An area of background and pseudo-absence point generation that has received comparatively little research, is if and how the quantity of points in relation to presences, otherwise known as prevalence (the number of presences within the total population of presence and absence/pseudo-absence points), affects SDM performance and subsequent transferability. The research by Barbet-Massin *et al.* (2012) highlights models typically performed best when the number of pseudo-absences were equal to the number of presences. Similarly, a more recent study by Liu *et al.* (2019) shows that model performance typically plateaued when the number of background points was between 1 and 3 times the number of presences, and no benefit to performance was gained by increasing the number of background points further. Additionally, both studies show that the optimal number of points varied according to the algorithm used, with particular focus on Maxent, suggesting a large number of background points are used i.e. 10,000 (Barbet-Massin *et al.*, 2012; Liu *et al.*, 2019).

This figure of 10,000 background points has long been used in SDM studies (Phillips & Dudik, 2008; Phillips *et al.*, 2009; Mateo *et al.*, 2010), on the premise that it is large enough to provide a good quantity of information to the model but not too large to increase computational time (Senay *et al.*, 2013). Even before the work by Barbet-Massin *et al.* (2012), the 10,000 points were recommended by other researchers (Phillips & Dudik, 2008). Additionally, the default number of background points in Maxent is 10,000, which is perhaps another reason the use of this value is so common in species distribution modelling (Elith *et al.*, 2011). However, this rather arbitrary value of 10,000 points could be problematic depending on the scale of the research. For example, in a global study, 10,000 may be too few points for sufficient accuracy in predictions, or in a local study it may prove too many points over a limited environmental predictor gradient (Renner & Warton, 2013). This could result in difficulties for the model to discriminate between presence and background or pseudo-absence points, leading to poor predictive performance (Shabani *et al.*, 2018).

The study by Barbet-Massin *et al.* (2012) typically underpins the number of pseudo-absence points used in many other studies (e.g. Brown & Yoder, 2015; Messina *et al.*, 2016; Préau *et al.*, 2020), yet their findings relied on simulated species as did the work by Liu *et al.* (2019). To date, there has been very little research into how model performance is affected by varying numbers of background points using data for real species. Moreover, these previous studies have only explored the impact the number of points has on model performance in the area it was developed for. With increasing use of model transfers, there is also a need to understand if and how the number of background points used affects the subsequent transferability of models.

Here, using three common SDM approaches, I explore the efficacy of the established rules of thumb for the number of background points using presence data for a diverse set of 20 real species. I then take the research further, undertaking spatial transfers for all 20 species and showing how prevalence impacts transferability. As well as comparing performance at difference levels of prevalence, I will contrast results with the default 10,000 point value often used. In particular, I assess:

1. How the number of background points affects model performance in the reference area (where it was developed).
2. How the number of background points affects model performance in the target area (where it was transferred to).
3. If there is a clear optimal prevalence for background points, and whether that varies by species and modelling algorithm in both reference and target areas.

2.2 Methods

The regions selected for investigation were the Island of Great Britain and Island of Ireland, hereafter referred to as Britain and Ireland. These locations were selected due to size, range of environmental conditions and environmental similarity with one another, in theory allowing more successful model transfers (Sequeira *et al.*, 2018b). In addition, both areas had an abundance of species occurrence data, which allowed a wide range of taxa to be selected. Methods are summarised below and more compressively detailed in Table A1, Appendix III, using the standardised ODMAP reporting protocol (Zurell *et al.*, 2020).

2.2.1 *Species and environmental data acquisition*

The environmental data downloaded were the 19 bioclimatic variables from WorldClim version 2, at a resolution of 30 arc-seconds, roughly 1 km^2 per grid cell (Fick & Hijmans, 2017). These 19 variables are derived from monthly rainfall and temperature values from the period of 1970 to 2000. They represent annual trends, seasonality and extreme or limiting environmental factors, giving a range of biologically important variables. For a full list of the 19 variables, see Appendix IV.

Species occurrence data was acquired from GBIF (Global Biodiversity Information Facility), an open access data repository (GBIF, 2020), containing over 1 billion occurrence records which are widely used in SDM studies (e.g. Di Febbraro *et al.*, 2013; Fan *et al.*, 2018; Préau *et al.*, 2020). Twenty species were selected (Table 2.1) from a range of different taxonomic groups; amphibians, birds, insects, mammals, plants, and reptiles to enable a wide-ranging study, rather than drawing conclusions gathered from one species or group. Species within the groups were chosen based on data availability, rarity/commonness and their distribution being constrained by climatic variables rather than human influences. For example, the only reptile species common to both Britain and Ireland is *Z. vivipara* (common lizard), which was therefore selected. Similarly, there are only 3 amphibian species common to both areas: *E. calamita* (natterjack toad) which is rare in both areas and had too few occurrence points, *R. temporaria* (common frog) which is too widespread as subsequently discussed, therefore *L. vulgaris* (smooth newt) was selected. Similarly, there are few mammal species common to both areas with distinct niches determined by climate whose range is not determined by human activities, hence the selection of *L. timidus* (mountain hare).

Whilst there are numerous other species that could have been selected, those that were extremely widespread and common, such as *R. temporaria, Cyanistes caeruleus* (Eurasian blue tit), *Rattus norvegicus* (brown rat) and *Urtica dioica* (common nettle) were not chosen for use in this study. This was due to their ubiquity throughout the geographic and environmental space in the study, causing issues with the models not being able to discriminate between suitable and unsuitable climatic areas (Segurado & Araújo, 2004; Tsoar *et al.*, 2007). Similarly, species whose range is not defined by climate but other factors i.e. interspecific interactions and anthropogenic pressure such as *Cervus elaphus* (red deer), *Crex crex* (corncrake) and *Sciurus vulgaris* (red squirrel) were also not selected for use in this study as the bioclimatic variables would not have been good predictors of their range (Rödder & Lötters, 2010; Guisan *et al.*, 2013).

The final twenty species chosen covered a wide range of environmental conditions and geographic locations within the study areas and contained substantial variation in traits and rarity. The occurrence records were acquired from a 30-year period to match the bioclimatic predictor variables. However, the rarer species had fewer recordings in Ireland during this time period, therefore the year criteria was extended to 2010 to provide more records for *A. scirpaceus* (reed warbler)*, B. ibis* (cattle egret)*, R. hipposideros* (lesser horseshoe bat) and *L. megera* (wall brown). Records were filtered to retain occurrences only from the countries of the United Kingdom and Ireland, with their basis of recording from observations rather than museum specimens or material samples, and accepted presences which fall within the species' International Union for Conservation and Nature (IUCN) defined range, and therefore records most likely to be true. These filters were applied to ensure data was as reliable and accurate as possible.

Table 2.1 List of species included in this study, along with the number of presence points in Britain and Ireland. Data from GBIF.

Species name	Common name	Kingdom	Class	Presences	
				Britain	Ireland
Acrocephalus scirpaceus	Reed warbler	Animalia	Aves	2184	74
Asplenium scolopendrium	Hart's tongue fern	Plantae	Polypodiopsida	4505	297
Bombus jonellus	Heath bumblebee	Animalia	Insecta	936	532
Bubulcus ibis	Cattle egret	Animalia	Aves	137	81
Chorthippus brunneus	Common field grasshopper	Animalia	Insecta	7865	203
Drosera rotundifolia	Round-leaved sundew	Plantae	Magnoliopsida	6243	97
Gonepteryx rhamni	Brimstone butterfly	Animalia	Insecta	5073	466
Lagopus lagopus	Red grouse	Animalia	Aves	2731	858
Lasiommata megera	Wall brown	Animalia	Insecta	3080	106
Lepus timidus	Mountain hare	Animalia	Mammalia	3774	5495
Linaria flavirostris	Twite	Animalia	Aves	2319	83
Lissotriton vulgaris	Smooth newt	Animalia	Amphibia	2790	162
Martes martes	Pine marten	Animalia	Mammalia	2056	1622
Narthecium ossifragum	Bog asphodel	Plantae	Magnoliopsida	8667	101
Quercus petraea	Sessile oak	Plantae	Magnoliopsida	3811	105
Rhinolophus hipposideros	Lesser horseshoe bat	Animalia	Mammalia	1202	554
Taxus baccata	English yew	Plantae	Pinopsida	6764	95
Tyria jacobaeae	Cinnabar moth	Animalia	Insecta	4902	112
Tyto alba	Barn owl	Animalia	Aves	7533	786
Zootoca vivipara	Common lizard	Animalia	Reptilia	3883	151

2.2.2 Data processing

The bioclimatic variable layers contained data for the whole earth, they were clipped to the area of interest (Britain and Ireland). Because the 19 bioclimatic variables were derived from the same core rainfall and temperature data, they were inspected for multicollinearity, which can cause issues with model fitting and produce unreliable results (Graham, 2003; Alin, 2010). Multicollinearity checks were carried out in R version 3.6.1, using the variance inflation factor and stepwise reduction from the ‘usdm’ package, version 1.1-18 (Naimi, 2017). Of the 19 variables, 12 exhibited strong collinearity (VIF > 10) and were removed from analysis, keeping the following 7 variables for use in the subsequent models: isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of warmest quarter (full bioclimatic variable information detailed in Appendix IV).

2.2.3 Modelling and analysis

Species distribution models were created using the ’sdm’ R package version 1.0-81 (Naimi & Araújo, 2016). Three algorithms were chosen: Generalised Linear Models (GLM) with linear terms using a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature classes available for automatic selection based on best fit for the data; Boosted Regression Trees (BRT) with family = Bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01. The algorithms were chosen due to their different approaches to modelling species distributions (regression based: GLM; machine learning: BRT and Maxent) and due to their popularity, arguably being the most commonly used in the species distribution modelling literature (Merow *et al.*, 2013; Srivastava *et al.*, 2019).

In the reference area, presence and background points were initially bootstrapped (resampled with replacement; Efron, 1982), before models were fitted using a 70:30 split for model training and testing, and then transferred to a bootstrapped sample in the target area, Ireland. This process was repeated for 1,000 iterations, which not only allowed for an estimate of variability in model performance, but also ensured performance was not based on the overreliance on any single point, therefore increasing robustness.

To test whether the quantity of background points affects model transferability, models were trained using 15 different levels of prevalence. A flat rate of 10,000 points, commonly seen in modelling studies (Hernandez *et al.*, 2008; Wisz & Guisan, 2009; Barbet-Massin *et al.*, 2012) was initially used. Then models were iteratively retrained using the prevalence values listed in Table 2.2, which were similar to those in simulation studies previously performed by Barbet-Massin *et al.*, (2012) and Liu *et al.* (2019). The 1,000 iterations of each model were carried out at each of the 15 prevalence levels for the 20 species, totalling 900,000 simulations in this study. Finally, models were transferred using the corresponding level of prevalence in the target area to assess performance. To view the prevalence values for each species when 10,000 background points were used, see Table A4, Appendix V.

Table 2.2 Comparison of prevalence and the equating ratio of presences to the number of background points used in this research.

Prevalence	Ratio of presence & background points
0.90	1:0.11
0.75	1:0.33
0.66	1:0.5
0.50	1:1
0.33	1:2
0.25	1:3
0.20	1:4
0.17	1:5
0.14	1:6
0.13	1:7
0.11	1:8
0.10	1:9
0.09	1:10
0.06	1:15

The area under curve (AUC) of the receiver operator characteristic (ROC) was employed to test model performance. AUC evaluates the ability of a model to discriminate a continuous variable into a two-group classification, in this case either presence or absence of a species (Gonçalves *et al.*, 2014). AUC was chosen because this statistic does not use an arbitrarily user-defined threshold, instead testing a range of thresholds which removes user-generated bias (Peterson *et al.*, 2008). In addition, the single figure output of the AUC can be used to directly compare performance across different modelling algorithms making it suitable for use here (Jiménez-Valverde, 2012). The AUC is given as a value from 0 to 1, with 1 indicating perfect fit of the model, whereas 0.5 means model fit is no better than random chance, therefore 0.5 and lower indicates poor predictive ability (Hanley & McNeil, 1982).

2.3 Results

2.3.1 Changing prevalence in the reference area

In the reference area of Britain, the models performed well; mean AUC values ranged between 0.775 and 0.850 for each algorithm and prevalence (Figure 2.1 and Tables A5 to A7 in Appendix VI). Maxent models showed the most variation in AUC per species across the range of prevalence values but performed best on average. The worst performance of maxent models typically occurred when prevalence was greater than 0.5, when there were fewer background points than presences. AUC was highest and plateaued between 0.833 and 0.841, prevalence was between 0.5 and 0.06. However, BRT and GLM models did not follow this pattern, in fact for BRTs, AUC was fairly similar across the range of prevalence values with only 0.01 difference between highest, (mean = 0.834, 95% confidence interval = ±0.001) and lowest (0.824, ±0.001).

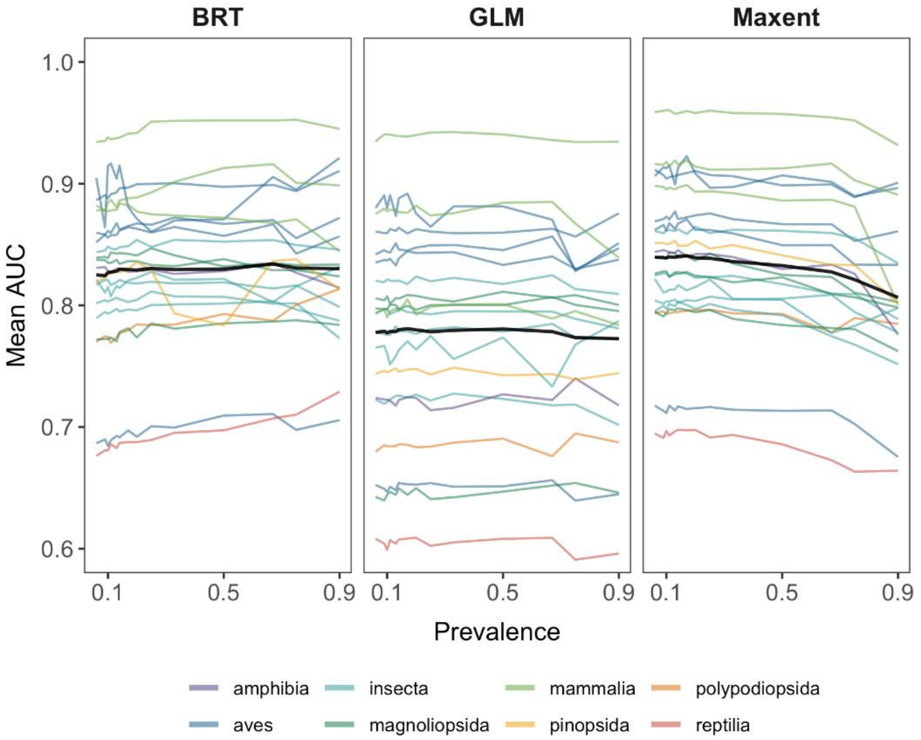


Figure 2.1 AUC values across the range of prevalence values for the 3 model algorithms in the reference area of Britain. Coloured lines represent the mean values of the 20 species modelled, coloured by class, and the black line signifies the mean across the range of data. Means were generated from the 1000 bootstrapped iterations.

2.3.2 Changing prevalence in the target area

When the models were transferred, resulting AUC values were not as high in the target area of Ireland and there was greater variability in AUC values between species and the prevalence values tested (Figure 2.2 and Tables A8 to A10 in Appendix VI). However, the pattern displayed by the mean across all species was broadly like that in the reference area, but perhaps not as pronounced. GLMs performed the best of the three algorithms at all prevalence values, with fairly consistent AUC values (0.633 ±0.002 to 0.642 ±0.002) across the range, however there was considerable variation in performance between species. Despite Figure 2.2 showing what appears to be a slight decline in mean performance for Maxent as prevalence increased, this was only a difference in AUC of 0.012, with the range across all prevalence levels of 0.584 (±0.002) to 0.607 (±0.002). BRTs showed the most variability; AUC values ranged from 0.567 (±0.002) to the highest AUC of 0.597 (±0.002) when prevalence was 0.2.

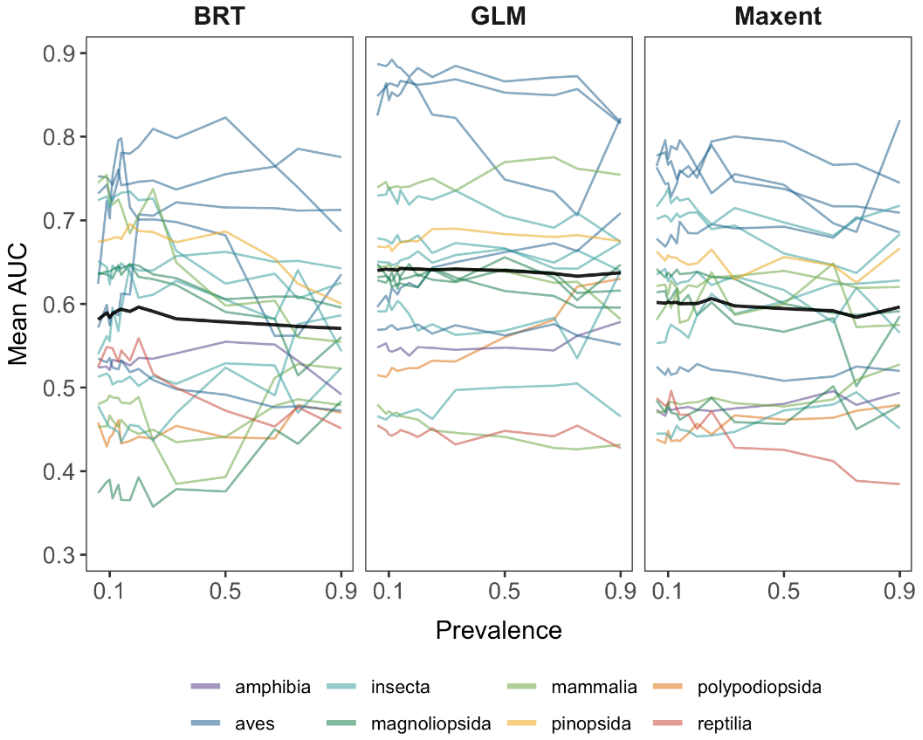


Figure 2.2 AUC values across the range of prevalence values for the 3 model algorithms in the target area of Ireland. Coloured lines represent the mean values of the 20 species modelled, coloured by class, and the black line signifies the mean across the range of data. Means were generated the 1000 bootstrapped iterations.

2.3.3 10,000 background points in the reference area

In the reference area when models were trained with 10,000 background points, there was little difference in performance compared to models using the varying levels of prevalence (Figure 2.3). The mean AUC of GLMs was 0.778 (±0.001), with only a difference of less than ±0.01 in mean AUC values across all levels of prevalence. The mean AUC value of Maxent models was 0.837 (±0.001) and similarly only had a difference in mean AUC of ±0.01 when prevalence was between 0.5 and 0.06. When there were fewer background points than presences, i.e. prevalence <0.5, performance decreased, with AUC values lower by 0.03 when compared to performance of 10,000 background points. Conversely, the mean AUC values from BRTs were higher by between 0.015 and 0.3 at every prevalence than when 10,000 points were used.

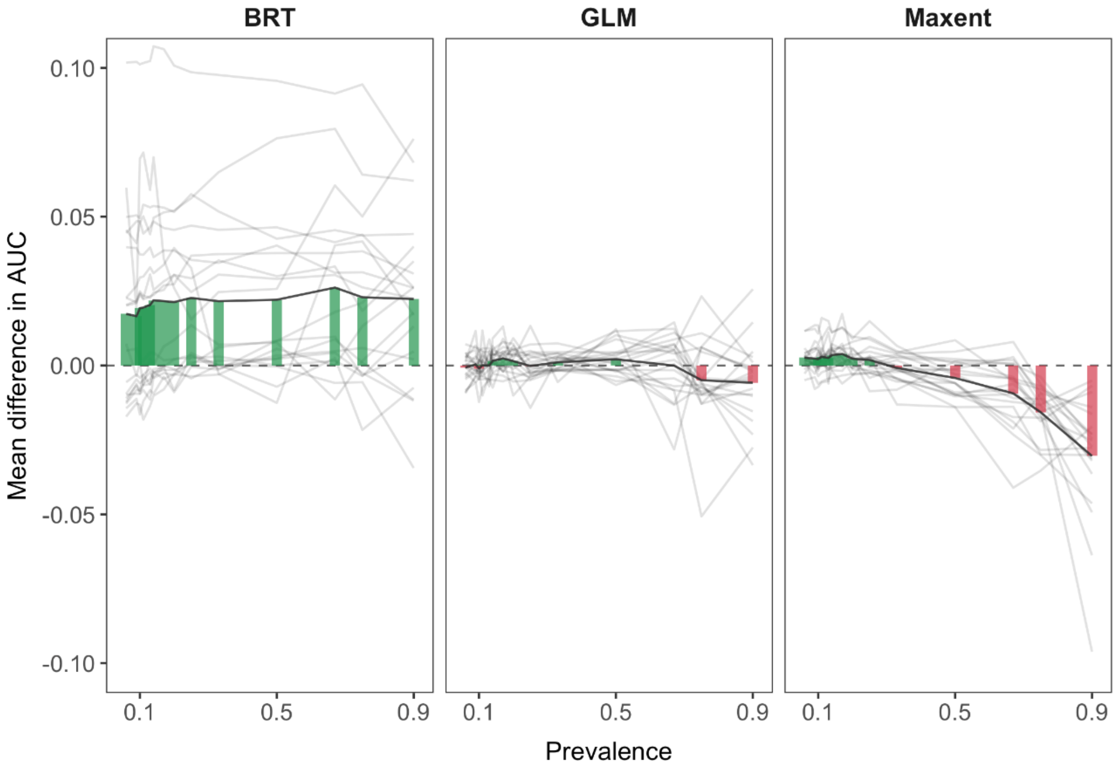


Figure 2.3 Difference in AUC values across the range of prevalence values compared to the AUC produced when models used 10,000 background points in the reference area of Britain. Light grey lines represent the mean difference values of the 20 species modelled. The dark grey line and coloured bars indicate the mean across the range of species, with green bars signifying mean performance was better than 10,000 points, red indicating worse performance.

2.3.4 10,000 background points in the target area

When comparing performance between models using 10,000 background points and the set prevalence levels, results in the target area were broadly similar to those shown in the reference area but with considerably more variation between species. The mean AUC for GLMs and Maxent showed little difference and the least variation, with the mean differences in AUC across all prevalence values of around ±0.01 (Figure 2.4, Tables A7 to A9). The greatest difference to 10,000 points for BRTs occurred when prevalence was 0.9, producing an AUC lower than that at 10,000 points by 0.024.

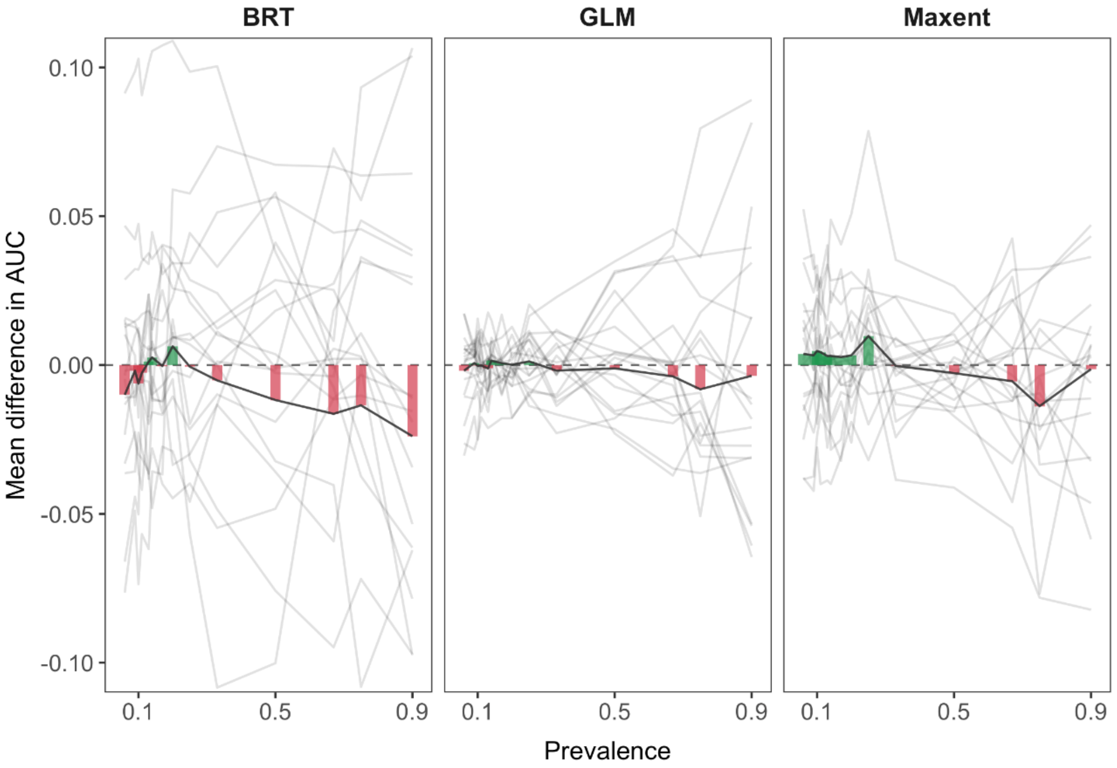


Figure 2.4 Difference in AUC values across the range of prevalence values compared to the AUC produced when models used 10,000 background points in the target area of Ireland. Light grey lines represent the mean difference values of the 20 species modelled. The dark grey line and coloured bars indicate the mean across the range of species, with green bars signifying mean performance was better than 10,000 points, red indicating worse performance.

2.4 Discussion

Whilst there have been studies examining the influence of background point prevalence on model predictive performance (e.g. Stokland *et al*., 2011; Barbet-Massin *et al.*, 2012; Liu *et al.*, 2019), there is a stark lack of knowledge surrounding how this affects model transferability. Therefore, this study examined the effect prevalence has on the predictive performance and transferability of SDMs, using three of the most common modelling algorithms and occurrence data for 20 species. Changing the number of background points generally had little effect on the mean predictive performance of models in either reference or target areas, apart from at very high levels of prevalence where performance declined. The default value of 10,000 background points was shown to perform well, with mean performance like that produced when testing the varying levels of prevalence. There was substantial variation in the predictive performance between individual species, but the overall pattern of how performance varies at differing levels of prevalence was broadly consistent between species. Predictive performance varied by algorithm and performance was better in the reference area than when models were transferred to the target area.

2.4.1 Effects of changing prevalence in the reference area

This study shows that the number of background points a model is trained with, does impact on performance albeit negligibly. The trend was distinct in the reference area, varying by algorithm, but with consensus between species exhibiting comparable results. Performance amongst GLMs was generally highest when prevalence was 0.5, however when fewer background points were used and prevalence increased, performance declined slightly. Whereas in contrast, increasing the number of background points gave broadly the same performance as when prevalence was 0.5. Such results are similar to those in the study by Liu *et al.* (2019), highlighting GLM performance did not increase until very high of background points were used (16 times the number of presences), and even then, increases in performance were not significant. However, Barbet-Massin *et al.* (2012) note that using 10,000 background points gave the best result, which was not the case in this study, but they note that GLMs were less influenced by the number of background points than other algorithms, which can be seen here with the comparatively small changes in AUC (Figure 2.1 and Table A5).

Results from Maxent displayed a similar trend to GLMs, but more pronounced; with prevalence lower than 0.5 performance remained generally the same, however when prevalence increased to fewer background points than presences, there was a distinct decline in performance. While the default and commonly used number of background points in Maxent is 10,000 (Phillips & Dudik, 2008), here it has been shown that even low numbers of background points provide excellent performance (e.g. *B. ibis*, prevalence = 0.5, n = 137, AUC = 0.907). Additionally, Liu *et al.* (2019) note using large numbers of background points, such as 10,000, has no benefit when presences are less than 160. However, in this study regardless of the number of presences, an equal number of background points and presences gave good performance for a range of species (see *L. megera*, *T. jacobaeae* etc, Table A6). What is clear and consistent through the range of species, is that performance is most affected when prevalence is greater than 0.5. Therefore, when using Maxent, the number of background points should be equal to or greater than the number of presences.

A reason for the trends shown by GLMs and Maxent, i.e. low numbers of background points/high prevalence giving lower performance compared to a prevalence of 0.5 and less, can be attributed to the overall purpose of these points. When using fewer background points than presences, points are not providing enough information to characterise the environment, in turn causing model predictions to be poor (Phillips *et al.*, 2009). Whereas when the number of background points increases, there are enough to provide sufficient information, leading to an accurate characterisation of the environment and greater ability to predict a species' true distribution (Phillips *et al.*, 2006). However, by increasing the number of background points further, model performance does not continue to increase as no extra information can be gained above a certain threshold (Liu *et al.*, 2019), in this case at a prevalence of between 0.5 and 0.25. Additionally, further increasing the number of background points may in fact act as a hinderance through increasing computational time (García-Callejas & Araújo, 2016).

BRT performance increased with prevalence (Figure 2.1 and Table A4), but generally remained constant across the range of background point values. This trend was also noted by Liu *et al.* (2019), who go on to suggest BRTs performed best when background points equalled the number of presences, but also show a decrease in performance at lower prevalence values. The use of an equal number of background points and presences was also recommended by Barbet-Massin *et al.* (2012), who show the greatest performance was achieved with this method. However, slightly different results were observed by Stokland *et al.* (2011), with low numbers of background points providing the worst performance. Although, Stokland *et al.* (2011) go on to show, variation in AUC between differing quantities of background points was not considerable and almost the same for a couple of species, which was reflected in this research by the consistent AUC values across the range of background point values here.

Whilst many SDM studies base the number of background points used on the research by Phillips & Dudik (2008), Stokland *et al.* (2011), Barbet-Massin *et al.* (2012), and Liu *et al.* (2019), either virtual species or low numbers of real species were used to make the recommendations. Virtual species are often used to ensure bias and the choice of species with their idiosyncrasies do not influence results. However, these will always be present when modelling real species (Jarnevich *et al.*, 2015), therefore testing the validity of recommendations of background point prevalence is important. By using a range of real species, this study shows previous recommendations are largely applicable to SDM studies modelling real species distributions. Though there were subtle differences in performance, using an equal number of background points and presences i.e. a prevalence of 0.5, generally provided high predictive performance for all three algorithms, which has also been shown to be the case when using other machine learning methods (see Sor *et al*., 2017). However, if seeking the best performance possible, sensitivity analysis such as this should be carried out.

2.4.2 Effects of background point prevalence in the target area

The results for models transferred to the target area were less clear, albeit with a broadly similar trend to those in the reference area. Model performance again was highest when lower prevalence values were used, generally below 0.5, in line with the study by Liu *et al.* (2019). However, differences were then observed; BRT and Maxent performance typically declines with an increase in prevalence/decrease in the number of background points, albeit negligibly. In contrast, GLMs remained relatively consistent across the range of prevalence values (Figure 2.2). Similar trends were observed in the studies focusing on background point sensitivity in the area models were trained (e.g. Barbet-Massin *et al.*, 2012; Sor *et al., 2017;* Liu *et al.*, 2019), but not to the same extent which is perhaps an effect of transferring a BRT. With this in mind, it is recommended that when transferring models using these three algorithms, a prevalence of 0.5 or lower is used.

The lack of studies investigating the impact of the background point prevalence on model transferability makes comparing results a challenge. But what is clear is that transferred models largely stick to the trend displayed in the reference area, and the trends highlighted in studies investigating background point sensitivity in the area models were trained (e.g. Barbet-Massin *et al.*, 2012; Liu *et al.*, 2019). However, when models are transferred, the additional variation in performance can be owed to the underlying issues associated with transferability (Dobrowski *et al.*, 2011; Werkowska *et al.*, 2017). As such, transferred models typically display decreased performance, as observed across all species and algorithms in this study (Tables A7 to A9) and is a common observation in the wider transferability literature (see Zanini *et al.*, 2009; Torres *et al.*, 2015; Roach *et al.*, 2017; Sequeira *et al.*, 2018a)

These declines in performance may be attributed to niche dissimilarity between the reference and target areas (Torres *et al.*, 2015), quality of data (Aubry *et al.*, 2017) and environmental equilibrium of the species (Václavík & Meentemeyer, 2009; Varela *et al.*, 2009), which have been shown to be the most common determinants of model transferability. These causes of decline in performance are particularly apparent with the *L. timidus*, where the considerable drop in performance from an AUC value >0.9 at all prevalence levels in the reference area to around 0.6 in the target area with each modelling algorithm, due to differences in niche similarity between the populations in Britain and Ireland (Whelan, 1985; Watson & Wilson, 2018).

Similarly, the drop in performance of transferred models of *B. jonellus* amongst other species in this study, may have been due to an underprediction of distribution in the target area caused by data quality. There were more recordings in the reference area, which is to be expected due to the greater size, however there were generally less records in target proportional to the area. Perhaps this is, in fact, because the species was absent, but it could be due to lack of surveys therefore models were reporting false negatives (Rondinini *et al.*, 2006). These issues are likely to be commonly encountered when transferring models to novel environments and different datasets of a species' occurrence are used. Despite studies on transferability becoming increasingly common (Sequeira *et al.*, 2018b), there remain fundamental challenges such as these, surrounding the concept and practice of transferring models (Yates *et al.*, 2018).

2.4.3 10,000 background points

The commonly used and default 10,000 background point quantity has often been recommended, as it is large enough to provide enough information for a model to perform well, yet not too large to impact computational time (Senay *et al.*, 2013). However, in this study, 10,000 points did often not provide the best predictive performance (Figure 2.3). Whilst this varied by species and algorithm, typically once prevalence was 0.5 or lower, there were only small differences in AUC (~0.005) of models using 10,000 points or between 1 and 15 times the number of presences.

Barbet-Massin *et al.* (2012) suggested 10,000 points offer the best performance when using regression methods. Yet here with GLMs, performance was often higher with a prevalence of 0.5 or less. This was the case in both reference and target areas, regardless of the number of presences a species had e.g. the least abundant, *B. ibis* with only 137 presence records and the most abundant, *N. ossifragum* with 8,667 presences. Although, as previously stated, the differences in AUC values produced were negligible when comparing the use of 10,000 points or any of number of background points within the prevalence range tested (0.06 – 0.9). This perhaps shows GLMs are not overly sensitive to the number of background points they use, which was also demonstrated by Barbet-Massin *et al.* (2012), whose research focusing on pseudo-absences, shows the method used to generate these points had a greater influence on a model's predictive accuracy, rather than prevalence.

The default and suggested number of background points in Maxent models is 10,000 (Phillips & Dudik, 2008; Elith *et al.*, 2011). However, 10,000 points did not give the highest AUC values in either the reference or target areas. The number of background points providing the highest AUC again varied by species, and in some cases a prevalence of 0.5 gave better performance than using 10,000 regardless of the number of presences (e.g. *G. rhamni* and *L. timidus*). A similar trend to Figure 2.3 is displayed by Phillips and Dudik (2008), although their study of Maxent's sensitivity to change in background points differed from this research by using set values of background points equal for all species tested. They show performance peaked and plateaued with 10,000 background points, where in this study, this was when prevalence was 0.25. Additionally, Liu *et al.* (2019) show that Maxent models only benefit from using 10,000 background points when the number of presences of a common species were less than 160 and no advantage to performance was gained outside this situation. Perhaps this trend was not apparent in the study by Phillips and Dudik (2008) due to the relatively low numbers of presences, compared to those used here and by Liu *et al.* (2019).

There was considerable difference in behaviour of BRTs using 10,000 points. Whilst 10,000 points have been used in BRT SDMs and proven to predict distribution well (e.g. Domisch *et al.*, 2013), here, in the reference area, the mean AUC values were higher when using any other number of background points (Figure 2.3). However, 10,000 points did still provide good performance (AUC >0.8) for many species (Table A4), just not the highest. None of the studies that researched BRT sensitivity to prevalence suggest using this value (Stokland *et al.*, 2011; Barbet-Massin *et al.*, 2012; Liu *et al.*, 2019), but it is not clear why, other than low performance.

For all three algorithms the mean difference in AUC between 10,000 background points and a prevalence of 0.5 or lower, whether positive or negative were small, typically between 0.005 and 0.01. In addition, this did not appear to vary according to the number of presences of a species. Further highlighting the statement by Barbet-Massin *et al.* (2012) that the number of background points only had a minor effect on predictive performance. This perhaps indicates models are not sensitive to the number of points they are trained with which has been observed in this study.

2.4.4 Is there an optimal number of background points?

The results show there is no optimal number of background points that gives the highest predictive performance for all species and algorithms, and whether predicting in the area a model was trained or transferring to novel environments. In the reference area, the trends were comparable across the 20 species (Figure 2.1) but the best performing prevalence differed slightly between algorithm and species. Regardless of these minor differences, the general trend in all species and algorithms shows prevalence has a minimal impact on performance once above 0.5, largely reflecting results from other studies (e.g. Stokland *et al.*, 2011; Barbet-Massin *et al.*, 2012; Liu *et al.*, 2019).

The greater variability of results from transferred models displayed in Figure 2.2 further highlights the prevalence providing the best performance, changes by species and algorithm, with the underlying performance attributed to the commonly described issues surrounding transferability (Guisan & Thuiller, 2005; Rapacciuolo *et al.*, 2012). Literature shows there is still great uncertainty when transferring models. with many outstanding questions surrounding the subject area (Werkowska *et al.*, 2017; Sequeira *et al.*, 2018b; Yates *et al.*, 2018). However, whilst the results here show mixed transferability and high variability between species, the initial low prevalence values from 0.06 to 0.05 provided the best performance for the three algorithms, which goes someway to providing a new insight into how to improve model performance and transferability.

Despite this research showing there is no optimal number of background points across all algorithms, such as the 10,000 points suggested for Maxent and regression methods by Phillips & Dudik (2008) and Barbet-Massin *et al.* (2012), and used in a range of studies with different algorithms (see; Hernandez *et al.*, 2008; Reiss *et al.*, 2011; Barbet-Massin *et al.*, 2018), high performance was still be achieved using this value. Although, here, sensitivity to the number of background points was examined as a value relative to the number presences i.e. prevalence, rather than a number of a fixed values used across focal studies (see Phillips &

Dudik, 2008; Stokland *et al.*, 2011), meaning it is impossible to say a fixed value of 1,000 or 10,000 background points provides the best performance. However, for the majority of models, using a prevalence value of 0.5 or lower produced the best results, only marginally different to those using background 10,000 points (average difference in AUC ~0.005).

Furthermore, Santika (2011) shows that the effect of prevalence on predictive performance has a strong methodological foundation and is primarily influenced by the performance measure and the threshold selection method. Whilst this study solely used AUC as the assessment metric, which has its critics (see Lobo *et al*., 2008; Jiménez-Valverde *et al*., 2011; Ruete and Leynaud, 2015), rather than a combination including threshold dependent measures such as TSS or Kappa. Other studies using single assessment metrics found similar trends (e.g. Stokland *et al.*, 2011; Liu *et al.*, 2019), as did research that used multiple assessment metrics (see Sor *et al*., 2017). Additionally, Barbet-Massin *et al.* (2012) used a combination of TSS and AUC, finding that both measures were highly correlated and suggested that the choice of the assessment metric did not influence performance or results.

Ultimately, what number of background points to use in SDMs should be determined by the degree of accuracy needed. In the reference area, data shows there can be too few background points (prevalence <0.5). But a prevalence of 0.5 and above yields good results, in line with Sor *et al.* (2017) and Liu *et al.* (2019). For transfers, using a prevalence value of between 0.5 and 0.2 will provide some degree of certainty that the most appropriate and best performing prevalence has been selected, with only minor differences in performance.

2.5 Conclusion

This study shows that the number of background points used to train a model has little impact on model performance and transferability, but that algorithm and the species modelled had a greater impact on predictive performance. That being said, the greatest impacts of changing prevalence, albeit minimal, were observed when using Maxent. For all three algorithms testes, it is recommended that a mid-range prevalence i.e. 0.5 (equal numbers of background points and presences) is used, which will provide high predictive performance and transferability. Furthermore, if the best possible performance is required, a small array of models should be fitted to find which performs best, followed by sensitivity analysis, changing the number of background points until an optimum is found.

Chapter 3 - Does predictor resolution influence model transferability?

3.1 Introduction

High resolution environmental data is a much sought-after resource, whether it is climatic, landcover, elevation and terrain, or bathymetric. These types of data are used in a variety of fields, to look at the relationships between species and their environments (Copping *et al.*, 2018), to analyse flood risk (Bouzahar *et al.*, 2018), to understand the effects of land use change on climate (Tran *et al.*, 2017), and to predict the distribution and prevalence of plant pests and disease (Brown *et al.*, 2018). Many of these studies typically use as high a resolution of data as possible, perhaps based on the assumption that high resolution means more information, which in turn equates to increased accuracy and precision (Ross *et al.*, 2015; Fisher *et al.*, 2018).

The easy access and use of high-resolution data, has been facilitated by advances in technology in the past decade or so, allowing fine scale environmental data to be collected locally and globally with less time and financial cost (Tang & Shao, 2015; Ouma, 2016). A prime example of this is the Copernicus programme, using earth observation satellites to provide a variety of marine, terrestrial and atmospheric data of Europe, at resolutions as high as 20 m per pixel (European Comission, 2015). Another example is the UK environment agency’s digital surface model data, covering more than 75% of the UK at a resolution of 2 m, or the newer 25 cm resolution data in a handful of areas (Environment Agency, 2014). Additionally, the two data sources listed, along with multiple others, are open source, which allows researchers around the world unparalleled access to data. But with the continual advances in technology pushing the available resolutions ever higher, it is important to try and understand if these higher resolutions are always beneficial in terms of providing more information and enhancing predictive performance of models which use such data.

In the fields of conservation biology and ecology, the primary use for environmental data is the inclusion as predictor variables in species distribution models (SDMs). Such models are used to explore the relationship between the spatial and temporal distribution of a species and the environment (Araújo & Guisan, 2006; Elith & Leathwick, 2009) and have become commonplace in conservation biology research. SDMs have typically been used to support conservation planning (Le Roux *et al.*, 2017), aid in the management of threatened or invasive species (Dullinger *et al.*, 2009; Wilson *et al.*, 2011), understand phylogeographic patterns (Willis *et al.*, 2008; Pearman *et al.*, 2014), and to identify potential sites likely to hold unknown populations of a species (Fois *et al.*, 2015).

Whilst it is common to see the highest resolution data available used in research, in reality the aims of the study should dictate the most appropriate resolution (Guisan & Thuiller, 2005; Guisan *et al.*, 2007b; Lauzeral *et al.*, 2013). Millar & Blouin-Demers (2012) conducted a study at a regional scale, modelling a species' range within a Canadian province using a 25 m resolution predictor data. The aim was to assess effectiveness of management plans for the species, which with more coarse data, may not have correctly identified key features within the habitat. Whereas, over a similar sized area, in Fennoscandia, Hof *et al.* (2012) use environmental predictor data at a resolution of 1 km, to predict the potential range of a species. The coarser data was appropriate here because the researchers were interested in how a species' range might shift, and not the individual features within a habitat defining a species' range (Pearson & Dawson, 2003).

The research of Willis and Whittaker (2002), then expanded by Pearson and Dawson (2003), highlights the most suitable environmental predictors based on the scale of the study. For example in a terrestrial study, if conducting research at a global or regional level, they recommend climate as the most appropriate predictor, whereas at the opposite end of the scale, at local level, soil type and biotic interactions are recommended as preferred predictors. However, climatic variables have been used over a range of scales and remain the most commonly used predictors in SDM studies (Gardner *et al.*, 2019). This is not only due to the ease of access, but because climate is has been shown to be one of the main constraints to species' distributions (Soberón & Peterson, 2005).

Another benefit to using climate as a predictor is that datasets often come in a range of resolutions, allowing research over different scales. For example the WorldClim dataset, provides 19 bioclimatic variables in four resolutions from coarse scale at a 10 arc-minute resolution, with each cell roughly covering a 344 km^2 area at the equator, to the higher resolution data, at 30 arc-second resolution, with each cell covering around 0.86 km^2 (Figure 3.1, Fick & Hijmans, 2017). The difference in resolution between 10 arc-minutes and 30 arc-seconds is 3 orders of magnitude, which can impact model performance (Lauzeral *et al.*, 2013).

Multiple studies have shown that higher resolution climatic predictors lead to better model performance. Ross *et al.* (2015) compared predictions of habitat occurrence using three resolutions, showing models using the highest resolution data performed best. Similarly, Kaliontzopoulou *et al.* (2008) and Scales *et al.* (2017) show the use of coarse resolution data risks inaccurate model performance. However, this trend is not always the case, as Guisan *et al.* (2007a) show changing resolution did not severely impact model performance, and Tobalske (2002) found models performed better when using a coarse resolution. Although, the most comprehensive study of scale by Seo *et al.* (2009) and the general consensus in the literature (e.g. Gottschalk *et al.*, 2011; Moudrý & Šímová, 2012; Connor *et al.*, 2018) suggests predictive models typically perform better at higher resolutions.

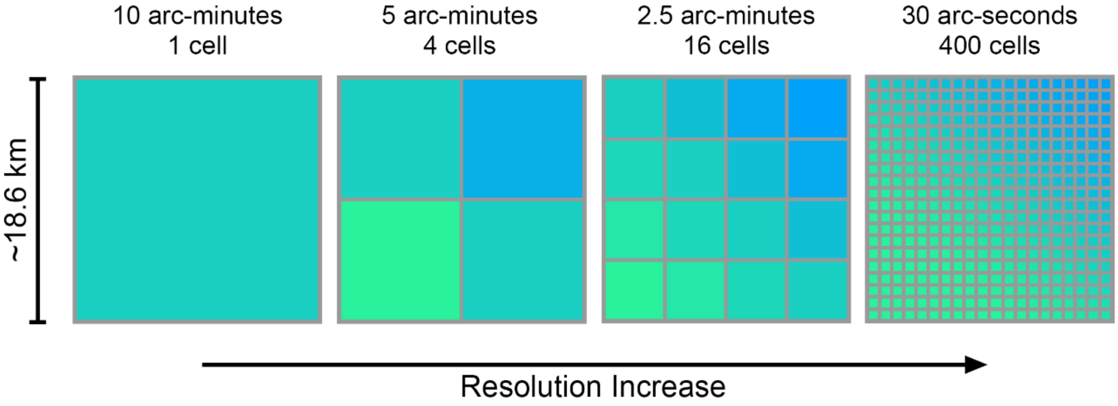


Figure 3.1 Representation of an environmental data layer, comparing the resolution and number of cells within a given area, at the four resolutions offered by WorldClim.

Whilst multiple studies explore how resolution of predictor variables influences model performance, and how best to select the resolution of predictors based on the scale of the research being undertaken (e.g. Pearson & Dawson, 2003; Boyce, 2006; Seo *et al.*, 2009), very few have considered how this impacts model transfers. Currently, there is little evidence as to how resolution impacts SDM accuracy when they are used beyond the time or geographic range they were trained, i.e. transferred into novel spatial or temporal environments (Manzoor *et al.*, 2018). This process, known as transferring a model has many uses. For example, highlighting areas vulnerable to invasions (Hudgins *et al.*, 2017; Fan *et al.*, 2018), predicting the potential future range of species in response to climate change (Lawler *et al.*, 2006; Dobrowski *et al.*, 2011), assisting in the regulation of disruptive and damaging anthropogenic activities (Mannocci *et al.*, 2017) and to aid in informing on suitable areas for the reintroduction of species (Schadt *et al.*, 2002).

The main benefit of transferable models in conservation research is that one can make inferences about species, when response data is unavailable in the area the model is transferred to (Wenger & Olden, 2012). Thus, models tend to be transferred for two reasons: Firstly, in academic exercises to provide insight and understanding into the methods of transfers and how to improve them, particularly in data rich areas. Secondly, models are transferred through necessity, when there is either a lack of or no data (i.e. when modelling invasive species or future range due to climate change), or it is unfeasible to collect data (i.e. too expensive to sample the deep sea environment; Yates *et al.*, 2018).

In order to verify predictions and ascertain the accuracy of the transferred models, an independent dataset in the area models were transferred to would be needed (Petitpierre *et al.*, 2017). This is often not available, hence research from the first scenario (academic studies) is used to provide insight into best practice when models are transferred in the second situation (necessity). Using the insights and guidelines provided by transferability research in data rich areas (i.e. Werkowska *et al.*, 2017; Sequeira *et al.*, 2018b) can potentially reduce uncertainty allowing model transfers to be a beneficial solution in conservation research.

However, when transferring a model to predict areas suitable for a species' re-introduction in another country, using environmental, elevation or climate data, the data sources may differ between the area models were trained and transferred to (target and reference areas). This in turn could mean differences in resolution of predictor data between the target and reference areas (Moudrý & Šímová, 2012). How this impacts predictive performance of transferred models remains unclear. As does, if there are a choice of predictor data resolutions in both the reference and target area, which should be used? Coarse resolution for quick and broad results, or the highest resolution for more information but longer processing time? Whilst predictor resolution should be based on the aims of the study and how much detail is needed to answer the questions, they also should be based on the knowledge of how predictive performance differs by resolution (Austin & Van Niel, 2011; Sequeira *et al.*, 2018a). How predictor resolution affects predictive performance of a transferred model (i.e. the models transferability) remains unanswered, and is only one of many important questions surrounding the theory and practice of model transferability (Yates *et al.*, 2018).

To address this knowledge gap and provide an insight into how spatial scale affects the performance of transferred models, the following questions will be answered:

1. Does higher-resolution predictor data provide better model performance in the reference area?
2. When transferring a model, does target area predictor data resolution impact predictive performance and transferability?
3. When transferring a model to the target area, does reference area predictor data resolution impact predictive performance and transferability?
4. Should models be transferred into the same resolution data as the model was trained at?

3.2 Methods

The regions selected for investigation were the Island of Great Britain and Island of Ireland, hereafter referred to as Britain and Ireland. These locations were chosen due to size, range of environmental conditions and environmental similarity with one another, in theory allowing more successful model transfers (Sequeira *et al.*, 2018b). In addition, both areas had an abundance of species occurrence data, facilitating analysis across a wide range of taxa with correspondingly varied ecological characteristics. Methods are summarised below, with comprehensive details including data and model development using the standardised ODMAP reporting protocol (Zurell *et al.*, 2020), displayed in Table A2, Appendix III.

3.2.1 Data acquisition

The environmental data used, were the 19 bioclimatic variables from WorldClim version 2 (Fick & Hijmans, 2017). The data was downloaded in the four available resolutions: 30 arc-seconds, with each cell equal to 0.86 km^2 at the equator; 2.5 arc-minutes equal to 21.5 km^2 at the equator; 5 arc-minutes, equal to 86 km^2 at the equator; and 10 arc-minutes, equal to 344 km^2 at the equator (Figure 3.2, WorldClim, 2020). The 19 bioclimatic variables represent annual trends, seasonality and extreme or limiting environmental factors, giving a range of biologically important variables. They are all derived from monthly rainfall and temperature values over a 30-year period, from 1970 to 2000. For a full list of the 19 variables, see Appendix IV.

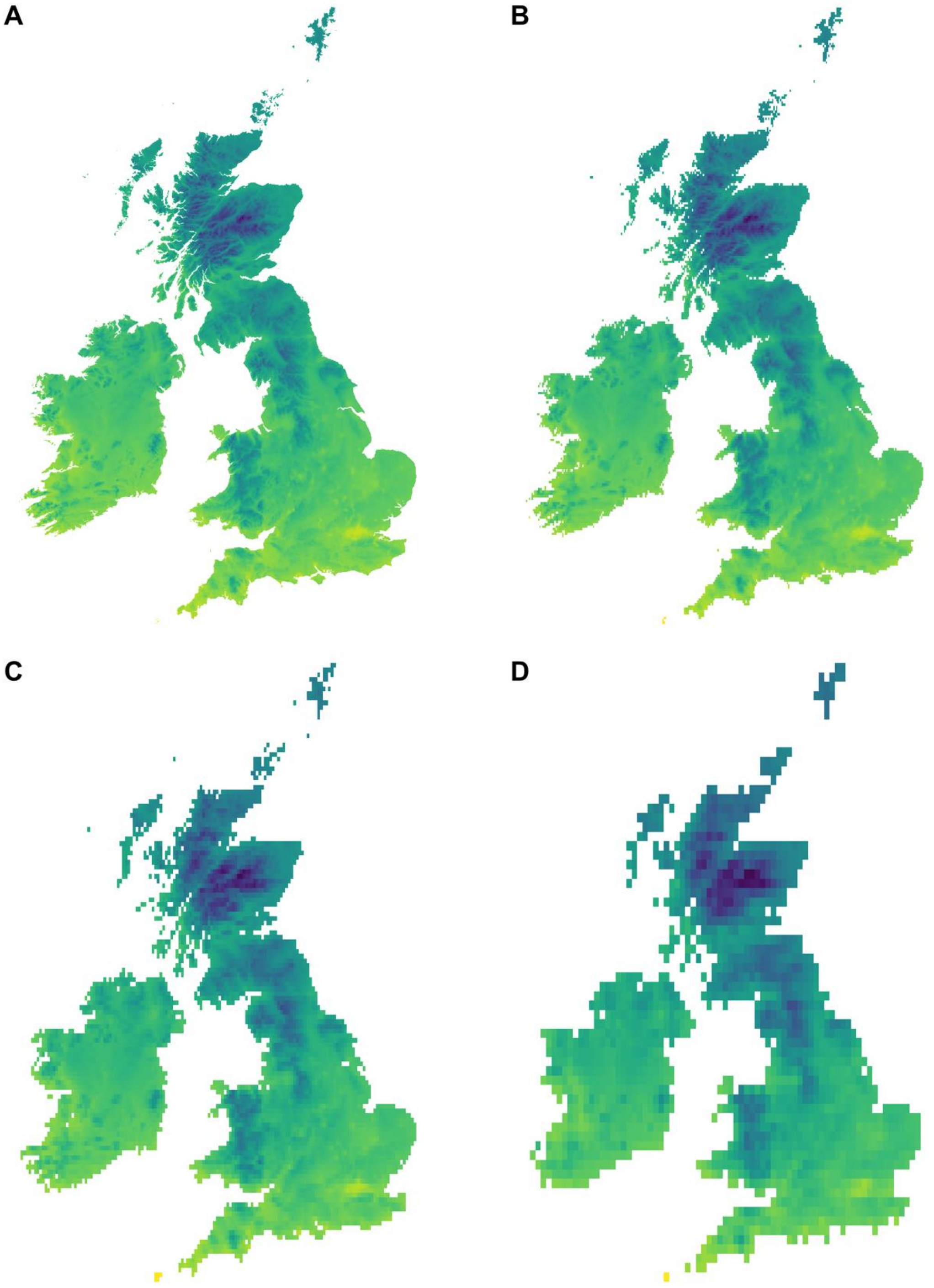


Figure 3.2 Comparison of resolution using mean annual temperature (Bio 1, of the WorldClim dataset) of the British Isles. The four resolutions displayed are the four which WorldClim data is available: A; 30 arc-seconds, B; 2.5 arc-minutes, C; 5 arc-minutes and D; 10 arc-minutes. As resolution decreases, maps become more pixelated as cells are aggregated, losing detail. This is best observed on the coast.

The Global Biodiversity Information Facility (GBIF) was accessed to search for suitable species to model in this study (GBIF, 2020), with records widely used in SDM research (e.g. Di Febbraro *et al.*, 2013; Fan *et al.*, 2018; Préau *et al.*, 2020). The database was filtered to retain records from only the United Kingdom and Ireland, accepted presence records which fall within the species' IUCN defined range, and occurrences from observations, rather than museum specimens or material samples to ensure records were as accurate as possible. Twenty species were then selected and downloaded (Table 3.1). Species were specifically selected to cover a range different taxonomic groups: amphibians, birds, insects, mammals, plants, and reptiles. Additionally, the species were from a broad range of habitats and geographic areas with different requirements and contained variation in their traits and rarity, allowing for more widely applicable inferences to be drawn.

Furthermore, extremely widespread, and common species, for example *Cyanistes caeruleus* (Eurasian blue tit), *Rattus norvegicus* (brown rat) and *Urtica dioica* (common nettle) were not selected for use in this study. This was primarily due to their ubiquity throughout the geographic and environmental range of the study, causing issues with the models not being able to discriminate between suitable and unsuitable climatic areas. Similarly, species whose range is not defined by climate but other factors i.e. interspecific interactions and anthropogenic pressure such as *Cervus elaphus* (red deer), *Crex crex* (corncrake) and *Sciurus vulgaris* (red squirrel) were also not selected for use in this study as the bioclimatic variables would not have been good predictors of their range (Rödder & Lötters, 2010; Guisan *et al.*, 2013).

Table 3.1 List of species included in this study

Species name	**Common name**	**Kingdom**	**Class**
Acrocephalus scirpaceus	Reed warbler	Animalia	Aves
Asplenium scolopendrium	Hart's tongue fern	Plantae	Polypodiopsida
Bombus jonellus	Heath bumblebee	Animalia	Insecta
Bubulcus ibis	Cattle egret	Animalia	Aves
Chorthippus brunneus	Common field grasshopper	Animalia	Insecta
Drosera rotundifolia	Round-leaved sundew	Plantae	Magnoliopsida
Gonepteryx rhamni	Brimstone butterfly	Animalia	Insecta
Lagopus lagopus	Red grouse	Animalia	Aves
Lasiommata megera	Wall brown	Animalia	Insecta
Lepus timidus	Mountain hare	Animalia	Mammalia
Linaria flavirostris	Twite	Animalia	Aves
Lissotriton vulgaris	Smooth newt	Animalia	Amphibia
Martes martes	Pine marten	Animalia	Mammalia
Narthecium ossifragum	Bog asphodel	Plantae	Magnoliopsida
Quercus petraea	Sessile oak	Plantae	Magnoliopsida
Rhinolophus hipposideros	Lesser horseshoe bat	Animalia	Mammalia
Taxus baccata	English yew	Plantae	Pinopsida
Tyria jacobaeae	Cinnabar moth	Animalia	Insecta
Tyto alba	Barn owl	Animalia	Aves
Zootoca vivipara	Common lizard	Animalia	Reptilia

3.2.2 Data processing

Once the bioclimatic had been downloaded, they were sorted and processed using ArcMap 10.5 and GADM version 3.6, level 1 shapefiles of Britain and Ireland (Hijmans *et al.*, 2012) to clip the 19 bioclimatic variable layers at each resolution, to the area of interest. This reduced file size and subsequently decreased processing time. As the bioclimatic variables were derived from the same core rainfall and temperature data, multicollinearity checks were carried out to reduce and remove collinear variables which can cause issues with model fitting and subsequently produce unreliable results (Graham, 2003; Alin, 2010). Checks were performed in R version 3.6.1, using the variance inflation factor and stepwise reduction from the ‘usdm’ package, version 1.1-18 (Naimi, 2017). Of the 19 variables, 12 exhibited strong collinearity (VIF > 10) and were removed from analysis, keeping the following 7 variables for use in the subsequent models: isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of warmest quarter.

3.2.3 Modelling and analysis

Species distribution models were created using the ’sdm’ R package version 1.0-81 (Naimi & Araújo, 2016). Three presence-background/pseudo-absence modelling algorithms were chosen: Boosted Regression Trees (BRT) with family = Bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01; Generalised Linear Models (GLM) using linear terms and a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature classes available for automatic selection based on the fit of the data. These algorithms were chosen due to their different approaches to modelling species distributions (regression based: GLM; machine learning: Maxent; classification tree and machine learning: BRT), their popularity in the literature and their high performance during transfers compared to other algorithms (Elith *et al.*, 2006; Merow *et al.*, 2013; Srivastava *et al.*, 2019). Background points were randomly generated in the study area, at an equal number to the number of species presences, based on findings from chapter 2 and recommendations in the literature (Sor *et al*., 2017; Liu *et al.* 2019). In the reference area, presence and background points were first bootstrapped (sampled with replacement; Efron, 1982), before models were fitted using a 70:30 split for model training and testing at one resolution, and then transferred to a bootstrapped sample in the target area, Ireland, at all four available resolutions, as demonstrated by Figure 3.3. This process was repeated for 1,000 iterations with each of the four predictor resolutions in the reference area. This bootstrapping approach was used to ensure model performance was not based on the overreliance on any single point, making this study more robust. Additionally, the 1,000 iterations allowed for an estimate of variability in model performance which allowed test statistics to be generated.

The area under curve (AUC) of the receiver operator characteristic (ROC) was employed to test model performance. AUC was chosen because this statistic removes any potential user-generated bias by providing a scaled assessment metric (Peterson *et al.*, 2008). In addition, AUC evaluates the ability of a model to discriminate a continuous variable into a two-group classification, in this case either presence or absence of a species (Gonçalves *et al.*, 2014). The single-figure output of the AUC can be used to directly compare performance across different modelling approaches, making it suitable for this study (Jiménez-Valverde, 2012). The AUC is given as a value from 0 to 1, with 1 indicating perfect fit of the model, whereas 0.5 means model fit is no better than random chance, AUC <= 0.5 indicates poor predictive ability (Hanley & McNeil, 1982).

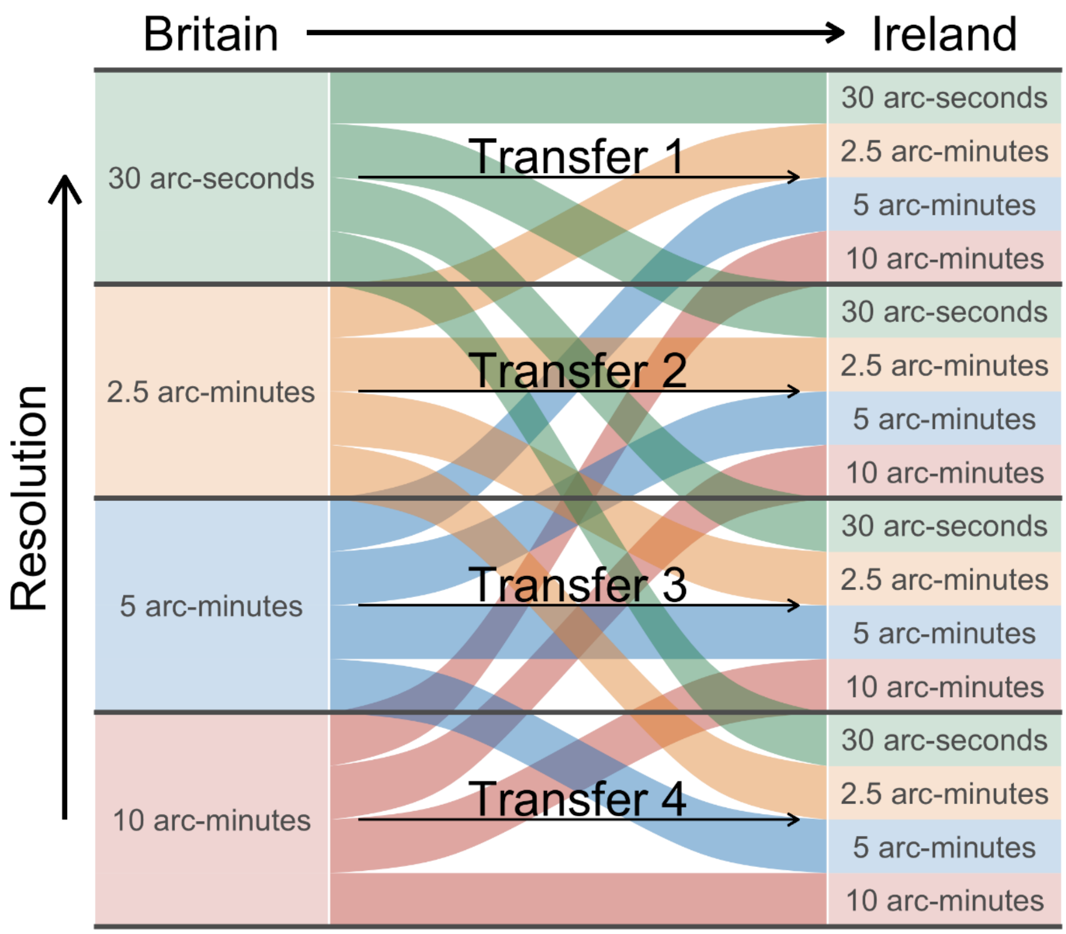


Figure 3.3 Flow diagram of model transfers from the reference area (Britain) the target area (Ireland). Models were trained at each of the four resolutions and subsequently transferred, with distribution predictions made at each resolution in the target area.

3.3 Results

3.3.1 Predictor resolution in the reference area

Overall models performed well in the reference area of Britain, with performance varying by species, modelling algorithm and resolution of predictor variables (Figure 3.4). BRTs performed the best, with a maximum mean AUC across the 20 species of 0.918 (95% confidence interval ± 0.001) when using a resolution of 10 arc-minutes. The AUC decreased with an increase in resolution, to a minimum mean AUC across the 20 species of 0.836 (± 0.001) when using predictor variables at a 30 arc-second resolution. The same pattern of performance at each resolution can be observed across GLMs and Maxent models too, with Maxent showing very little difference in mean AUC to BRTs; maximum mean AUC 0.911 (± 0.001) and minimum mean AUC 0.833 (± 0.001). Whereas GLMs had lower mean AUC values by around 0.5: maximum mean AUC 0.864 (± 0.001), minimum mean AUC 0.780 (± 0.001). Additionally, the trend of higher performance at coarser resolutions was observed consistently across the 20 species for the 3 algorithms (Tables A11 to A13, Appendix VII).

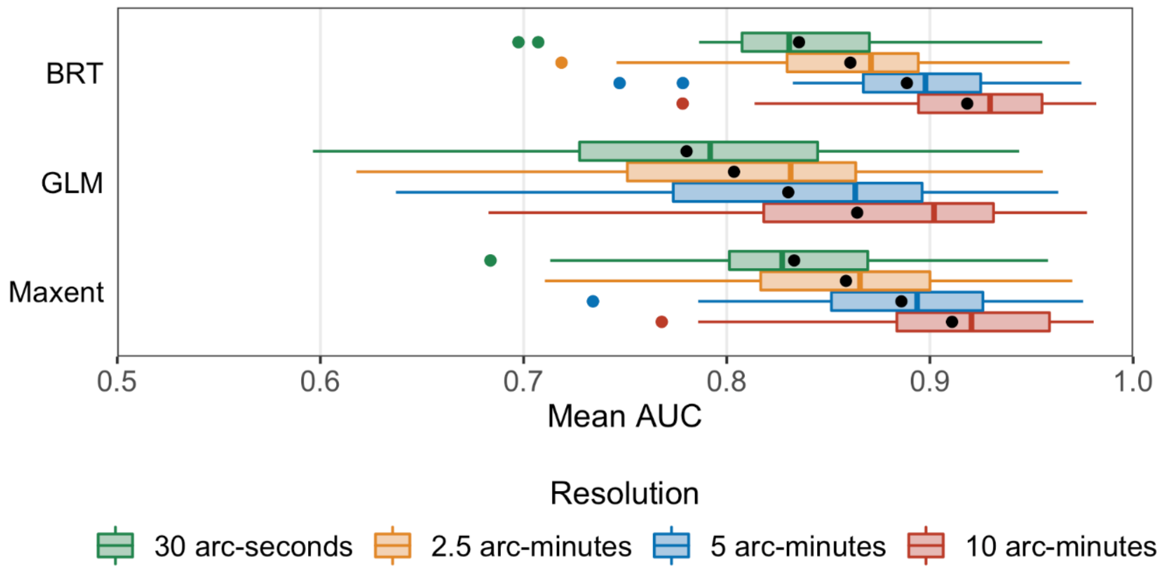


Figure 3.4 Boxplots of AUC for the three modelling approaches at each of the four resolutions in the reference area. Black points indicate the cross-species mean per modelling approach.

3.3.2 Predictor resolution in the target area

In the target area, performance was lower than in the reference area. However, the highest AUC values came from the resolutions opposite to those in the reference area; the best performing models were those transferred to the highest resolution (30 arc-seconds, Figure 3.5) and the poorest performing were those transferred to the coarsest resolution (10 arc-minutes). Additionally, models trained at higher resolutions provided better performance in the target area. Therefore, the best performing models were those trained at a 30 arc-second resolution and transferred to a 30 arc-second resolution. Although differences between those trained at a 10 arc-minute resolution and 30 arc-second resolution were small (mean difference in

AUC = 0.011), with the main differences in performance coming from the resolution of predictor data the models were transferred to (Figure 3.5).

The performance by algorithm was the inverse of that in the reference area: GLMs with the greatest mean AUC value of 0.64 (± 0.002), when models were trained at 30 arc-seconds and transferred to a 30 arc-second resolution. This was higher than the values from BRTs and Maxent (0.579 ± 0.002 and 0.595 ± 0.002) by 0.061 and 0.45 respectively. The mean AUC values of BRTs and Maxent were comparable across the range of resolutions, consistently lower than those produced by GLMs, although differences were not considerable and AUC values were more similar when using coarse resolutions.

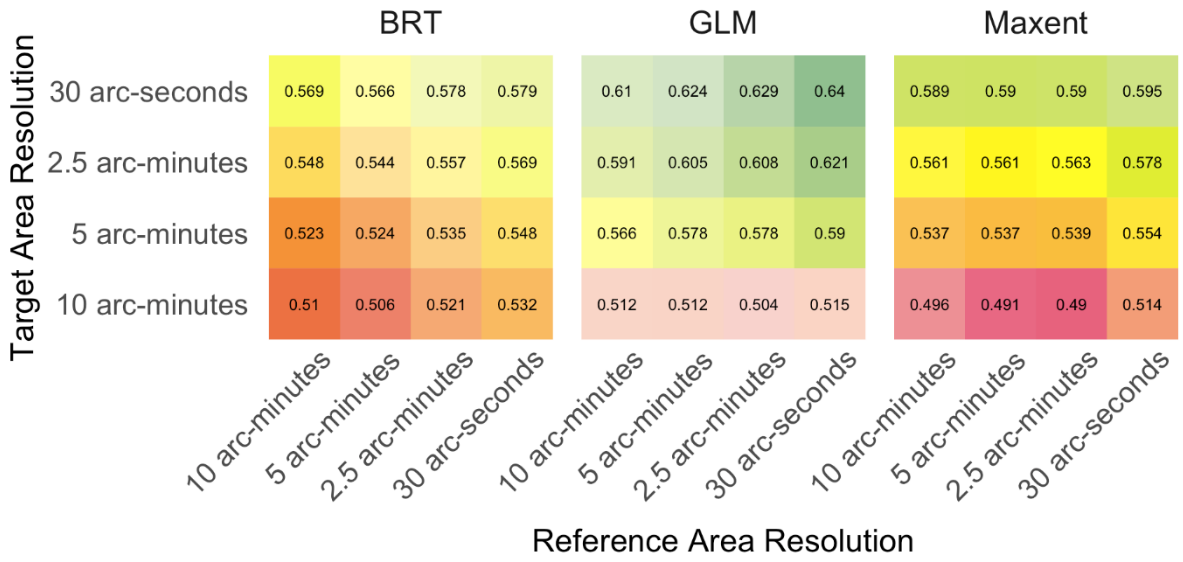


Figure 3.5 Heatmap of AUC for model transfers using each combination of predictor resolutions between reference and target areas. Heatmaps are plotted per modelling approach. Colour indicates cross-species mean (green: high; red: low) and opacity represents variance, using standard deviation (opaque: low; transparent: high).

The variability in mean AUC values between species in the target area was greater than that in the reference area (Tables A14 to A16 in Appendix VII). The species which had the best performing models was *A. scirpaceus*, with AUC values of 0.866 (± 0.002) when using a GLM from a 30 arc-second resolution to a 30 arc-second resolution. This only dropped slightly when transferring from a coarse to fine resolution, i.e. 10 arc-minutes to 30 arc-seconds (0.831 ± 0.002). However, considerable declines in performance for *A. scirpaceus* using GLM were observed when transferring to a coarse resolution, regardless of the reference area resolution; 30 arc-seconds to 10 arc-minutes, AUC = 0.583 (± 0.002) and 10 arc-minutes to 10 arc-minutes AUC = 0.565 (± 0.003). This pattern is repeated across the three algorithms used, with the greatest difference in AUC between models at an individual species level, observed when the resolution in the target area was highest. Differences decreased when coarse resolution data was used in the target area and AUC values were more similar between the three approaches. This trend was largely followed by all 20 species (Tables A13 to A15).

3.4 Discussion

Whilst there have been many studies examining how predictor data resolution impacts model performance (e.g. Tobalske, 2002; Guisan *et al*., 2007a; Scales et al., 2017), results appear to be contrasting. Furthermore, how this applies to a model when it is transferred to a novel environment has not been researched in as much detail and remains unclear. Therefore, this study investigated the influence of predictor resolution on predictive performance in both the reference and target areas, using the 4 commonly used resolutions of a popular climatic predictor dataset.

A clear pattern can be observed in the results, with coarser resolution of predictor enhancing model performance in the reference area (Britain) and fine resolution of predictors enhancing model performance in the target area (Ireland).

3.4.1 Resolution and predictions in the reference area

In the reference area, model performance was highest when coarse resolution predictor data was used (10 arc-minutes, Figure 3.4). This is in line with findings by Tobalske (2002) who observed greater model performance at coarser resolutions, similarly, Lowen *et al.*, (2016) show the highest resolution did not provide the best predictive performance. These results differ from a large portion of the literature that suggests higher resolution predictor data offers the best predictive performance (see; Kaliontzopoulou *et al.*, 2008; Seo *et al.*, 2009; Ross *et al.*, 2015). However, such contrasting results may be due to the assessment metrics used, i.e. Ross *et al.* (2015) used threshold-dependent evaluation methods, rather than the threshold-independent AUC used here. But the main cause of differences is likely due to the predictor variables used: Kaliontzopoulou *et al.* (2008) for example, used landcover and topographic predictors, which are likely to change considerably over a small area, with coarse resolutions masking important features. Such changes are generally not experienced when using climatic predictors (Austin & Van Niel, 2011), potentially explaining why these studies showed fine resolution predictors performed better. Moreover, using climate predictors, Guisan *et al.*, (2007a; b) show changing resolution does not severely impact predictive performance, noting that with a coarsening of data, performance can either increase or decrease. This is also reflected by Farashi & Alizadeh-Noughani (2018) whose models show an initial increase in performance with coarsening of resolution, before eventually decreasing, but differences were not considerable and were comparable to results displayed in this study (Figure 3.4).

Enhanced model performance at the reference site when using the coarsest resolution climatic predictors was consistent across all 20 species and the three algorithms. (Tables A10 to A12). Similar results were also observed by Seo *et al.* (2009) and Farashi & Alizadeh-Noughani (2018), and although there were differences in which resolution provided the greatest predictive performance, there were consistent trends across the algorithms used, as shown in this study, highlighting the validity of results. However, the differences in the resolution providing the best performance between studies is likely to be attributed to the choice of focal species, the algorithm used and/or the region being modelled, as demonstrated by Guisan *et al.* (2007b).

Whilst the results here are clear, showing the coarse resolution data (10 arc-minute resolution) allowed the greatest predictive performance (Figure 3.4), the lack of consensus in the literature (e.g. Seo *et al.*, 2009; Ross *et al.*, 2015; Farashi & Alizadeh-Noughani, 2018) highlights that there is no one rule or recommendation applicable for all situations. In fact, which resolution will provide the greatest performance is driven by the choice of predictors, how well the model is fitted and the accuracy of presence data (Guisan *et al.*, 2007b; Scales *et al.*, 2017). To find the resolution which provides the greatest predictive performance, appropriate variables should be chosen based on the focus of research, underlying questions being answered and the scale of the study as outlined by Pearson & Dawson (2003) and Lauzeral *et al.* (2013). In addition, it is recommended that a range of available predictor variable resolutions be tested in sensitivity analysis, such as in this study.

3.4.2 Impact of resolution on model transferability

When transferring models, there are two areas where predictor resolution may influence model performance; firstly, that in the reference area used to train the model and secondly, the resolution used in the target area to evaluate the transferred model. Here, in contrast to predictions made in the reference area, when transferring models, the best performance came from those trained using higher resolution data, the inverse of the best performing resolution for predictions in the reference area. One of the only other studies that investigated the impact of predictor resolution on transferability also found coarse resolutions to be the worst performing (Manzoor *et al.*, 2018). However, there were differences between this study and that by Manzoor *et al.* (2018), namely the resolution of data used; here the highest resolution was 30 arc-seconds, whereas that was the lowest resolution used by Manzoor *et al.* (2018).

The differing results of best resolution in the reference area according to whether models were transferred or not, may in part be due to the models being able to generally characterise a species' distribution well in the reference area regardless of resolution. Hence the relatively small differences in performance (AUC values) when changing resolution in the reference area, which is further highlighted by Guisan *et al.* (2007b), who suggest models are not overly sensitive to resolution change. Regardless, the results displayed here largely follow the general SDM resolution literature (i.e. Kaliontzopoulou *et al.*, 2008; Seo *et al.*, 2009; Ross *et al.*, 2015; Scales *et al.*, 2017) suggesting higher resolution data does provide better performance.

Of the aspects tested, the resolution of predictor data in the target area exerted the greatest influence on predictive performance of transferred models, rather than the comparatively small increases in performance provided by increasing the resolution of predictor data the model was trained with in the reference area. Perhaps due to better fitting data in the target area or increased spatial accuracy, as detailed by Elith & Leathwick (2009). This trend was not observed by Manzoor *et al.* (2018) due to study design, transferring models to the same resolution that they were trained, therefore the differing influence of reference and transfer area resolution was not recorded.

A cause of the differences in which predictor resolution offered the best performance between predictions in reference and target areas may be attributed to the predictor variable values within the two areas. Whilst the target area is environmentally similar to the reference area, the physically smaller area of the target site may cause a greater environmental gradient and larger differences between adjoining grid cells of the climatic predictors. If this is the case, the coarser resolution data would ‘average’ those cells, masking the smaller details only observable at a finer resolution (Baniya *et al.*, 2012). Such trends are commonly experienced when using topographic and landcover variables (Austin & Van Niel, 2011; Manzoor *et al.*, 2018). Hence when modelling at a local or fine scale (< 1km scale), Pearson & Dawson (2003) recommend the use of topography and landcover.

The trend displayed here of finer resolution in both reference and target areas allowing better transferability was observed across all species and the three algorithms despite underlying differences in predictive performance. What causes a model to be transferable is perhaps one of the most studied areas of transferability research, with considerable differences in performance well documented in a range of situations (see; Elith *et al.*, 2006; Randin *et al.*, 2006; Peterson *et al.*, 2007). As observed here, transferred models often display decreased performance, with the most common determinants of a successful transfer attributed to niche similarity (Torres *et al.*, 2015), quality of data (Aubry *et al.*, 2017) and environmental equilibrium (Václavík & Meentemeyer, 2009; Varela *et al.*, 2009).

Regardless of the slight decreases in performance when transferring models, evidence to date (here and Manzoor *et al.*, 2018) shows that using higher resolution data equates to better predictive performance of transferred models. Whilst, the lack of literature into how predictor resolution impacts transferability makes comparing results a challenge, it does shows that even a minor and potentially overlooked aspect in the process of transferring models can influence the ability to predict species distributions accurately. Moreover, the results shown here of differing optimal resolutions for predicting distribution in the reference area and target area adds further uncertainty to results, unless sensitivity analysis can be performed, and results validated in the target area. Nevertheless, this is another challenge for data poor transfers, adding to the transferability challenges addressed by Werkowska *et al.* (2017), Sequeira *et al.* (2018b), and Yates *et al.* (2018).

3.4.3 Should models be transferred with the same predictor resolution?

In this study, the best performing model transfers used the same highest resolution predictor data (30 arc-seconds) in both the reference and target areas. It is commonplace that the same resolution data is used for transfer, as this requires only one dataset to be acquired and prepared for use (e.g. Dobrowski *et al.*, 2011; Rapacciuolo *et al.*, 2012; Beaumont *et al.*, 2016). However, this might not always lead to the highest transferability. Trivedi *et al.* (2008) projected species' ranges from 50 km to 5 km under future climate scenarios, showing that whilst changing resolution did not significantly impact performance, using fine resolution data did cause issues with heterogeneity in predictors, likely due to the smoothing of the data when downscaling (Nogués-Bravo & Araújo, 2006). However, Suárez-Seoane *et al.* (2014) recorded similar results to the results here but to a greater degree, possibly due to the greater range in resolutions (10 km t0 50 m). Perhaps similar differences in performance would have been observed here if the data used was also downscaled to a higher resolution.

The results of this study and those produced by Trivedi *et al.* (2008) and Manzoor *et al.* (2018) not only highlight how model performance can be impacted by resolution in both the reference and transfer areas, but also demonstrate that transferability can be situation specific and differs per application. Therefore, there is no definitive answer as to whether models should be transferred with the same resolution data in the reference and target areas, particularly as the resolution used in an SDM is often dictated by both data availability and aims of the research, where predictors are frequently downscaled or upscaled to the required resolution (e.g. Thuiller *et al.*, 2005; Lauzeral *et al.*, 2013; Suárez-Seoane *et al.*, 2014).

3.5 Conclusion

Predictor resolution matters. However, the impact that resolution has on predictive performance of models and model transfers is not straightforward. Whilst there is no 'correct' or 'best' resolution to use, as findings are unlikely to be applicable to all studies, this research has shown that selecting predictor resolution for a model transfer based on the optimum resolution at the reference site may not always lead to the highest transferability. Consequently, when appropriate and data allows, sensitivity analysis should be performed to find the best resolution for transferring models. However, in data poor areas where sensitivity analysis is not possible, transferring models at a range of resolutions should be considered.

Chapter 4 - The impact of modelling approach on transferability

4.1 Introduction

Investigating the geographic distribution of species and factors that influence this has long been a focus of study in the fields of conservation biology and ecology. Central to this research is the use of species distribution models (SDMs) to investigate the relationship between a species and the environment (Araújo & Guisan, 2006). These important tools have been used to identify priority areas for nature reserve design and designation (Ferrier *et al.*, 2002; Fajardo *et al.*, 2014), investigate the drivers behind a species' presence in certain locations (Copping *et al.*, 2018), to inform and assess sampling strategies in species distribution research (Guisan *et al.*, 2006; Marini *et al.*, 2010), and to guide in ecological restoration and species reintroduction projects (Schadt *et al.*, 2002; Wilson *et al.*, 2011; Angelieri *et al.*, 2016).

Whilst the origins of SDMs can be traced back to the works of Grinnell (1904), it was not until late in the 20th century that quantitative and statistical research, combined with the mapping of species distributions occurred. The earliest approaches to modern SDMs were arguably the works by Nix (1986) using envelopes to map a species' distribution, and Ferrier (1984) using linear regression to predict species distribution using environmental variables. Since these studies, and aided by significant improvements in technology, there is now a whole suite of modelling algorithms available to investigate species distributions (Elith & Leathwick, 2009).

Envelopes, like the original model used by Nix (1986), along with distance based algorithms, form the profile family of algorithms and are still used today in the form of BIOCLIM and Domain (see; Guisan *et al.*, 2007; Kearney *et al.*, 2010; Battini *et al.*, 2019). They have been shown to accurately predict species distributions, however these algorithms do have drawbacks, primarily the tendency to often overpredict a species’ distribution due to the rectangular hull used (Elith *et al.*, 2006; Araújo & Townsend, 2012) and the high susceptibility to prevalence (Hernandez *et al.*, 2006; Phillips *et al.*, 2006), respectively.

Still one of the most commonly used families are regressions (Elith *et al.*, 2006). These algorithms predict the response variable as a function of a predictor variable (Franklin, 2010). This in its most basic form is based on the assumption that the relationship can be described by a straight line, which implies a constant change in the predictor, results in a constant change of the response variable (Guisan & Zimmermann, 2000). However, this is often not the case with ecological data, therefore the ‘simple’ linear regression is often extended into a generalised linear model (GLM), which can use multiple predictor variables and non-normal data through the use of link functions (Zuur *et al.*, 2009). This can be further extended into a generalised additive model (GAM), which can fit models semi-parametrically, thus allowing more complex relationships between the predictor and response to be modelled (Elith & Leathwick, 2009; Guisan *et al.*, 2012).

Becoming increasingly popular as the focus of SDMs shifts from explanation to prediction, are the machine learning based models (Elith *et al.*, 2006; Elith & Leathwick, 2009). With their foundations in the data mining and computer science fields, this family have the ability to learn and improve predictions of training data automatically, often through many iterations of the model being tested (Bhattacharya, 2013; Gobeyn *et al.*, 2019). Popular algorithms in this family are random forests (RF) and boosted regression trees (BRT), neural networks, native bayes and support-vector machines (SVM). These models often perform well in ecological studies and are able to deal with complex data and learn patterns, unlike traditional statistical models such as GLMs (Elith *et al.*, 2006).

Arguably the most popular machine learning approach in SDM studies, is maximum entropy modelling (Maxent; Phillips *et al.*, 2006). Maxent has the ability to fit complex and non-linear models thanks to its six features (functions and transformations), which are selected to avoid overfitting (Merow *et al.*, 2013; Guisan *et al.*, 2017). Maxent has been shown to outperform other algorithms on numerous occasions (Elith *et al.*, 2006; Peterson *et al.*, 2007; Shabani *et al.*, 2016), which perhaps adds to its popularity along with ease of use. However, it is this ease of use that has drawn criticism, particularly as a ‘black-box’ model, where it is simple to input data and get results without a real understanding of the processes, which can lead to the wrong choice of settings and produce unreliable outputs (Morales *et al.*, 2017; Rapacciuolo, 2019).

One of the newest approaches to SDMs is the use of ensemble forecasts (Araújo & New, 2007; Marmion *et al.*, 2009). Whilst BRTs and RFs are ensembles of regression trees, producing many models and averaging, it is common now to see an ensemble of different algorithms such as GLM, Maxent and RF combined into one ensemble forecast (see; Crimmins *et al.*, 2013; Ranjitkar *et al.*, 2014; Jones & Cheung, 2015). Such forecasts are attractive as literature shows that predictions can be considerably different between individual modelling algorithms (Segurado & Araújo, 2004), therefore the accuracy of predictions can markedly improve through the use of an ensemble (Araújo *et al.*, 2005; Marmion *et al.*, 2009). Additionally, the uncertainty of predictions associated with single models can be reduced (Grenouillet *et al.*, 2011).

The shift in focus of SDM studies to prediction, particularly through extrapolation into novel environments, is an area of research that has gathered much attention since the early 2000's (Werkowska *et al.*, 2017). When the model is used in an environment, temporally or spatially different to that in which it was trained, this cross-applicability is known as transferability (Sequeira *et al.*, 2018b). Transferable models have been used to outline areas likely to be susceptible to invasions (Thuiller *et al.*, 2005b; Fan *et al.*, 2018), to predict species range shifts due to projected climate change (Stewart *et al.*, 2015; Préau *et al.*, 2019), and to highlight areas likely to hold previously undiscovered populations of a species (Chunco *et al.*, 2013; Fois *et al.*, 2015)

Despite the focus on transferable models for over a decade, there remains challenges and the need for a greater understanding of how and what impacts model transferability (Sequeira *et al.*, 2018b). Yates *et al.* (2018) outline challenges surrounding model transfers, posing the question "Do Specific Modelling Approaches Result in Better Transferability?", which has been one of the most studied aspects of model transferability (Guisan *et al.*, 2007a; Meynard & Quinn, 2007; Heikkinen *et al.*, 2012; Beaumont *et al.*, 2016; Norberg *et al.*, 2019). However, the literature does not appear to have a strong consensus regarding the "best" modelling algorithm for transfers.

Elith *et al.* (2006) showed the more recent methods such as BRTs and Maxent consistently predicted species distribution more accurately than the more established regression-based methods. Likewise, Huang and Frimpong (2016) demonstrate BRTs were the best performing model when transferred, as do Guisan *et al.* (2007), followed by GAMs and GLMs which outperformed Maxent. In contrast Bellard *et al.* (2013) found the performance of Maxent to be far superior to that of a GLM. Similarly, Rapacciuolo *et al.* (2012) show Maxent to be one of the top performing algorithms, outperforming GLMs and RFs. Yet, Mi *et al.* (2017) show the predictive performance of RFs is higher than that of Maxent, but Dobrowski *et al.* (2011) show the more established statistical methods (GAMs and GLMs) outperformed RFs when transferred. See Table 4.1 for a list of studies comparing modelling approaches.

Table 4.1 List of studies comparing modelling approaches. The table indicates the algorithm used, whether transferability was studied, the main findings from this research and the reference for the study. References used in this table are listed in Appendix VIII

Study	**Models used**	**Transferability**	**Main findings**
Vayssières et al. (2000)	CART, GLM	NO	CART outperformed GLM
Seguardo & Araújo (2004)	ANN, CART, ENFA, GAM, GLM	NO	No method was superior in all circumstances
Elith et al. (2006)	BIOCLIM, BRT, BRUTO, DOMAIN, GAM, GARP, GDM, GLM, LIVES, MARS, MAXENT	YES	Novel methods (BRT, MAXENT) outperformed established methods (BIOCLIM, DOMAIN, GLM)
Randin et al. (2006)	GAM, GLM	YES	GAM performed better than GLM
Guisan et al. (2007)	BIOCLIM, BRUTO, BRT, DOMAIN, GAM, GDMSS, GLM, MARS, MAXENT, OM-GARP	NO	BRT and MAXENT outperformed BIOCLIM, DOMAIN, GLM
Meynard & Quinn (2007)	CART, GAM, GARP, GLM	NO	GAM outperformed other methods
Pearson et al. (2007)	GARP, MAXENT	NO	MAXENT performed better than GARP
Townsend Peterson et al. (2007)	GARP, MAXENT	YES	Only small differences in performance between MAXENT and GARP
Wisz et al. (2008)	BIOCLIM, DOMAIN, GLM, GAM, BRUTO, MARS, BRT, GARP, MAXENT, LIVES	NO	GBM and MAXENT were the best performing
Elith & Graham (2009)	GLM, BRT, RF, MAXENT, GARP	YES	Models performed similarly
Marmion et al. (2009)	ANN, CTA, ENSEMBLE, GBM, GAM, GLM, MARS, MDA, RF	NO	Ensembles had increased accuracy over single models
Dobrowski et al. (2011)	GAM, GBM, GLM, RF	YES	GAM and GLM outperformed RF
Heikkinen et al. (2012)	ANN, CTA, GARP, GAM, GBM, GLM, MARS, MAXENT, MDA, RF	YES	GAM, GBM and MAXENT provide good prediction accuracy and transferability
Rapacciuolo et al. (2012)	ANN, CTA, GAM, GBM, GLM, MARS, MAXENT, RF, SRE	YES	Maxent performed better than GLM and RF
Wenger & Olden (2012)	ANN, GLM, RF	YES	ANN and RF provide excellent performance but poor transferability
Bellard et al. (2013)	ENSEMBLE, FDA, GBM, GLM, MARS, MAXENT, RF	YES	Maxent was superior to GLM
Qiao et al. (2015)	BIOCLIM, GAM, GARP, GBM, GLM, MARBLE, MAXENT, RF	NO	No single best algorithm
Huang & Frimpong (2016)	BRT, LLR, MAXENT	YES	BRT performed best and was most transferable
Mi et al. (2017)	CART, ENSEMBLE, MAXENT, RF, TREENET	YES	RF provided best performance
Sor et al. (2017)	ANN, GLM, RF, SVM		ANN provided the best performance
Townsend Peterson et al. (2017)	ENSEMBLE, GAM, GARP, GBM, GLM, MAXENT, MVE, RF	YES	ENSEMBLES reduced uncertainty but did not out perform single models (GLM, MAXENT, RF)
Norberg et al. (2019)	BC, BORAL, BRT, ENSEMBLE, GAM, GJAM, GLM, GNN, HMSC, MARS, MISTN, MRTS, RF, SAM, SVM, XGB	YES	None of the models performed well for all prediction tasks

Regardless of the exhaustive list of studies investigating the “best model”, the lack of consensus and contrasting results, highlights model performance varies depending on the data, species, predictors and scale of the research in question (Elith & Leathwick, 2009; Sequeira *et al.*, 2018b). Norberg *et al.* (2019) compared 33 model algorithms, showing that performance varied, and no single algorithm performed well in all predictions. Furthermore Qiao *et al.* (2015) suggest there is no single “best” model, with performance dependent upon the situation, and go on to recommend using a suite of algorithms, which is where an ensemble approach may be beneficial.

This research investigates differences in model performance and transferability using 20 species and 9 different algorithms. This differs from the literature in a number of ways: 1) real species are modelled rather than virtual species commonly used in such studies (Elith & Graham, 2009; Qiao *et al.*, 2015). 2) The models used are from a combination of model families, adopting more recent techniques such as SVMs and takes advantage of ensembles (Huang & Frimpong, 2016; Manzoor *et al.*, 2018). And 3) the transfers are at a regional scale using high resolution data, rather than a global study or one using a coarse resolution, as seen commonly in the literature (Thuiller *et al.*, 2005b; Iturbide *et al.*, 2018b). To add to the literature and expand the transferability knowledge, the following questions will be answered:

1. Is there a single “best” algorithm in the area models were trained?
2. Is there a “best” transferable modelling algorithm?
3. How does model performance compare between the area the models were trained and the area they were transferred to?
4. Is transferability attributed to the algorithm or the species being modelled?

4.2 Methods

The regions selected for investigation were the Island of Great Britain and Island of Ireland, hereafter referred to as Britain and Ireland. These locations were selected due to size, range of environmental conditions and environmental similarity with one another, in theory allowing more successful model transfers (Sequeira *et al.*, 2018b). In addition, both areas had an abundance of species occurrence data, allowing the choice of species. To see a comprehensive outline of the methods using the ODMAP protocol, a standardised protocol for reporting SDMs (Zurell *et al.*, 2020), see Table A3, Appendix III.

4.2.1 Data acquisition

Predictor data used in this study were the 19 bioclimatic variables from WorldClim version 2 (Fick & Hijmans, 2017). The data was downloaded at a 30 arc-second resolution, with each cell equal to around 0.86 km^2 at the equator (WorldClim, 2020). The 19 bioclimatic variables represent annual trends, seasonality and extreme or limiting environmental factors, giving a range of biologically important variables. They are all derived from monthly rainfall and temperature values over a 30-year period, from 1970 to 2000. For a full list of the 19 variables, see Appendix IV.

Species occurrence data was acquired through the Global Biodiversity Information Facility (GBIF)., an online data repository (GBIF, 2020), whose occurrence records have been widely used in SDM research (e.g. Di Febbraro *et al.*, 2013; Fan *et al.*, 2018; Préau *et al.*, 2020). The database was filtered to display records from the United Kingdom and Ireland. Additional filters were then also applied, to provide only presence records which have been accepted to fall within the species’ IUCN defined range, the occurrence's recordings from observations rather than museum specimens or material samples to ensure records were as accurate as possible. Twenty species were then selected, see Table 4.2. Species were specifically chosen to cover a range different taxonomic groups from a broad range of habitats and geographic areas, with different requirements and contained variation in their traits and rarity. By selecting this wide range of species, a more compressive study could be conducted, rather than limiting conclusions to one species or taxonomic group.

Table 4.2 List of species included in this study.

Species name	**Common name**	**Kingdom**	**Class**
Acrocephalus scirpaceus	Reed warbler	Animalia	Aves
Asplenium scolopendrium	Hart's tongue fern	Plantae	Polypodiopsida
Bombus jonellus	Heath bumblebee	Animalia	Insecta
Bubulcus ibis	Cattle egret	Animalia	Aves
Chorthippus brunneus	Common field grasshopper	Animalia	Insecta
Drosera rotundifolia	Round-leaved sundew	Plantae	Magnoliopsida
Gonepteryx rhamni	Brimstone butterfly	Animalia	Insecta
Lagopus lagopus	Red grouse	Animalia	Aves
Lasiommata megera	Wall brown	Animalia	Insecta
Lepus timidus	Mountain hare	Animalia	Mammalia
Linaria flavirostris	Twite	Animalia	Aves
Lissotriton vulgaris	Smooth newt	Animalia	Amphibia
Martes martes	Pine marten	Animalia	Mammalia
Narthecium ossifragum	Bog asphodel	Plantae	Magnoliopsida
Quercus petraea	Sessile oak	Plantae	Magnoliopsida
Rhinolophus hipposideros	Lesser horseshoe bat	Animalia	Mammalia
Taxus baccata	English yew	Plantae	Pinopsida
Tyria jacobaeae	Cinnabar moth	Animalia	Insecta
Tyto alba	Barn owl	Animalia	Aves
Zootoca vivipara	Common lizard	Animalia	Reptilia

In Addition, widespread and common species, for example *Cyanistes caeruleus* (Eurasian blue tit), *Rattus norvegicus* (brown rat) and *Urtica dioica* (common nettle) were not selected for use in this study. This was primarily due to their ubiquity throughout the geographic and environmental range of the study, causing issues with the models being able to discriminate between suitable and unsuitable climatic areas. Similarly, species whose range is not defined by climate but other factors i.e. interspecific interactions and anthropogenic pressure such as *Cervus elaphus* (red deer), *Crex crex* (corncrake) and *Sciurus vulgaris* (red squirrel) were also not selected for use in this study as bioclimatic variables would not have been good predictors of their range (Rödder & Lötters, 2010; Guisan *et al.*, 2013).

4.2.2 Data processing

The 19 bioclimatic data layers were processed using ArcMap 10.5 and GADM version 3.6, level 1 shapefiles of Britain and Ireland (Hijmans *et al.*, 2012) to clip the global dataset to the areas of interest, removing unwanted data. Data was then opened in R version 3.6.1 to check for multicollinearity. These are colinear variables which can cause issues with model fitting and subsequently produce unreliable results (Graham, 2003; Alin, 2010). Checks were performed using the variance inflation factor and stepwise reduction from the ‘usdm’ package, version 1.1-18 (Naimi, 2017). Due to the way the 19 bioclimatic variables are generated and are derived from the same core rainfall and temperature data, 12 exhibited strong collinearity (VIF > 10) and were removed from analysis. The following 7 variables were kept for use in the subsequent models: Isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of the warmest quarter.

4.2.3 Modelling and analysis

Nine algorithms were chosen to model species distributions: Bioclim with default settings; Boosted Regression Trees (BRT) with family = Bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01; Domain using default settings; Generalised Additive Models (GAM) with a logit link function and smoothing λ = 0.6; Generalised Linear Models (GLM) with linear terms and a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature types available for automatic selection based on best fit of the data; Random Forests (RF) with the number of trees set to a maximum of 500, with the complexity automatically defined by model, according to the data; Support Vector Machine (SVM) set as a classification machine; Ensemble approach used weighted means of the previous 8 algorithms, based on their performance (AUC value) in each iteration, with greater weighting given to the better performing models.

These algorithms cover a range of model families; machine learning, profile methods and regression based models, and were selected due to their different approaches in modelling a species' distribution and prominence in the SDM literature (Table 4.3; Elith *et al.*, 2006; Qiao *et al.*, 2015). SDMs were created in R using the 'sdm' R package version 1.0-81 (Naimi & Araújo, 2016) and background points were randomly generated in the study area, at an equal number to the number of species presences, based on findings from chapter 2 and recommendations in the literature (Sor *et al.*, 2017; Liu *et al.* 2019). In the reference area, presence and background points were first bootstrapped (sampled with replacement; Efron, 1982), before models were fitted using a 70:30 split for model training and testing, and then transferred to a bootstrapped sample in the target area, Ireland. This process was repeated for 1,000 iterations, which not only allowed for an estimate of variability in model performance, but also ensured performance was not based on the overreliance on any single point, therefore increasing robustness.

Table 4.3 Modelling approaches used, with the family and a short explanation of the approach, along with references for the modelling method.

Method	**Model family & explanation**	**Reference**
Bioclim	profile: envelope	Nix (1986)
boosted regression trees: BRT	machine learning: decision trees with boosting	Friedman *et al*., (2000)
Domain	profile: distance-based	Carpenter *et al*., (1993)
generalised additive model: GAM	regression	Hastie & Tibshirani (1986)
generalised linear model: GLM	regression	Nelder & Wedderburn (1972)
Maxent	machine learning: maximum entropy	Phillips *et al*., (2006)
random forests: RF	machine learning: decision trees with bagging	Breiman (2001)
support vector machine: SVM	machine learning: supervised learning	Cortes & Vapnik (1995)
Ensemble	weighted mean of Bioclim, BRT, Domain, GAM, GLM, Maxent, RF & SVM. weights were based on performance (AUC values), with more weight given to the better performing models.	Araújo & New (2007)

Model performance was measured using the area under curve (AUC) of the receiver operator characteristic (ROC). AUC evaluates the ability of a model to discriminate a continuous variable into a two-group classification, in this case either presence or absence of a species (Gonçalves *et al.*, 2014). AUC was chosen because this statistic does not use an arbitrarily user defined threshold, instead testing a range of thresholds which removes user-generated bias by providing a scaled assessment metric from 0 to 1 (Peterson *et al.*, 2008). An AUC value of 1 indicates perfect fit, whereas 0.5 means the model fit is no better than random chance (Fawcett, 2006).

Therefore 0.5 and lower indicates poor predictive ability (Hanley & McNeil, 1982). The single figure AUC output can be used to directly compare performance across different algorithms and modelling approaches, making it suitable for this study (Jiménez-Valverde, 2012).

4.3 Results

4.3.1 Performance in the reference area

Model performance was generally excellent, with a mean AUC across all algorithms of 0.825 (Figure 4.1A). The best performing models used RFs (mean AUC 0.953) and the ensemble approach (0.899). These were followed by SVMs, GAMs, BRTs and Maxent with little difference performance, with mean AUC values of 0.857, 0.840, 0.836 and 0.834 respectively. GLMs, Bioclim and Domain were the poorest performing, with lower than average performance (0.781, 0.735 and 0.690 respectively; Figure 4.1A).

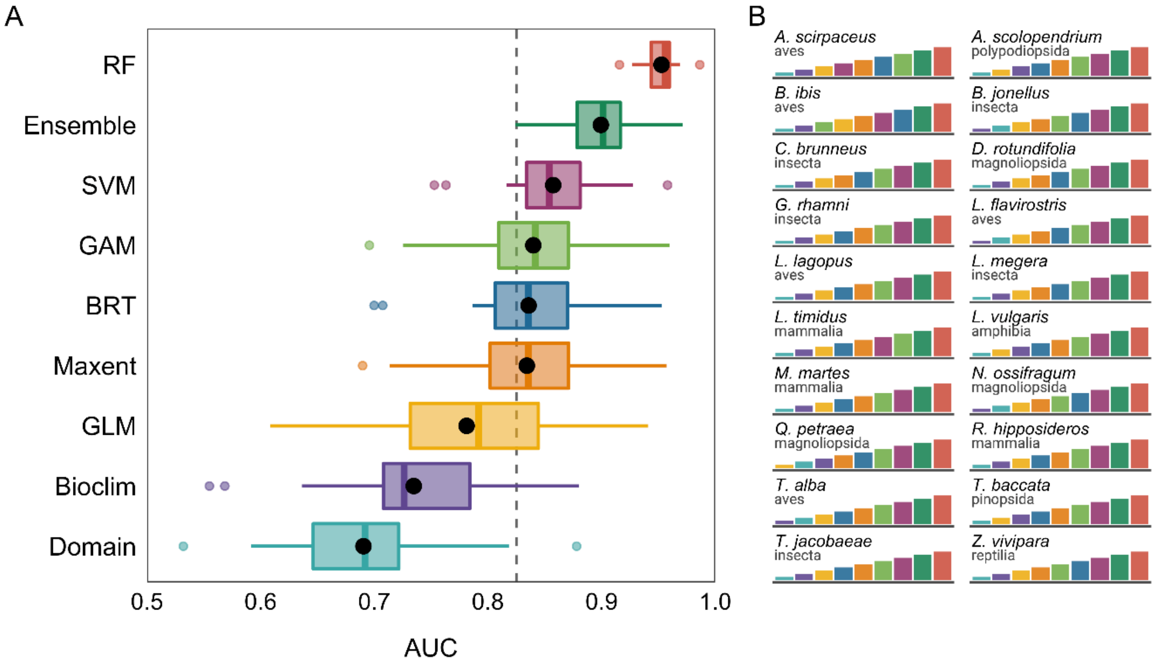


Figure 4.1 Model performance in the reference area. A) Boxplots showing model performance, with the black points representing the mean, and dashed line showing the mean value across all algorithms. B) Bar plots showing performance of ranked models per species. The tallest bar represents the model with highest mean AUC, the shortest bar represents the model with the lowest mean AUC. Bar colour corresponds with the colour per algorithm in A.

Performance varied by species; RFs and the ensembles were consistently ranked the top performing algorithm across the 20 species, and the profile methods, Bioclim and Domain were consistently ranked lowest (Figure 4.1B). However, there was no pattern in the ranking of the remaining 5 algorithms (BRT, GAM, GLM, Maxent and SVM), with them varying in rank per species modelled. For the full range of results by algorithm and species, including 95% confidence intervals, see Table A17 in Appendix IX. To visualise how predictive performance varies spatially by modelling approach, see Figure 4.2.

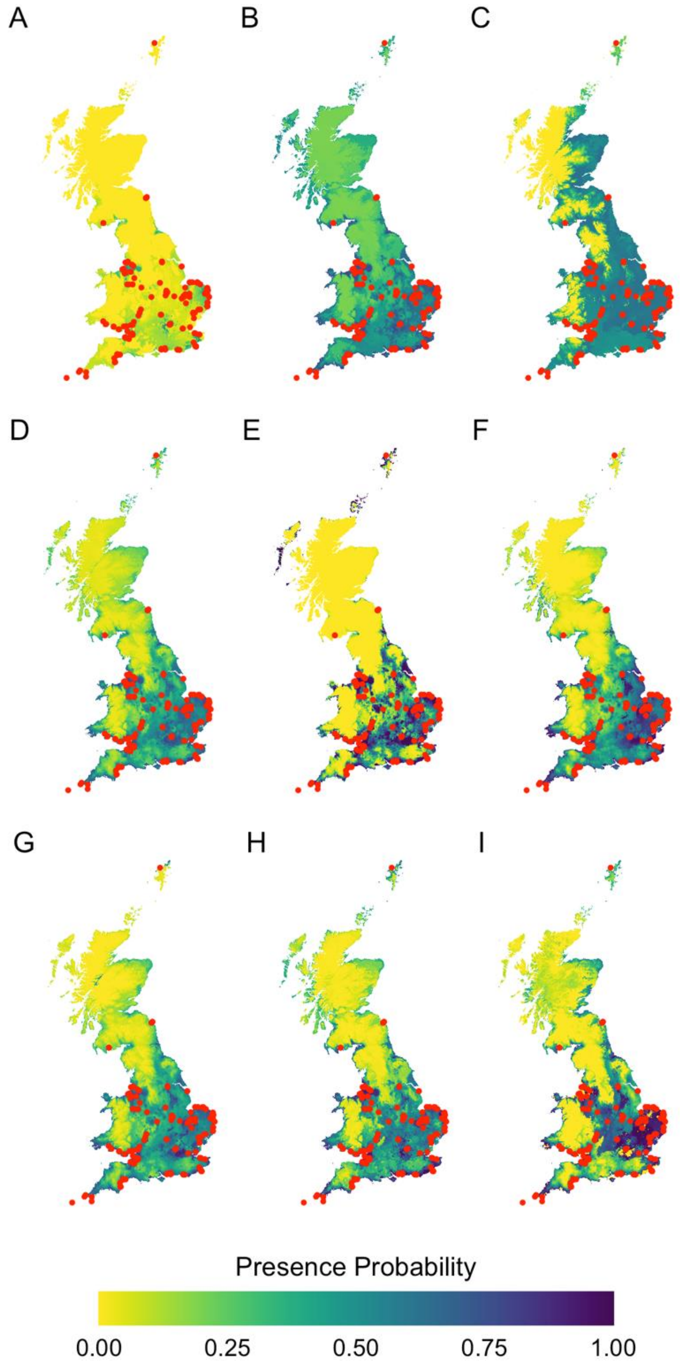


Figure 4.2 Maps of predicted relative probability of presence for *B. ibis* in the reference area for 1 of the 1,000 iterations, using the 9 modelling algorithms: A) BIOCLIM (AUC = 0.815), B) BRT (AUC = 0.918), C) Domain (AUC = 0.790), D) Ensemble (AUC = 0.935), E) GAM (AUC = 0.944), F) GLM (AUC = 0.895), G) Maxent (AUC = 0.931), H) RF (AUC = 0.964) & I) SVM (AUC = 0.878). Red points indicate recorded presences.

4.3.2 Performance of transferred models in the target area

Transferred models had poorer performance than those in the reference area, with a mean AUC of 0.576 across the nine modelling approaches and considerably more variation in AUC values. The best performing model was the GLM with a mean AUC value of 0.645 (Figure 4.3A). However, the range in AUC values was the largest of any of the modelling approaches (0.431 – 0.872). The ensemble approach again performed well, with the second highest mean AUC (0.642) comparable to results from the GLMs, but with less variance (0.501 – 0.813). Maxent, BRT, GAM, RF and SVM performed comparably, with mean AUC values of 0.602, 0.585, 0.571, 0.559 and 0.541 respectively. Similar to the reference area, Bioclim and Domain were the poorest performers with mean AUC values of 0.528 and 0.514.

Despite the mean AUC values suggesting poor performance, this was not the case for all species modelled (Figure 4.3A). There were some AUC values considerably higher than the mean, for example, GLM performance modelling *A. scirpaceus* was 0.872 and SVM performance for *B. ibis* was 0.801. The full range of results including 95% confidence intervals are displayed by species and algorithm in Table A18 Appendix IX. In addition, for maps showing how predictions of relative probability of presence for *B. ibis* in the target area differ per modelling algorithm, see Figure 4.4.

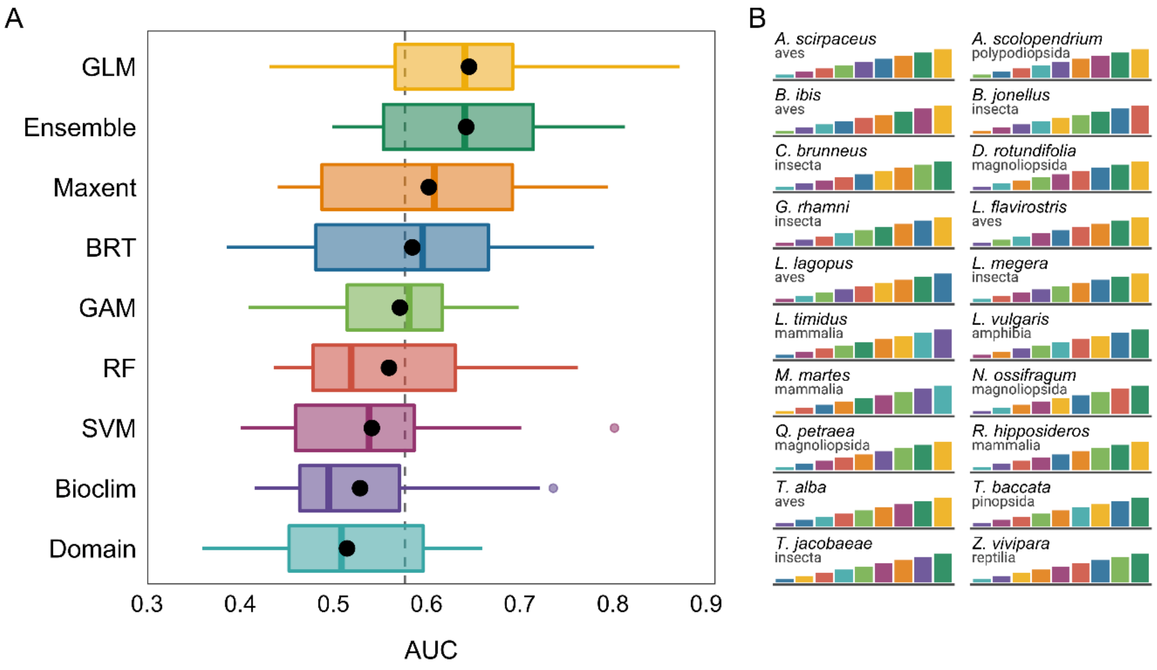


Figure 4.3 Model performance in the target area. A) Boxplots showing model performance, with the black points representing the mean, and dashed line showing the mean value across all algorithms. B) Bar plots showing performance of ranked models per species. The tallest bar represents the model with highest mean AUC, the shortest bar represents the model with the lowest mean AUC. Bar colour corresponds with the colour per algorithm in A.

The ranking of algorithms by performance showed substantial differences between species. GLMs were ranked top for 10 of the 20 species (Figure 4.3B), but also towards the bottom of the rankings in a few instances. Unlike in the reference area, Bioclim and Domain were not always ranked in last place, appearing towards the top of the rankings for 2 species. The ensemble approach was ranked highly throughout, appearing in the top three models for the majority of species (Figure 4.3B).

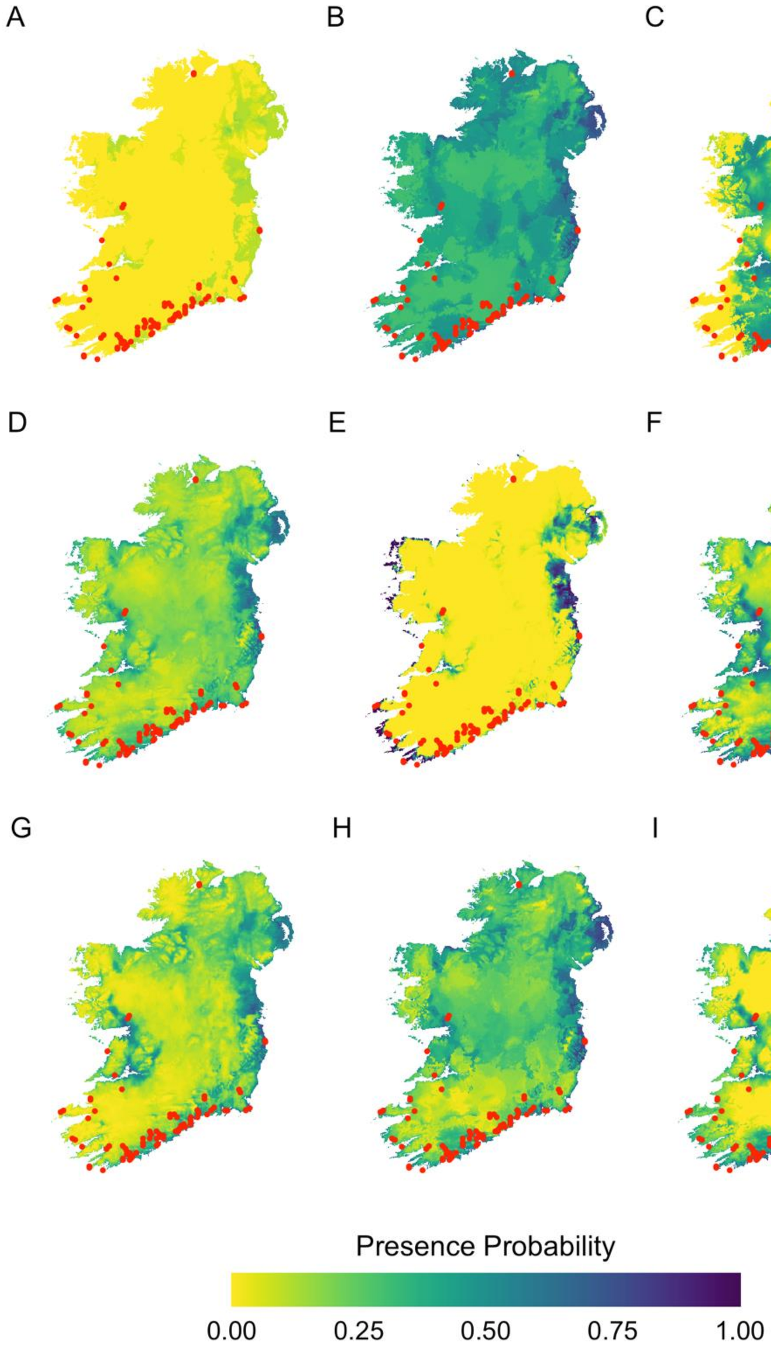


Figure 4.4 Maps of predicted relative probability of presence for *B. ibis* in the target area for 1 of the 1,000 iterations, using the 9 algorithms: A) BIOCLIM (AUC = 0.614), B) BRT (AUC = 0.737), C) Domain (AUC = 0.627), D) Ensemble (AUC = 0.842), E) GAM (AUC = 0.762), F) GLM (AUC = 0.878), G) Maxent (AUC = 0.776), H) RF (AUC = 0.668) & I) SVM (AUC = 0.834). Red points indicate recorded presences.

4.3.3 Change in model performance between reference and target areas

There were differences in model transferability, which varied by species modelled and algorithm used (Figure 4.5). GLMs were perhaps the most transferable, appearing closest to the dashed line in Figure 4.5, indicating similar performance between reference and target areas. To quantify difference in performance, percentage change in mean AUC was calculated, allowing comparison between algorithms and species (Table 4.4). Here, the mean performance for GLMs was 17.4% lower in the target area than the reference area. RFs were the least transferable with a decrease in performance of 41.3% in the target area compared with that in the reference area. In addition, in Figure 4.5, the points representing RF appear furthest from the dashed line in Figure 4.5, despite relatively high performance in both areas. For a list of differences in performance between reference and target areas for each species and the mean, see Table 4.4.

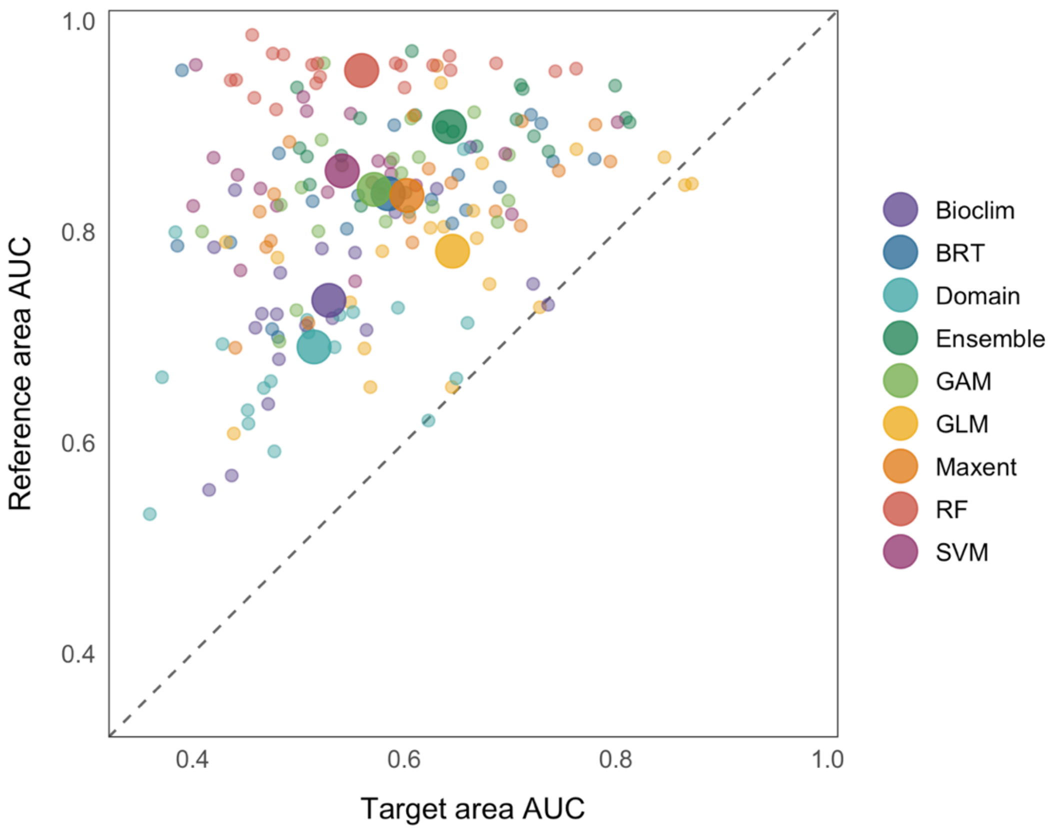
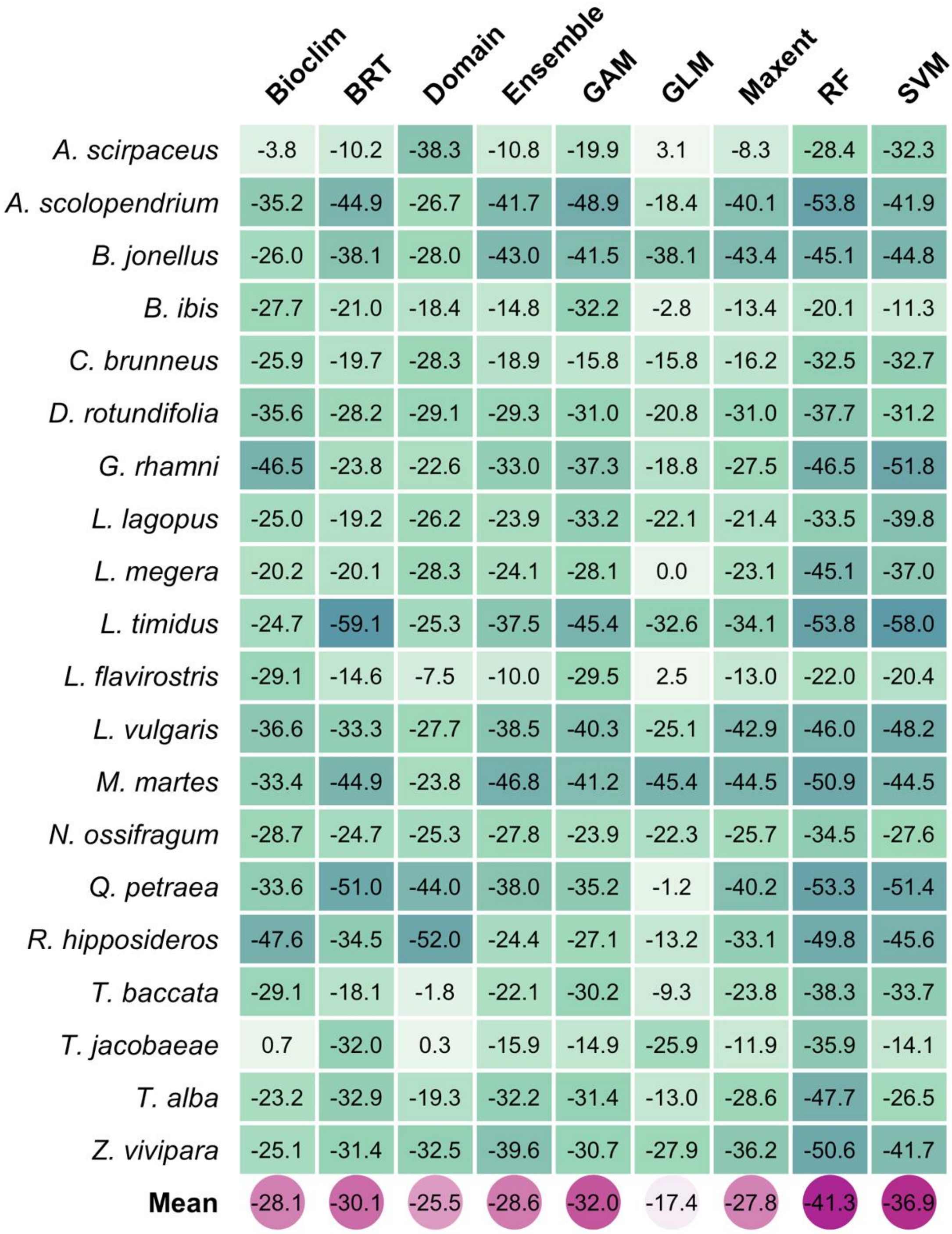


Figure 4.5 Scatterplot of target area vs reference area model performance. Small points represent mean AUC per species, large points represent the mean AUC across all species and point colour indicates the algorithm. Points on the left of the dashed line show better performance in the reference area, points on the right indicate better model performance in the target area, points on the line represent the same performance in both areas.

Table 4.4 Change in model performance from the reference to target area. Differences are expressed as percentage change (%), per species and algorithm. Lighter colours represent small change in mean AUC, darker indicate greater changes. Mean change across all species is represented in the final row by the points.



	Bioclim	BRT	Domain	Ensemble	GAM	GLM	Maxent	RF	SVM
A. scirpaceus	-3.8	-10.2	-38.3	-10.8	-19.9	3.1	-8.3	-28.4	-32.3
A. scolopendrium	-35.2	-44.9	-26.7	-41.7	-48.9	-18.4	-40.1	-53.8	-41.9
B. jonellus	-26.0	-38.1	-28.0	-43.0	-41.5	-38.1	-43.4	-45.1	-44.8
B. ibis	-27.7	-21.0	-18.4	-14.8	-32.2	-2.8	-13.4	-20.1	-11.3
C. brunneus	-25.9	-19.7	-28.3	-18.9	-15.8	-15.8	-16.2	-32.5	-32.7
D. rotundifolia	-35.6	-28.2	-29.1	-29.3	-31.0	-20.8	-31.0	-37.7	-31.2
G. rhamni	-46.5	-23.8	-22.6	-33.0	-37.3	-18.8	-27.5	-46.5	-51.8
L. lagopus	-25.0	-19.2	-26.2	-23.9	-33.2	-22.1	-21.4	-33.5	-39.8
L. megera	-20.2	-20.1	-28.3	-24.1	-28.1	0.0	-23.1	-45.1	-37.0
L. timidus	-24.7	-59.1	-25.3	-37.5	-45.4	-32.6	-34.1	-53.8	-58.0
L. flavirostris	-29.1	-14.6	-7.5	-10.0	-29.5	2.5	-13.0	-22.0	-20.4
L. vulgaris	-36.6	-33.3	-27.7	-38.5	-40.3	-25.1	-42.9	-46.0	-48.2
M. martes	-33.4	-44.9	-23.8	-46.8	-41.2	-45.4	-44.5	-50.9	-44.5
N. ossifragum	-28.7	-24.7	-25.3	-27.8	-23.9	-22.3	-25.7	-34.5	-27.6
Q. petraea	-33.6	-51.0	-44.0	-38.0	-35.2	-1.2	-40.2	-53.3	-51.4
R. hipposideros	-47.6	-34.5	-52.0	-24.4	-27.1	-13.2	-33.1	-49.8	-45.6
T. baccata	-29.1	-18.1	-1.8	-22.1	-30.2	-9.3	-23.8	-38.3	-33.7
T. jacobaeae	0.7	-32.0	0.3	-15.9	-14.9	-25.9	-11.9	-35.9	-14.1
T. alba	-23.2	-32.9	-19.3	-32.2	-31.4	-13.0	-28.6	-47.7	-26.5
Z. vivipara	-25.1	-31.4	-32.5	-39.6	-30.7	-27.9	-36.2	-50.6	-41.7
Mean	-28.1	-30.1	-25.5	-28.6	-32.0	-17.4	-27.8	-41.3	-36.9

4.4 Discussion

This study examined nine different algorithms to ascertain whether a single model is able to produce high predictive performance in both the area it was trained and in a novel environment. The performance differed greatly between modelling approaches; in the reference area results were fairly consistent across the 20 species, with RFs and the ensemble approach performing excellently and the profile methods of Bioclim and Domain performing poorly. When models were transferred, there was much more variation in which algorithm performed best, changing between each species. However, the ensemble approach again was one of the highest and most consistent performing algorithms.

4.4.1 Model performance in the reference area

Whilst predictive performance was generally high, it did vary considerably by algorithm, with the machine learning methods outperforming the profile methods. Like the study by Elith *et al.* (2006), models can be split by performance into three groups, with somewhat similar results, particularly with Bioclim and Domain classed in the poorest performing group. However, the subsequent groups containing models which performed better, were different, primarily due to the inclusion of RF, SVM and the ensemble in this study. Regardless, of the differences in grouping, the order of models by performance and variation in AUC between algorithms was comparable, highlighting BRT and Maxent performed better than GLMs. Similarly, Reiss *et al.* (2011), show Bioclim as the worst performing and GLM ranked in the middle. Again, the machine learning methods provided the greatest predictive performance, although Maxent performed better than RF and SVM, which differs from findings in this study. Differences in the order of algorithm by performance between studies are only small, and most likely due to differences in the species modelled and the predictors used, which has been shown by Syphard & Franklin (2009) to be a major contributor to differences in model performance.

Interestingly, Maxent is one of, if not the most popular species distribution modelling algorithms (Yackulic *et al.*, 2013), owed to its high predictive performance, and has been shown to outperform a number of other approaches (see Elith *et al.*, 2006; Reiss *et al.*, 2011). Yet here, whilst performance was high (mean AUC 0.834), Maxent was ranked the 5th best performing, highlighting other algorithms performed better. This has also been well documented in the literature: Shabani *et al.* (2016) show BRT and RF had greater predictive accuracy than Maxent, with the same being observed by Oppel *et al.* (2012). Though there is consensus that Maxent generally performs better than profile and regression approaches, when compared to other machine learning methods, results appear to vary by study, further indicating performance may be attributed to the species and predictors used.

The ensemble approach, recently embraced in SDM studies, has here shown high predictive performance, only bettered by RF. However, arguably the main benefit to their use is not only the high performance, but consistency and less variability in predictions compared to a single model approach. Crimmins *et al.* (2013)highlight this, with high predictive performance by an ensemble, and much less variation than single model algorithms, particularly regression-based methods, which has also been demonstrated in numerous other studies (see Grenouillet *et al.*, 2011; Liu *et al.*, 2019). Furthermore, Marmion *et al.* (2009) show that significant increases to predictive accuracy can be gained through using an ensemble, although Araújo & New (2007) suggest similar levels of accuracy can also be gained by traditional methods of model improvement. Ultimately, the performance of an ensemble approach may be bettered by a single model algorithm, such RF here and shown by Crimmins *et al.* (2013), and GAM in the study by (Ranjitkar *et al.*, 2014). But the lower variability leading to less uncertainty in results from ensembles is hard to achieve with a single model approach, which are more susceptible to influence from species idiosyncrasies and model artefacts (Araújo & New, 2007). Therefore, the use of an ensemble can lead to increased reliability, thus greater confidence in predictions, so where possible, using an ensemble approach is recommended.

The consistency of results across the range of species in the reference area, shown by Figure 4.1B, indicates the differences in performance were not impacted by species or environmental influences, but primarily the underlying modelling algorithm. Therefore, the top performing algorithm, RF, could be considered the single best model here, however, the literature does not typically state such findings. Whilst RF has been shown as the best performing on numerous occasions (see Grenouillet *et al.*, 2011; Ren-Yan *et al.*, 2014; Shabani *et al.*, 2016; Mi *et al.*, 2017), there are also studies with contrasting results, with approaches such as GLM, GAM, multivariate adaptive regression splines (MARS), generalized boosting method (GBM) and Maxent performing better than RF (see Reiss *et al.*, 2011; Bucklin *et al.*, 2015; Norberg *et al.*, 2019). Consequently, perhaps there is no single best algorithm, instead, those which have a higher probability of performing well, such as other more recent machine learning methods and occasionally regressions. Therefore, for the best results in SDM studies, a suite of algorithms should be employed, including an ensemble approach, enabling the identification of which approach performs best to meet the aims within a given context.

4.4.2 Performance of transferred models

When models were transferred, predictive performance in the target area was generally lower than the reference area, with substantial variation between algorithms and individual species modelled. This pattern of reduced performance on transfer has been well documented, with Randin *et al.* (2006) showing large declines in performance when GAMs and GLMs were transferred to a new region. Similarly, Wenger & Olden (2012) found machine learning methods (artificial neural networks, ANN and RF) also performed poorly when transferred, as did Duque-lazo *et al.* (2016) using ANN, BRT, Maxent and RF. This reduced performance was observed in machine learning approaches here (BRT, Maxent, RF, SVM), and was most pronounced in predictions by RFs, with performance in the target area on average 41% lower than that in the reference area. The weak performance of RFs using an independent dataset has been observed on numerous occasions and attributed to the tendency of RFs to overfit (see Heikkinen *et al.*, 2012; Barbet-Massin & Jetz, 2014; Luan *et al.*, 2020), in spite of measures such as bagging to prevent overfitting, as described by Breiman (2001). Furthermore, Randin *et al.* (2006) suggest overfitting reduces model transferability, which is in line with the findings here.

Despite the greatest declines in performance of transferred models coming from machine learning approaches, their predictive performance when transferred was still superior to that of the profile methods. The poorer transfer performance of profile methods has been highlighted in numerous studies, with Bioclim and Domain seen to perform relatively poorly in novel environments (see Rödder & Lötters, 2010; Qiao *et al.*, 2015; Shabani *et al.*, 2016). Qiao *et al.* (2015) suggest Bioclim has a tendency to be conservative in predictions, often underpredicting range, whereas Domain has been shown to often overpredict habitat suitability (Wiens *et al.*, 2009; Sarquis *et al.*, 2018), both of which were experienced here (Figure 4.2), attributing to the poor performance when transferred. Furthermore, there does not appear to be any studies recommending the use of such profile methods over regressions or machine learning approaches, which almost always perform better (Elith *et al.*, 2006).

Here, GLMs were the top performing model when transferred, which has often been observed in similar studies, although there have been mixed results: Duque-lazo *et al.* (2016) suggest GLMs provided the most desirable combination, providing high model performance and good transferability. The same was observed by Heikkinen *et al.* (2012), although GAM and Maxent offered greater transferability, whereas Mainali *et al.* (2015) show GLMs gave highly unrealistic predictions when transferred, and again better performance was achieved by GAM and Maxent. In addition, here GLMs could be considered the most transferable approach due to the smallest change in performance between reference and target areas, indicating the desirable traits described by Duque-lazo *et al.* (2016). However, whilst GLM transferability was high for the majority of species, there were several species where performance was poor, which resulted in the most variation of any algorithm (AUC values 0.431 – 0.832) and the ranking by performance varied from 1st to 9th place. This highlights performance is not equal for all species, as also shown by Rapacciuolo *et al.* (2012) particularly with GLMs. The variation in performance of GLMs is likely caused by non-analogue conditions and non-stationarity, i.e. environmental conditions that differ between the reference and target areas and where the relationships between variables do not stay constant when transferred, which results in a poorly fitting model for some species, hence the varied performance (Zuur et al., 2009; Yates et al,. 2018).

As described here, there does not appear to be a single best algorithm or modelling approach for high predictive performance and transferability. Qiao *et al.* (2015) and more recently, the comprehensive study by Norberg *et al.* (2019) further outline this, suggesting that no single algorithm can perform well in all tasks, with model performance differing depending the species modelled. Instead, perhaps the best approach is in fact an ensemble of multiple algorithms. The ensembles used in this study, not only performed well once transferred, but contained the least variability in results and were constantly ranked amongst the highest performing approaches for all species. Similar results have been observed in multiple studies, with Shabani *et al.* (2016) suggesting the predictions made by the best single algorithm approach are often less reliable than predictions from an ensemble. However, Rodríguez-Rey *et al.* (2013) show ensembles do not solve bias or idiosyncrasies, therefore may not improve transferability. Regardless, there will always be some degree of uncertainty when transferring models, but using an ensemble approach can reduce this through averaging multiple algorithms (Araújo & New, 2007; Grenouillet *et al.*, 2011), rather than solely relying upon single algorithms which have been shown to produce highly variable results (Evans *et al.*, 2013; Iturbide *et al.*, 2018b). Therefore, to increase reliability of predictions, it is recommended not only a suite of algorithms are used, but additionally, the use of an ensemble should be employed.

4.4.3 Causes of transferability

This study has shown that when models are transferred, they do not perform equally across the focal species, which demonstrates the modelling algorithm is not the only factor influencing transferability. In fact, an array of studies have shown there are multiple factors attributed to the species or environment which can exert the same, if not greater influence on transferability. For example, Dobrowski *et al.* (2011) and Eskildsen *et al.* (2013) show certain traits of their species modelled allowed for greater transferability, whereas Heikkinen *et al.* (2012) and Rapacciuolo *et al.* (2012) show transferability was attributed to taxonomic group. However, whilst both Heikkinen *et al.* (2012) and Rapacciuolo *et al.* (2012) investigated the same three groups, there was disagreement in which was most transferable: Rapacciuolo *et al.* (2012) shows butterflies were more transferable than plants, which in turn transferred better than birds, but Heikkinen *et al.* (2012) found the order of most transferable to be birds, then butterflies and finally plants, which was also the order observed here.

Why models of some taxon are more transferable than others is an outstanding question posed by Yates *et al.* (2018), however evidence so far indicates transferability is attributed to species' traits. Soininen & Luoto (2014) show dispersal mode and trophic position are influential. Similarly, Eskildsen *et al.* (2013 and Wogan (2016) suggest models of mobile species are less transferable than those with low dispersal ability. However, this was not the case here; perhaps the best performing were models of *B. ibis*, a highly mobile bird species, whose range has been rapidly shifting northwards in recent years due to climate warming (Maddock and Geering, 1994; Christmas *et al*., 2010; Youcefi *et al*., 2019). Whereas in contrast, sessile species such as plants, showed poor model transferability. Perhaps the causes of such results are not attributable to the species' traits, but instead due to the underlying data quality. Moran-ordonez *et al*. (2017) suggest data quality and availability increases for large and more conspicuous species, which in turn can lead to increased model performance (Seoane *et al*., 2005). This is probably the case here as charismatic and easily identifiable species such as birds, are more likely to be recorded than sessile plant or amphibian species, unless for specific surveys or projects. Moran-ordonez *et al*. (2017) go on to show that in fact data quality has a considerably higher influence on model performance than that of species traits, which they suggest is marginal. Nevertheless, this question remains unanswered, with research here and in the literature showing transferability is likely attributed to a combination of species' traits, algorithm selection and data quality (Moon *et al.*, 2017; Werkowska *et al.*, 2017).

The influence of environmental predictors on transferability can be owed to how the species interacts with the environment, where often, differences in the species-environment relationship occur between the reference and target areas. This has been a key driver of failed and poor performing model transfers (see Torres *et al.*, 2015; Roach *et al.*, 2017), and explains the poor transferability by models of *L. timidus*, where there are differences in niche between the populations in Britain and Ireland (Whelan, 1985; Watson & Wilson, 2018). These non-stationary relationships have been identified as a key challenge facing transferability (Yates *et al.*, 2018). Yet there does appear to be ways to take non-stationarity into account such as using a spatially larger training dataset to capture as many variations in the species-environment relationship (Paton & Matthiopoulos, 2015; Luan *et al.*, 2020). Or the use of a mechanistic models which are typically based on the intrinsic properties underlying the relationships, rather than the extrinsic, observation based, correlative SDMs (Buckley *et al.*, 2010; Peterson *et al.*, 2015).

Another driver of transferability and perhaps one experienced in every study is the quality of data used (Lauzeral *et al.*, 2013; Aubry *et al.*, 2017). Dormann *et al.* (2008) suggest data quality is one of the most influential factors in model performance and more recently, Aubry *et al.* (2017) show accurate identification of species has greater influence than the spatial extent and positional uncertainty, therefore occurrences used should be verifiable. Whilst records used here were verifiable, data quality may still have impacted transferability. For example, when comparing maps of the observed and predicted range of *B. jonellus* in the target area*,* there appears to be discrepancies*,* which lead to poor model performance*.* These differences could be due to lack of presence records which lead models to report false negatives during transferred model validation, leading to poor performance (Rondinini *et al.*, 2006).

The issues outlined here are common in transferability studies (see Strauss & Biedermann, 2007; Wenger & Olden, 2012; Wang & Jackson, 2014) and likely to always be encountered at some level. Whilst action can be taken to mitigate uncertainty and improve transferability as discussed, the nature of transferring into novel environments will always contain a degree of uncertainty. The research here has largely shown results in line with the current literature, providing further insight into successful transfers and the issues transferable models face. However, despite the depth of literature generated in recent years (i.e. Verbruggen *et al.*, 2013; Petitpierre *et al.*, 2017; Werkowska *et al.*, 2017; Sequeira *et al.*, 2018b; a), there remain fundamental challenges surrounding the concept and practice of transferring models, which will likely need answering per situation, based on the aims of the research being undertaken (Yates *et al.*, 2018).

4.5 Conclusion

This research has shown the modelling approach does have an impact on predictive performance and transferability. Results were largely in line with current literature showing machine learning methods performed highly in the reference area but were susceptible to overfitting and performance was weaker in the target area. In addition, results from transferred models appeared to be influenced by external factors which need to be considered when transferring models into novel environments. Nevertheless, to find the desired traits of high performance and transferability, it would be wise to use a selection of different algorithms to identify the most suitable to answer the research question. Furthermore, the use of an ensemble is highly recommended as they have shown high performance, low variability, and high transferability. Moreover, predictions produced by ensembles have increased reliability over single algorithm approaches, which have been shown to produce unrealistic predictions and vary considerably due to external influences.

Chapter 5 - Exploring the transferability of a generic risk-based mechanistic model of plant disease

5.1 Introduction

The introduction of organisms to new geographical areas is one of the greatest threats to global biodiversity (Mainka & Howard, 2010; Doherty *et al.*, 2016; Early *et al.*, 2016). The direct relationship between introductions and human movement has caused exponential increases in introductions in the past few centuries (Reid *et al.*, 2005; Hulme, 2009), where humans have both intentionally and inadvertently moved organisms around the globe (McNeely, 2006; Early *et al.*, 2016). These included domestic, agricultural and pest plants and animals, and disease-causing biota (viruses, bacteria and fungi) of humans, animals, and plants (Hulme, 2009; Pyšek & Richardson, 2010). Once an introduced organism becomes established in its new environment, the lack of predators adapted to deal with such organisms, or adaptations of prey and competitors often allows them to spread and reproduce prolifically and be considered an invasive species (Neubert & Parker, 2004). Whilst there are a number of definitions of invasive species, the general consensus appears to suggest they are organisms introduced outside their normal or native range, whose establishment and spread can modify habitats and ecosystems with or without causing economic or environmental damage (Beck *et al.*, 2008). Most invasive species significantly impact native biodiversity either directly through predation or competition, as a vector for disease, through habitat modification and destruction or by altering the dynamic between native species (Vilà *et al.*, 2011; Katsanevakis *et al.*, 2014).

Due to the significant environmental and economic impacts caused by invasive biota and the number and complexity of pathways for introduction, the consequential management has become a major task (Pyšek & Richardson, 2010; Hulme, 2015).

The effective prevention and control of invasive organisms requires a comprehensive list of known introduced biota, their point of introduction and information on life history in order to determine how far and fast they will spread (Hulme, 2009, 2015; Keller *et al.*, 2011). A number of countries and regions now have strict guidelines in place to minimise the risk of introducing non-native biota through trade and transport (Eschen *et al.*, 2015; Garcıa-de-Lomas & Montserrat, 2015; Piero *et al.*, 2015), combined with extensive research into the spread of certain high risk organisms which can improve early-warning, detection and eradication schemes (Piero *et al.*, 2015; Carboneras *et al.*, 2017).

Despite the increases in awareness and regulations of biosecurity to minimise spread of organisms, historic, pre-regulation and illegal (intentional and accidental) introductions are still having severe impacts on environments, biodiversity and economies today (Herborg *et al.*, 2003; Epanchin-niell, 2017). Some of the largest impacts from introduced biota on economies around the world are caused by the threat from plant diseases, often spread by invasive insects (Vurro *et al.*, 2010; Fisher *et al.*, 2013; Paini *et al.*, 2016; Hyatt-Twynam *et al.*, 2017). Economically, the impacts of plant pathogens are vast. It is estimated that in the USA, crop losses caused by pathogens exceed US$ 33 billion per year (Pimentel *et al*., 2001, 2005). Similarly, pathogens affecting trees and forestry, have cost over US$ 7 billion per year in loss of forest products (Pimentel *et al*., 2001). Additionally, the threat from plant pathogens to world food production will not only impact economies but will have a huge social impact. To meet global demand, projections show a 50% increase in production is needed, but currently pathogens still destroy up to 16% of production (Chakraborty & Newton, 2011).

In recent years, there appears to have been an increase in emphasis placed on plant pathogen surveillance and management projects (Harvell *et al.*, 2002; Pautasso *et al.*, 2010). Surveillance is used to detect invading pathogens before they spread out of control. However, as is often the case, epidemics are not discovered until already at a high prevalence. This tends to be due to a lack of quantitative information on pathogens' entry point and transport along with movement and reproduction dynamics, combined with a general lack of understanding of effective surveillance schemes (Park *et al.*, 2011). Parnell *et al.* (2015), show that simple models can be used to aid early detection surveillance by delivering valuable insights into complex systems, this can be used to subsequently inform decisions on surveillance resource allocation to detect the pathogen before it reaches high prevalence.

With the increasing availability and capability of epidemiological models, combined with the greater understanding on how diseases not only affect biodiversity but also global food security, the continued monitoring of infectious diseases is essential to ensure the effective control and management of future emerging epidemics (Vurro *et al.*, 2010; Paini *et al.*, 2016). One particular pathogen with a considerable amount of surveillance and research into its spread and control is *Huanglongbing, (HLB, syn. Citrus Greening Disease).* HLB is one of the world's most devastating plant pathogens and potentially the most destructive to the global citrus industry (Gottwald, 2010; Gottwald *et al.*, 2007).

5.1.1 Citrus greening

First described in 1927 in India by Husain & Nath (1927), but thought to originate in China in the 1800's, HLB has now spread throughout most of the world's major citrus growing regions, except the Mediterranean (Bové, 2006; Gottwald & McCollum, 2017). Whilst HLB is associated with three bacteria (*Candidatus* Liberibacter asiaticus, Las, *Candidatus* Liberibacter africanus, Laf, and *Candidatus* Liberibacter americanus, Lam), it is Las that is most prevalent and has perhaps had the greatest impact (Hall *et al.*, 2013). HLB is primarily spread by the Asian citrus psyllid (ACP, *Diaphorina citri*), a small sap-eating insect, originally from sub-tropical Asia, but now present in several Central American countries and states in the USA (Halbert & Manjunath, 2004; Monzo *et al.*, 2015). Florida was the first American state to confirm ACP, recorded in 1998 with HLB later confirmed in 2005, subsequently, ACP and HLB have both been recorded in Arizona, California and Texas (Gottwald, 2010; Narouei-Khandan *et al.*, 2016).

Once a tree becomes infected with HLB, the disease attacks the plant’s vascular system causing defoliation, abnormalities in the size, shape and quality of fruit, decreased yield and eventually death (Grafton-cardwell *et al.*, 2013). However, despite some of the more obvious effects, the disease is difficult to detect due to a long and variable asymptomatic period, often ranging between months and several years (Gottwald, 2010; Lee *et al.*, 2015). HLB can be spread rapidly, with up to 12,000 psyllids recorded on a single tree (Lee *et al.*, 2015), which unsurprisingly has led to high HLB prevalence rates. 100% of citrus groves in Florida are infected, with more than 80% of trees infected within those groves (Singerman & Useche, 2015; Craig *et al.*, 2018). The impacts of this infection have been severe. Before the introduction of HLB, the citrus industry in Florida employed over 76,000 people and supplied around 95% of the orange juice in the US (Singerman & Useche, 2015). However, between the years of 2000 and 2016, the citrus producing area decreased by 42% and total production decreased by 68% (Court *et al.*, 2017). In addition, it has been estimated that HLB has caused an $8.9 billion loss in revenue (Hodges &

Spreen, 2012; Spreen *et al.*, 2014). These impacts combined, continue to threaten the future viability of the citrus industry in Florida. With citrus the second largest fruit crop in the world (FAO, 2017), if the disease were to become as prevalent in other citrus producing regions as it is in Florida, the outcome could be devastating.

Despite almost a century of research into HLB, no cure has been found and its control remains largely unsuccessful (Gottwald & McCollum, 2017). There is currently a swathe of research being undertaken around the world, investigating the disease, its vector, and a range of its epidemiological aspects to try and gain a better understanding of this disease and reduce its impact in citrus growing regions (Lee *et al.*, 2015; Narouei-Khandan *et al.*, 2016; Gottwald & McCollum, 2017; Shimwela *et al.*, 2018). Parnell *et al.* (2014) successfully created a simple model that predicts risk of spread of HLB within Florida. Using this technique, high risk areas can be targeted for monitoring and implementation of control measures (Hyatt-Twynam *et al.*, 2017). With the disease now confirmed in other US states, there is great utility in testing whether the Florida model can be used to predict the risk of HLB spread in other states (i.e. the transferability of the model).

5.1.2 Model transferability with pest species

The concept of spatial or temporal cross-applicability of a model previously known as generality, but now trending towards the term transferability (Guisan & Thuiller, 2005; Wenger & Olden, 2012), is becoming an increasingly popular area of research within the ecological modelling field. This is essentially the extrapolation of an existing model to spatially or temporally extend its use into areas the model was not created and tested in (Elith & Leathwick, 2009; Sequeira *et al.*, 2018b). Transferable models have been used in a range of applications, from informing on suitable areas for the reintroduction of species (Schadt *et al.*, 2002) to predicting the potential future range of species in response to climate change (Lawler *et al.*, 2006; Dobrowski *et al.*, 2011). However, perhaps one of the most common applications is highlighting areas vulnerable to species invasions (e.g. Thuiller *et al.*, 2005; Hudgins *et al.*, 2017; Petitpierre *et al.*, 2017; Fan *et al.*, 2018).

The main benefit of transferring models in ecological research, is that they can provide predictions of a species' distribution (amongst other types of responses) in areas lacking enough data to create a model (Wenger & Olden, 2012). A good example of this is with newly introduced species; a model can be created and parameterised in the species' native range and then transferred to the newly introduced range, to make reliable and robust predictions about that species' potential to spread (see; Verbruggen *et al.*, 2013; Petitpierre *et al.*, 2017). However, this is not always the case and often a transferred model will perform poorly (i.e. Torres *et al*., 2015; Capinha *et al*., 2018).

In recent years, there has been an increase in the understanding of the use and issues surrounding model transferability (see; Werkowska *et al.*, 2017; Sequeira *et al.*, 2018; Yates *et al.*, 2018). Furthermore, there has been a focus on how transferable models may be able to assist in studies researching the current and future spread of pests and invasive biota (Wenger & Olden, 2012; Godsoe *et al.*, 2014). A prime example of where a transferable model could be useful is with the current HLB epidemic in the world's citrus growing regions. With HLB now confirmed in California (Gottwald *et al.*, 2014) and the vector detected in parts of mainland Europe (Massimino *et al.*, 2017), but with no confirmed cases of HLB yet, creating a transferable risk model has the potential to aid in controlling spread in these regions before disease prevalence rates reach highs as seen in Florida (Craig *et al.*, 2018). The simple but powerful risk model created by Parnell *et al.* (2014) has the foundation to be transferable, with few predictors not spatially constrained to one location, and a generic framework for model creation and surveying risk.

With this in mind, this research will investigate and assess the transferability of the simple mechanistic risk model created by Parnell *et al.* (2014), by transferring the model from an area of established HLB infection, to those newly infected. This research will therefore increase the understanding of HLB spread not only in the USA but will also be relevant to areas of emerging infections such as Europe. In addition, the findings here will contribute to the knowledge surrounding model transferability, particularly when dealing with invasive biota, plant pathogen and mechanistic models. To achieve these aims, the following research questions will be explored:

1. To what extent can a simple generic risk-based model of HLB be spatially transferable?
2. How do different predictors affect model transferability?
3. And can accurate spread predictions be made to aid in the control and management of HLB?

5.2 Methodology

In this section I first discuss the source of data, the data sorting and processing, and how certain aspects were transformed, allowing the two data sets (California and Florida) to be comparable. In addition, I describe how the methods evolved and certain choices regarding subsequent modelling were made, based on the results of data exploration and transformation. Following this, I outline the methods used to model HLB spread in Florida, the changes that occurred to the initial model and various successive versions that contained different predictors. Finally, I summarise the process of transferring the model from Florida to California and highlight the methods used here. As the focus of this study is on the transferability of a spread model, the reasons why certain methods were chosen, and brief results of these choices are presented in this section to help show the flow of the decision-making process from modelling in Florida to the transfer in California.

5.2.1 Data acquisition

Citrus tree data was acquired for the states of California and Florida, provided by the United States Department for Agriculture, Animal and Plant Health Inspection Service. At the time of writing, HLB was confirmed in commercial citrus groves and residential trees in Florida and only in residential trees in California (Kumagai *et al.*, 2013; da Graça *et al.*, 2016). Therefore, there were differences in data between the states, namely the parameters recorded (Table 5.1) and the amount of the data points. This variation between datasets can be attributed to a number of factors, namely the differences in phase of infection between the two states, prevalence of the disease within the states (Figure 5.1), and the presence of HLB in commercial plantings in Florida and not California.

Table 5.1 Parameters included in the Florida and California HLB datasets. *XY co-ordinates in Florida were taken at the centre of each citrus grove, in California, the co-ordinates were for each residential citrus tree.

Variable	**Florida**	**California**
XY Co-ordinates*	X	X
Date Sampled	X	X
Host Plant Type	X	X
Disease Status	X	X
ACP Vector Abundance	X	X
Sampling Cycle	X	
Planting Age	X	
Grove Size	X	
Trees per Grove	X	

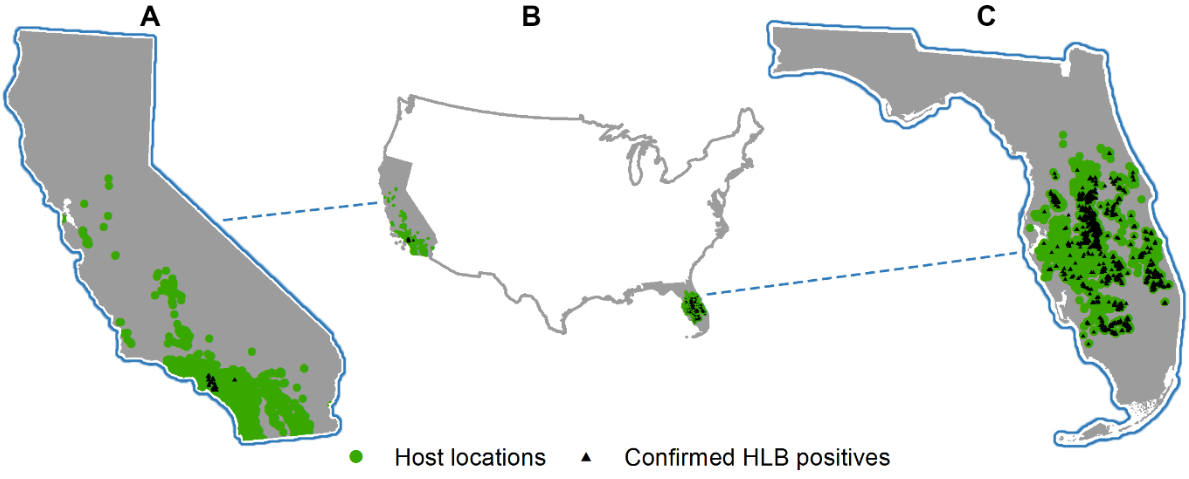


Figure 5.1 Maps showing citrus tree location and confirmed HLB positive locations. Maps were created with data used in this study and show: A) the state of California (2012 – 2017), B) an overview of locations in the USA, and C) the state of Florida (2010 – 2011).

The Florida data was collected in six, 6-week survey cycles from November 2010 to July 2011 (summary of data in Table 5.2). Surveys focused on commercial plantings, where citrus trees are grown in rectangular arrays of uniformly spaced trees of varying area known as blocks. In 2011, Florida contained over 70,000 plantings representing, 219,068 ha of citrus, with an average block size of 6.2 ha (USDA, 2012), predominantly located in the centre of the state (Figure 5.1). Host locations were recorded by a single discrete planting of citrus trees identifiable by the centroid coordinates of each location and in total, 30,064 plantings were surveyed through the six cycles. Various characteristics such as planting age and area were also recorded as shown in Table 5.2, (Parnell *et al.*, 2014).

In contrast, the California data was collected from residential citrus trees, as HLB was not yet known to occur in commercial plantings in California. Every residential citrus tree in high-risk areas of California was surveyed. This was carried out between March 2012 and December 2017, but with no real sampling cycles like Florida. Due to the vast number of residential citrus trees throughout the state, the number of data points was considerably higher; 222,203. However, because there were no planting records like commercial citrus, age, which was a key parameter in the initial model (detailed in the next section), could not be known. And as a consequence, some minor data transformations were required before any analysis began, to allow the two datasets to be more comparable.

Table 5.2 Summary of Florida data, with sampling dates, total number of trees and number of confirmed Huanglongbing (HLB) positive trees per cycle.

Cycle	**Total number of citrus trees**	**Observed positives**		**Dates of sample collection**
		New only	**Cumulative**	
1	2658	622	622	8 Nov - 30 Dec, 2010
2	3708	386	1008	3 Jan - 12 Feb, 2011
3	5525	390	1398	14 Feb - 25Mar, 2011
4	6336	187	1585	28 Mar - 6 May, 2011
5	6456	216	1801	9 May - 17 Jun, 2011
6	5381	29	1830	20 Jun - 29 Jul, 2011

5.2.2 Data sorting

Unlike the Florida data, there were no distinct cycles in California, and these were needed for use in the model, as detailed in section 5.2.4. Therefore, data was split into annual cycles from 2012 onwards. There was low prevalence in California (<1% infected), so if split into 6-week cycles corresponding to Florida, there would be many cycles without new positive trees confirmed, and the model would not function in the same way as Florida. For both the Florida and California data sets, HLB positive trees were cumulatively added to each cycle, however only the negative trees surveyed in each sampling cycle were added, as the negative status of trees in previous cycles could not be guaranteed unless surveyed again. The first cycle of California data in 2012, only had two trees confirmed with HLB, and there were no new confirmed infections until 2015. And although this is HLB positive data, it was not enough to use in the analysis, therefore the final California data contained 3 annual data cycles, from 2015 to 2017 (Table 5.3).

Table 5.3 Summary of citrus trees sampled in California, showing total number of trees and number of confirmed Huanglongbing (HLB) positive trees per cycle used in the analysis after data sorting. Due to the lack of new positive trees recorded in cycles 2 and 3, cycles 1 to 3 were not used in subsequent analysis.

Cycle	**Total number of citrus trees**	**Observed positives**		**Year of sample collection**
		New only	**Cumulative**	
1	45	1	1	2012
2	8688	0	1	2013
3	8212	0	1	2014
4	16828	3	4	2015
5	15759	6	10	2016
6	8858	98	108	2017

Once split into cycles, the vast number of data points in the California dataset presented issues with computational time. To overcome this, initially data was clipped; data points of host location can be seen throughout the state, as far north as the San Francisco area (Figure 5.1), however, HLB had only been confirmed to the Los Angeles area, so points outside of this range were removed. This left over 200,000 points and still presented issues with computation. Therefore, data needed to be aggregated whilst keeping the same detailed information. ArcMap 10.5 was used to create a grid over the spatial extent of the data points and the underlying HLB information was added to each grid cell. If one positive tree was included, the whole cell would count as an HLB positive location. Centroid points were generated in each cell and contained the HLB parameters shown in Table 5.3.

The optimum grid size for subsequent analysis should keep the data at a high resolution, give good predictive accuracy and have low computational time. To find this, seven grids were created ranging from 100 x 100m to 700 x 700m (the average size grove of the largescale citrus producers in Florida) and the centroid points were used in the model as tree location, using a 10 km dispersal distance (expert's opinion, outlined by Parnell *et al.*, 2014). The 300m grid not only produced results with the greatest predictive power (AUC = 0.819, Figure 5.2), but the area of the grid was similar to that of the mean grove size/citrus block in Florida (23.38 acres). The 100 meter and 200 meter grids had too many points to compute and were therefore left out of this analysis.

To test performance here and in subsequent analysis, the area under the curve (AUC) of the receiver operator characteristic (ROC) was employed. AUC is a widely used statistic in ecological modelling and is used to assess predictive accuracy by testing the ability of a model to distinguish true positives and negatives at a range of thresholds (Hanley & McNeil, 1982; Gonçalves *et al.*, 2014). AUC was used as this removes any potential user-generated bias exhibited in other metrics, by providing a scaled assessment metric between 0 and 1 (Peterson *et al.*, 2008). An AUC value of 1 indicates a model with perfect fit, whereas 0.5 means the model is no better than random chance. AUC values lower than 0.5 poor model predictive performance (Hanley & McNeil, 1982). AUC is arguably the best way to summarise a model's performance here, as the single number output generated can be compared across models (Fawcett, 2006; Jiménez-Valverde, 2012).

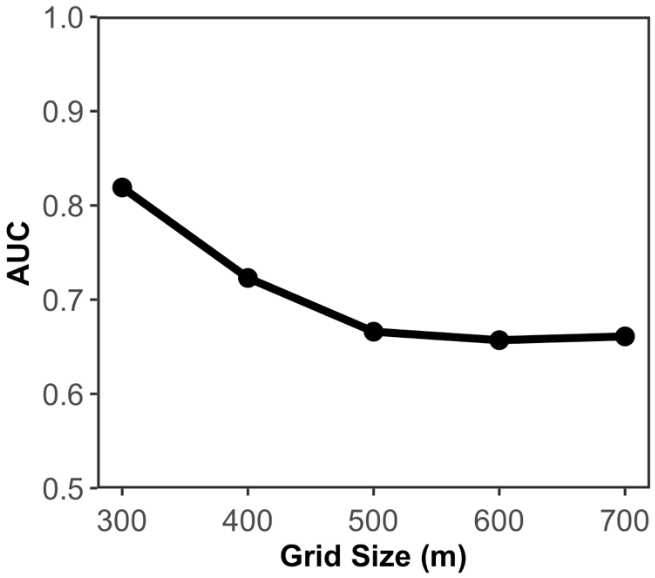


Figure 5.2 Plot comparing AUC values (Area Under Curve of the Receiver Operator Characteristic) generated using a 10 km dispersal distance for California HLB data in grid sizes from 300 x 300m to 700 x 700m.

5.2.3 Predictor variables

As HLB is spread by the vector ACP, abundance of the psyllid was investigated for use a predictor in the model. During HLB surveys, ACP abundance was recorded at each surveyed tree using the tap method: A white sheet is held under the tree being surveyed and a branch is tapped sharply with a PVC pipe 3 times. The insects are then counted (Monzo *et al.*, 2015). Consequently, ACP abundance was recorded for each tree sampled for HLB per cycle in Florida and California, however visible symptoms of HLB do not appear on the leaves for months to years after the initial infection (Lee *et al.*, 2015). To overcome this, ACP values from previous sampling surveys were interpolated for the locations of trees in each of the subsequent cycles.

Inverse Distance Weighting (IDW) interpolation was used in ArcMap (Figure A1, Appendix X). This is perhaps the simplest method for interpolating cell values on a surface in data deficient areas. IDW uses two variables to generate values; the size of the neighbourhood (area around the point being interpolated) expressed as the number of points, or as a radius of a given size, and the weighting given to the existing points (Balangcod, 2011; Gong *et al.*, 2014). A weighted average is then taken of the observed values within the neighbourhood, with weight as a function of inverse distance. Simply put, the further the existing point from the point being interpolated, the smaller its influence on the interpolated value.

To find the optimum settings before generating ACP values for use in the model, different power or weighting values were used. This is the value that controls the significance of other points on the interpolated value. Higher power values result in less influence from distant points (Watson & Philip, 1985; Asal, 2014; Gong *et al.*, 2014). Values between 0.5 and 3 are recommended to avoid overfitting and unexpected results (Shepard, 1968; Watson & Philip, 1985). Therefore, each cycle was interpolated 4 times with power values ranging from 0.5 to 3. The interpolated values were extracted for each point and the mean absolute error (MAE) was calculated (Figure 5.3). Watson & Philip (1985) note the optimal value for IDW power is when the mean absolute error is at its lowest. Therefore, the interpolated ACP data with the lowest MAE per cycle was selected for use in the subsequent analysis.

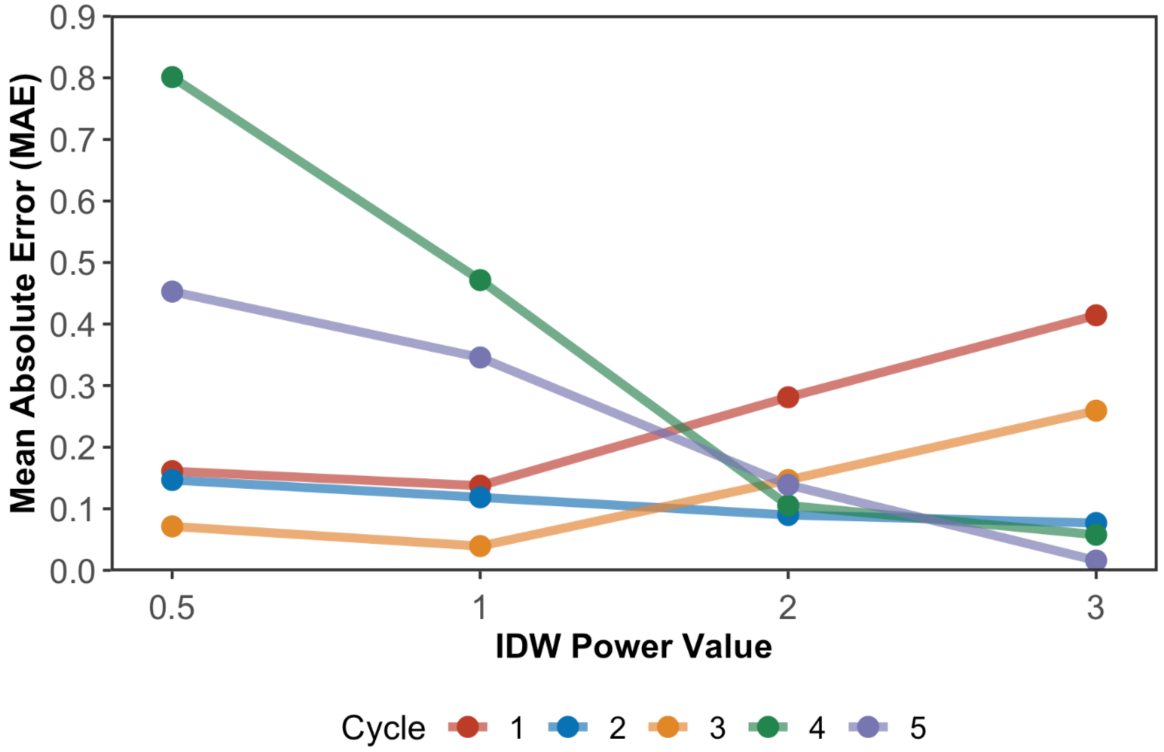


Figure 5.3 Plot showing the mean absolute error (MAE) of ACP values generated during the IDW process for each cycle in California. The power value associated with each MAE for each cycle is: cycle 1; 1, cycle 2; 3, cycle 3; 1, cycle 4; 3, cycle 5; 3.

Another set of predictors investigated was climate data. Shimwela *et al.*, (2018) and Narouei-Khandan *et al.*, (2016) have shown that climate variables are key predictors in the distribution of HLB. Therefore, to investigate whether climate can be used as a predictor in the HLB risk model and eventually transferred, the Worldclim Version 2 dataset at a resolution of 30 arc-seconds (Fick & Hijmans, 2017) was downloaded. This dataset contains the average monthly climate data for minimum, mean, and maximum temperature and precipitation between the years of 1970 and 2000. The main variables shown by Shimwela *et al.*, (2018) and Narouei-Khandan *et al.*, (2016) to contribute to HLB distribution were annual precipitation, precipitation in the wettest month, mean temperature in the driest quarter, and minimum temperature of the coldest month (Narouei-Khandan *et al.*, 2016; Shimwela *et al.*, 2018). So, these four variables were extracted for each of the citrus tree locations in California and Florida. However, these four climate predictors were not used in the final model as outlined in section 5.3.1.

5.2.4 Initial model

Initially, citrus data from Florida was analysed using methods based on those by Parnell *et al.* (2014), where a simple mechanistic model was developed as a generic risk model for plant pathogens. To estimate risk at a given location (i), two parameters were used, firstly the expected local epidemic size if the pathogen were to arrive. This is characterised by the basic reproductive number R_0, defined by Heffernan *et al.*, (2005) as “the expected number of secondary infections arising from a single individual during their entire infectious period”. This is proportional to the expected size of a local invasion or epidemic, therefore widely used in invasion science and plant epidemiology (Anderson & May, 1986). The second parameter is the probability, P, that the pathogen arrives and causes an epidemic at a given location, i.e. an uninfected tree, and is a measure of dispersal within a landscape. Therefore, risk estimation can be calculated as:

$$W_i = R_{0i} \text{ X } P_i$$

This model was developed using RStudio version 1.1.383, firstly by calculating R_0. Due to lack of detailed epidemiological data for HLB, it is not possible to explicitly calculate R_0, however, it has been shown by Parnell *et al.* (2014), that inverse age of a host location is proportional to the basic reproductive number R_0, which was calculated as:

$$R_0 = exp(rT)$$

Bassanezi & Bassanezi (2008) show younger trees to be more infectible, therefore, by reading data from their disease progress curves for HLB in citrus plants of varying ages, the epidemic growth rate (r) could be estimated. T, the generation interval, is known to be proportional to the initial growth rate of an epidemic (Wallinga & Lipsitch, 2007). $T = 5$ was used as a generation time for HLB. Probability of infection, P, was calculated by a dispersal kernel. This was a negative exponential function of the sum of all Euclidean distances from host location i to positive host location j in the previous cycle, with the mean dispersal distance α calculated from the exponent of the kernel shown to be $2/\alpha$: The dispersal kernel below was used:

$$K(\alpha, d_{ij}) = e^{-\alpha dij}$$

Once the model by Parnell *et al.* (2014) had been re-created in R, parameter estimation for α was carried out. Gottwald *et al.*, (2010) note average dispersal distance of ACP as 1.58 km and a relationship between HLB positive tree's up to 3.5 km apart, therefore during parameter estimation, iterations end at a maximum dispersal distance of 3.5 km. The model ran 15 times and the dispersal distance iteratively increased by 250 m, starting at 1 m. For each of the 15 risk estimations, ROC was generated, and AUC calculated to enable comparison between the 15 iterations. Parameter estimation was carried out for cycles 1 – 5, and the best-fit α value for each cycle calculated as the iteration with the highest AUC.

Following parameterisation, the model was used to predict risk of HLB spread in cycles 2 – 6 using the α value from each previous cycle. The performance of these spread models was validated again using ROC and AUC, due to the robustness and versatility of ROC and the ability for AUC to be used to compare performance of different modelling methods. This makes it highly recommended for use in a transferability study such as this (Liu *et al.*, 2011; Jiménez-Valverde, 2012). ROC and AUC were used throughout the process which also ensured consistency.

5.2.5 Distance only model

Data on planting age in California was not available, therefore, the expected local epidemic size (R_0) component of the model had to be changed. Subsequently, a revised version of the risk model was created. This contained only the probability of infection, P, calculated by the dispersal kernel previously outlined, essentially only using distance to predict risk:

$$W_i = P_i$$

The model works on the principle that the closer an uninfected tree (i) is to an infected tree (j), the greater the risk of infection. This is because disease spread is typically localised and relatively predictable, therefore distance is a very good proxy for risk of infection (Gilbert *et al.*, 1994; Gottwald *et al.*, 2010; Hyatt-Twynam *et al.*, 2017). Once again, using the methods previously outlined, parameter estimation was performed on cycles 1 – 5 (Figure 5.4) to find the best-fit parameter value to assign to α. The model was then used to perform risk estimations for cycles 2 – 6 using the newly generated α values from the previous cycle.

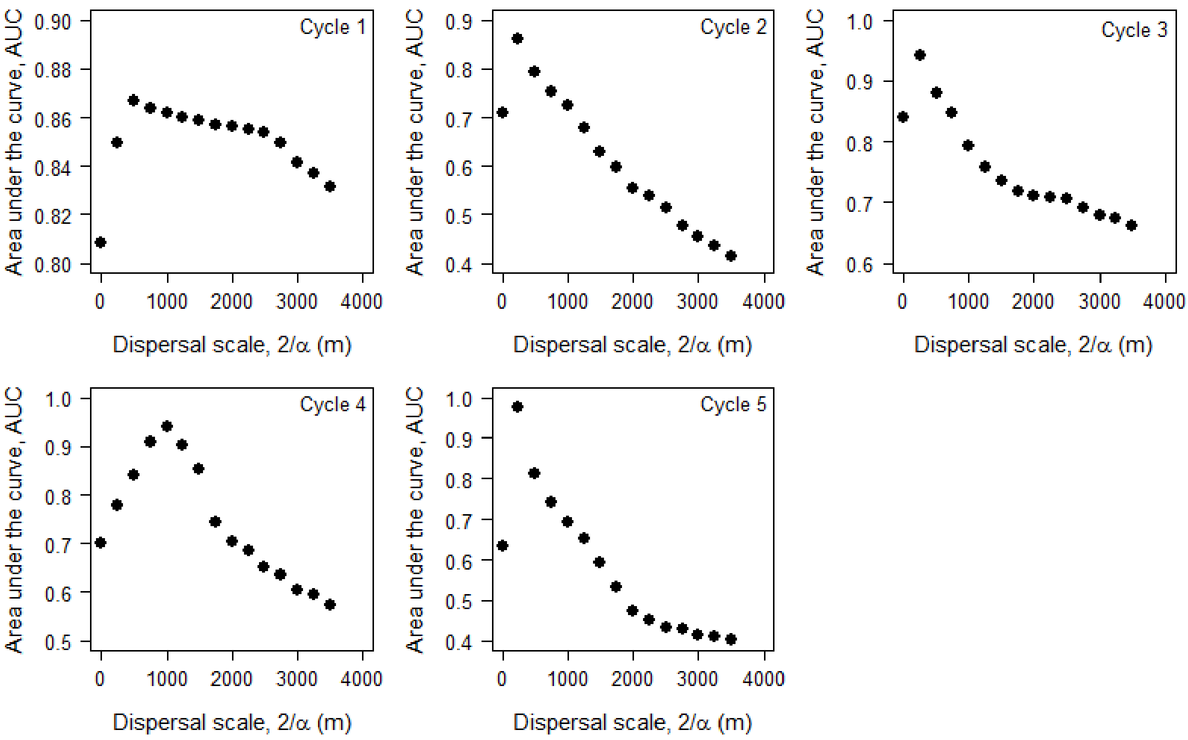


Figure 5.4 The change in area under the curve for ROC, with the mean dispersal distance $2/\alpha$ (m) for sampling cycles 1 – 5: cycle 1, maximum AUC = 0.849, mean dispersal distance, $2/\alpha$ at 500 m; cycle 2, maximum AUC = 0.860, mean dispersal distance, $2/\alpha$ at 250 m; cycle 3, maximum AUC = 0.941, mean dispersal distance, $2/\alpha$ at 250 m; cycle 4, maximum AUC = 0.940, mean dispersal distance, $2/\alpha$ at 1,000 m; cycle 5, maximum AUC = 0.977, mean dispersal distance, $2/\alpha$ at 250 m.

5.2.6 Host density model

To investigate further improvements to the model, additional known predictors of HLB and other plant pathogens were included. Host density has been demonstrated to be a major driver of disease epidemics (Gilbert *et al.*, 1994; Otten & Gilligan, 2006; Plantegenest *et al.*, 2007), therefore citrus tree density was calculated for each grove in Florida and the results rescaled to a range of 0 – 1 to ensure subsequent risk estimations were kept within this range for validation using ROC. The rescaled citrus tree densities were used in the model as the expected local epidemic size (R_0), and the best-fit parameter values (α) previously generated also used, resulting in:

$$W_i = R_{0i} \text{ X } P_i$$

This updated version of the model was then used to perform risk estimations for cycles 2 – 6 using the same methods previously outlined.

5.2.7 Vector density model

Another predictor investigated was vector abundance. Whilst there is not a vast array of literature outlining how vector density impacts plant disease prevalence, studies using other vector borne diseases, namely Malaria, have shown that increases in the vector to host ratio increases prevalence (Dye & Hasibeder, 1986; Focks *et al.*, 2000; Magori & Drake, 2013). This version of the model works in a similar way to the version which included host density as a predictor and is based on the theory that with more vectors there is more inoculum, therefore a greater chance of infection. ACP density was calculated for each grove and again rescaled to a range of 0 – 1 to ensure subsequent risk estimations were kept within this range. The new ACP density values were used in the model following model:

$$W_i = R_{0i} \text{ X } P_i$$

ACP values were used as the expected local epidemic size (R_0), again using the previously generated best-fit parameter values (α). Due to the asymptomatic period of HLB, ranging from months to years (Lee *et al.*, 2015), each cycle (2 to 6) was also tested with the interpolated vector values from previous cycles to account for lag in disease development.

5.2.8 Model transfer

The three updated versions of the model (distance only, host density and vector density) all performed well with high predictive power in Florida. However, the best model, used only distance as a predictor; adding host density and vector density as additional predictors reduced the model's power. Therefore, the version of the HLB risk model that used distance as the only predictor, was used to test transferability. Rather than developing a model and parameterising it in California, the distance only model using the previously calculated best-fit parameter values for α was used to generate risk estimates using the California data. The transferability of the model was tested on each of the three data cycles, using the three best-fit α parameter values and model performance again assessed using ROC and AUC.

5.3 Results

5.3.1 Climate data

Despite the four climate variables being shown as strong predictors of HLB distribution in Florida, the decision was taken not to include these climatic variables in the model. Figure 5.5 compares the four variables in Florida and California and shows considerable differences in climate between the two states. As a rule of thumb, extrapolating into an area with greater than 10% difference tends to yield poor results, and the differences in climate between the two states far exceeds 10% (Thuiller *et al.*, 2004; Sequeira *et al.*, 2018b). Therefore, with differences of this magnitude, the inclusion of climate variables as a predictor would decrease the model's predictive power rather than improve it.

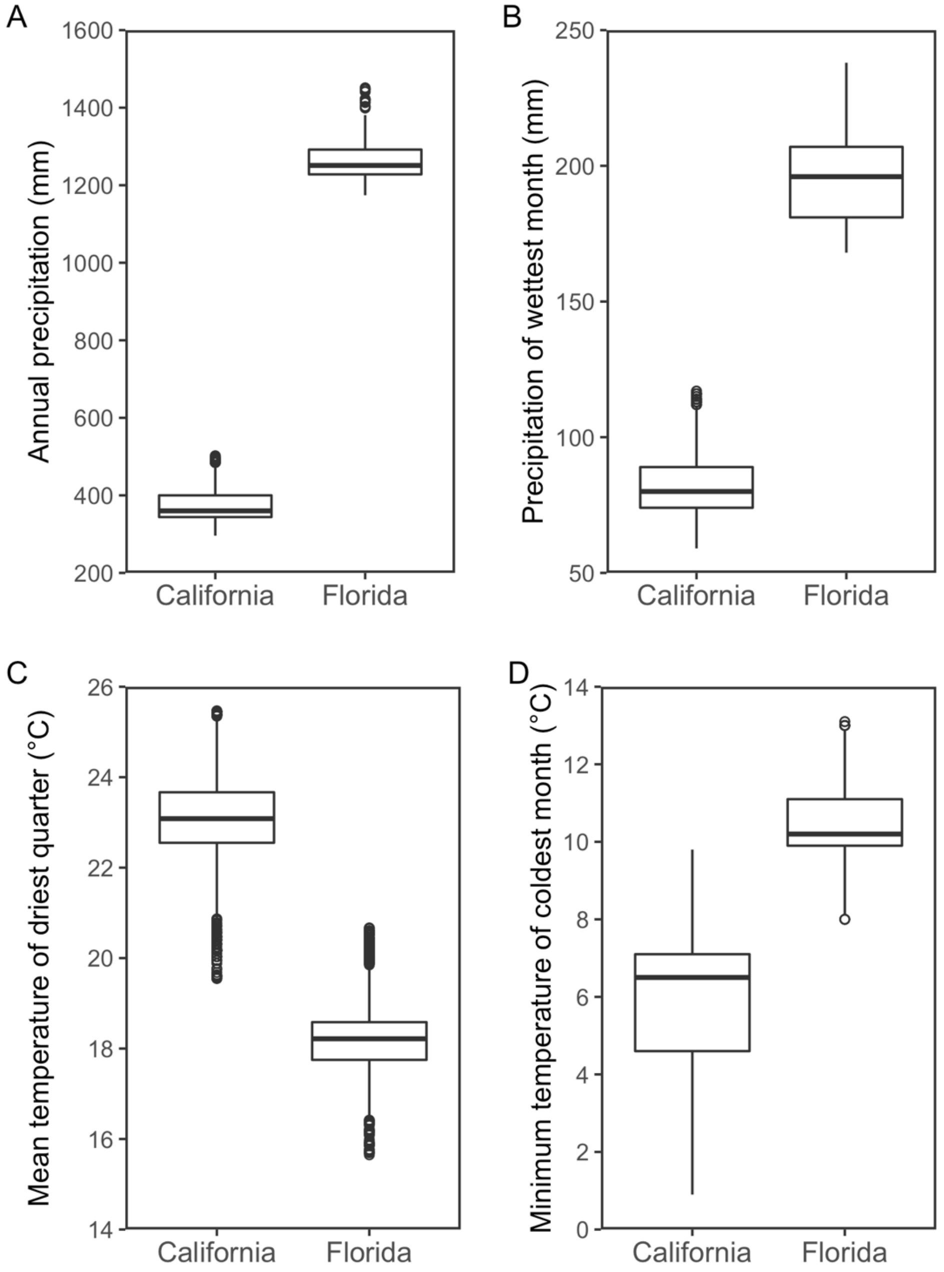


Figure 5.5 Boxplots of the four main climatic variables shown to be predictors of HLB distributions in California and Florida (Narouei-Khandan *et al.*, 2016; Shimwela *et al.*, 2018). A) shows differences in annual precipitation (mm) between the two states. B) shows the total precipitation of the wettest month (mm) for the two states. C) shows

the mean temperature during the driest quarter of the year (^{o}C), and D) shows the minimum temperature of the coldest month (^{o}C).

5.3.2 Distance only model

The distance only model performed well, accurately predicting which trees would become infected (Figure 5.6). This version of the model produced the highest AUC values; cycle 2, AUC = 0.867; cycle 3, AUC = 0.919; cycle 4, AUC = 0.948; cycle 5, AUC = 0.928; cycle 6, AUC = 0.986 (Figure 5.7). This shows performance generally improved through the cycles, with a difference of only 0.119 from the best predictions, cycle 6 and worst, cycle 2. Although performance improved, cycle 5 had a 0.02 lower AUC value than the value generated in cycle 4, however this is a negligible difference and the model still performed well, making accurate predictions for risk of HLB spread.

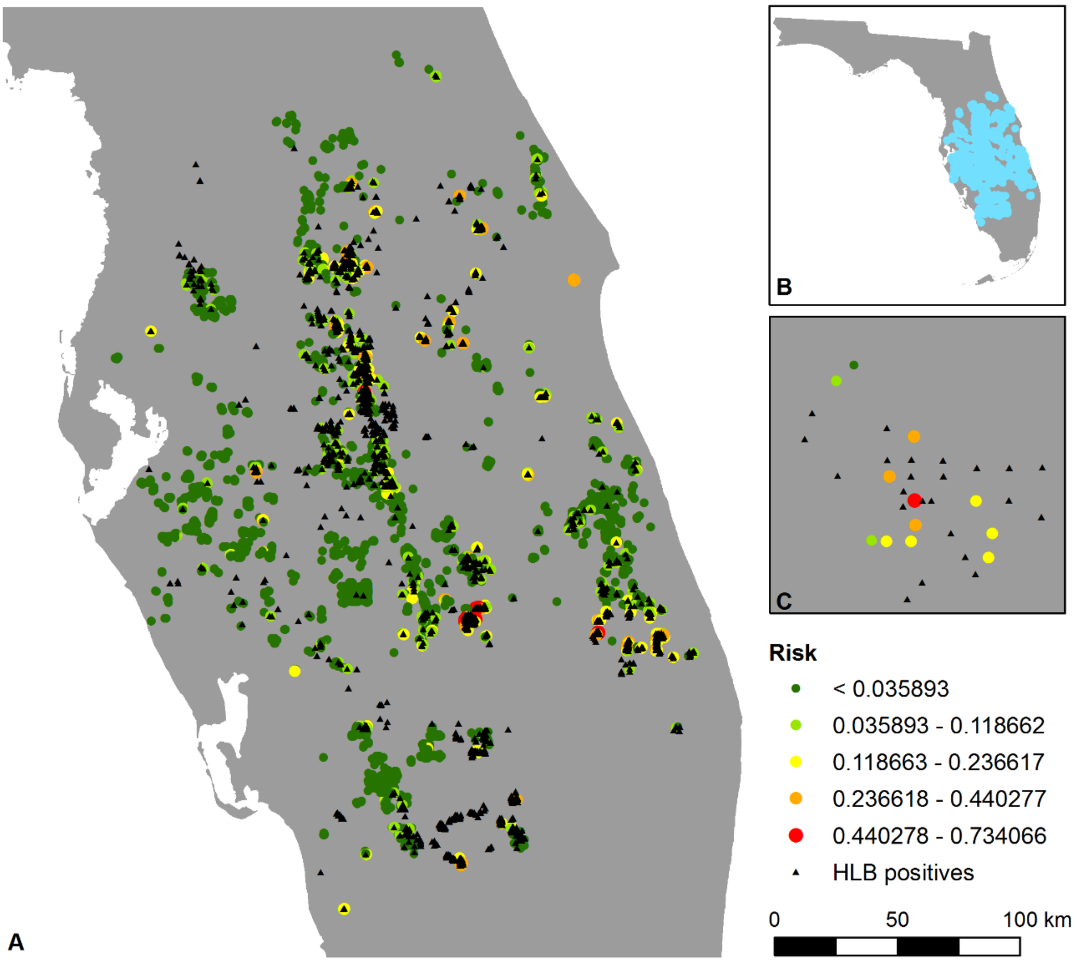


Figure 5.6 Map of risk of HLB spread in Florida, predicted for cycle 6. A) Whole state of Florida with all infected and uninfected trees. B) Position of trees sampled within the state. C) A more detailed image of an area within Florida showing risk of infection predicted from previous cycle positive locations (coloured circles) and actual positive trees in cycle 6 (triangles). For maps of cycles 2 to 5, see Appendix XI.

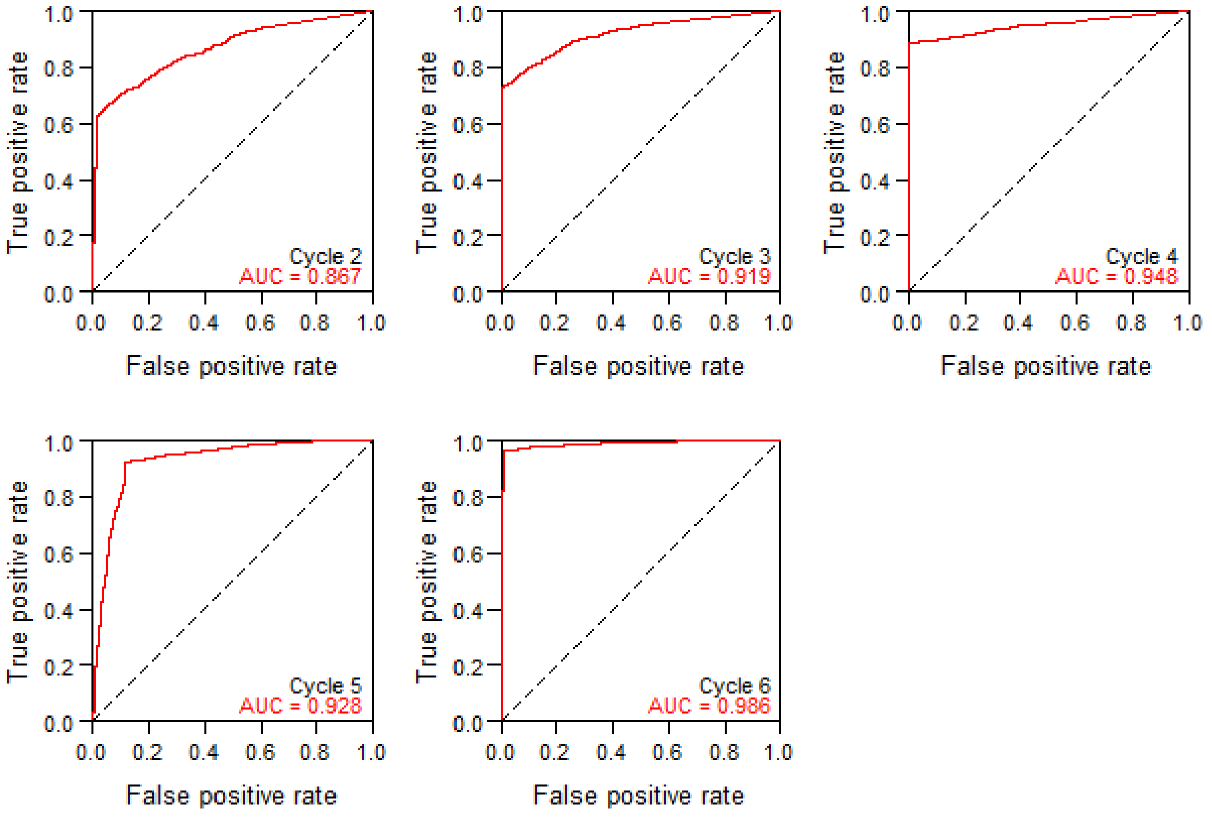


Figure 5.7 Receiver Operator Characteristic (ROC) curves for risk estimates in cycles 2 to 6. The solid red line indicates generated the risk estimate using the dispersal distance calculated in previous cycles. The Area Under the Curve (AUC), is displayed in the bottom right corner of the plot, and the dashed line denotes the no-discrimination line, equalling an AUC of 0.5.

5.3.3 Host density model

This version of the model contained an additional predictor; along with distance, host density (citrus trees) was used. ROC AUC values ranged from 0.865 in cycle 2, to 0.983 in cycle 6 (Table 5.4). Like the distance only model, performance increased through the cycles, again with the AUC of cycle 5, slightly lower than that of cycle 4, but only by 0.2. When comparing to the distance only model, this version using host density offered no improvement in performance, with lower AUC values, albeit only slightly, with an average difference of 0.0018.

Table 5.4 Comparison of Receiver Operator Characteristic (ROC) Area Under the Curve (AUC) values for cycles 2 to 6 using the distance only model and the model that used host density as an additional predictor.

Cycle	**AUC**	
	Dist. only	**Tree Density**
2	0.8669	0.8653
3	0.9192	0.9185
4	0.9484	0.9470
5	0.9281	0.9259
6	0.9862	0.9828

5.3.4 Vector density model

Again, another predictor was added to the distance only model, this time vector density. This was tested in a couple of forms: simply the density of psyllids at the time trees were sampled, corresponding with HLB surveying, and vector density interpolated from previous cycles which was used to investigate the asymptomatic period of HLB. As with previous models, the general trend was an increase in performance, shown by ROC AUC values through the cycles for both actual ACP values and those with a lag period (Table 5.5). Cycle 6 again generated risk estimates with the best performance; AUC ranged between 0.968 and 0.979, however the distance only model gave higher AUC values with 0.986 in cycle 6. Much like the previous host density model, this vector density version offered no improvements in performance to the original distance only model. Although the AUC values were only slightly lower; the model with actual sampled ACP density was on average 0.026 less than the distance only model. Interpolated ACP values offered a small improvement in performance over actual ACP values, but the AUCs were still lower than those from the original model.

Table 5.5 Receiver Operator Characteristic (ROC) Area Under the Curve (AUC) values for cycles 2 to 6, for the distance only model (No ACP), model using ACP density at time of HLB surveys, and ACP density with a lag time, using interpolated ACP densities from previous cycles, indicated by ACP-1, i.e. ACP density from 1 previous cycle, or ACP-5, ACP density from 5 cycles before the current.

Cycle	No ACP	ACP	ACP -1	ACP -2	ACP -3	ACP -4	ACP -5
2	0.8678	0.8654	0.8665	-	-	-	-
3	0.9191	0.9164	0.9176	0.9180	-	-	-
4	0.9500	0.9414	0.9464	0.9468	0.9458	-	-
5	0.9285	0.9126	0.9058	0.9149	0.9195	0.9168	-
6	0.9862	0.9755	0.9755	0.9675	0.9787	0.9792	0.9786

5.3.5 Model transfer

Of the three versions of the model, the most basic, containing distance as the only predictor was transferred to California. The other two versions offered no improvement in predictive performance and were therefore not transferred. ROC curves and subsequent AUC values were generated for each of the three cycles using the three dispersal distances calculated in Florida (Figure 5.8).

As shown in Figure 5.8, AUC values vary without a general trend, unlike when the model was used in Florida. The lowest AUC value was 0.488, in cycle 6 using a dispersal distance of 500 m, whereas the highest AUC value was 0.942 in cycle 5 using a dispersal distance of 250 m. There were consistencies in the AUC values for cycles 4 and 5; cycle 4 values remained low, between 0.600 and 0.633. In contrast, the AUC values for cycle 5 were considerably higher, between 0.926 and 0.942, meaning the predictions in cycle 5 were accurate and the model performed well. The AUC values for cycle 6 varied drastically, with a low of 0.488 and high of 0.602. These values indicate predictive performance was very poor and insufficient to provide useful results. Unlike in Florida where HLB appeared to spread in an outward fashion from existing positive points, the disease in California appears to have new foci each cycle, indicating long distance jumps (Figure 5.9 and Figures A6 – A13 in Appendix XII).

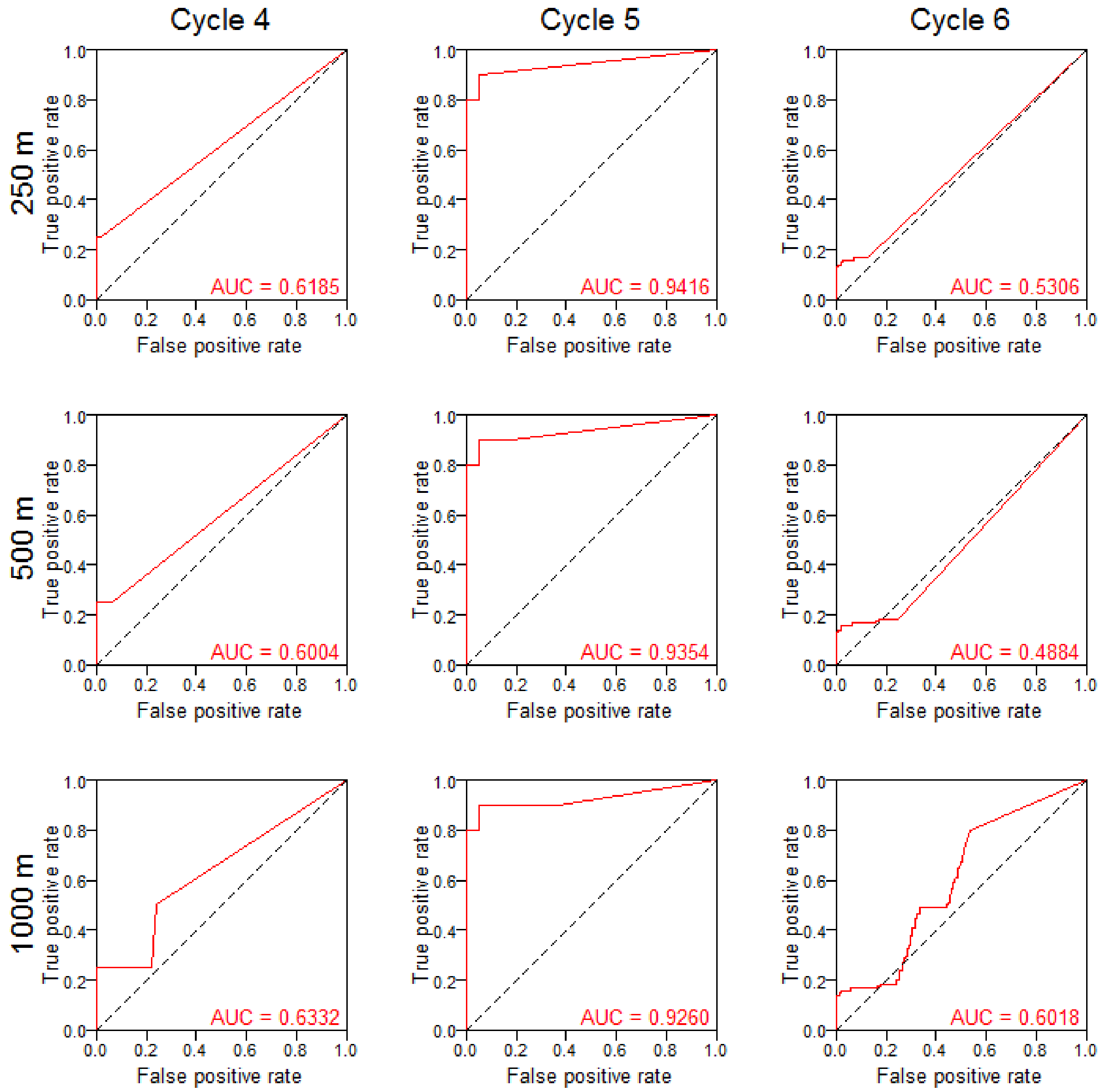


Figure 5.8 Receiver Operator Characteristic (ROC) curves of risk estimates for the three California cycles using the three dispersal distances generated from the Florida data set (250, 500 and 1,000 metres). The solid red line indicates the generated risk estimate using the dispersal distance calculated in previous cycles. The Area Under the Curve (AUC), is displayed in the bottom right corner of the plot, and the dashed line denotes the no-discrimination line, equalling an AUC of 0.5.

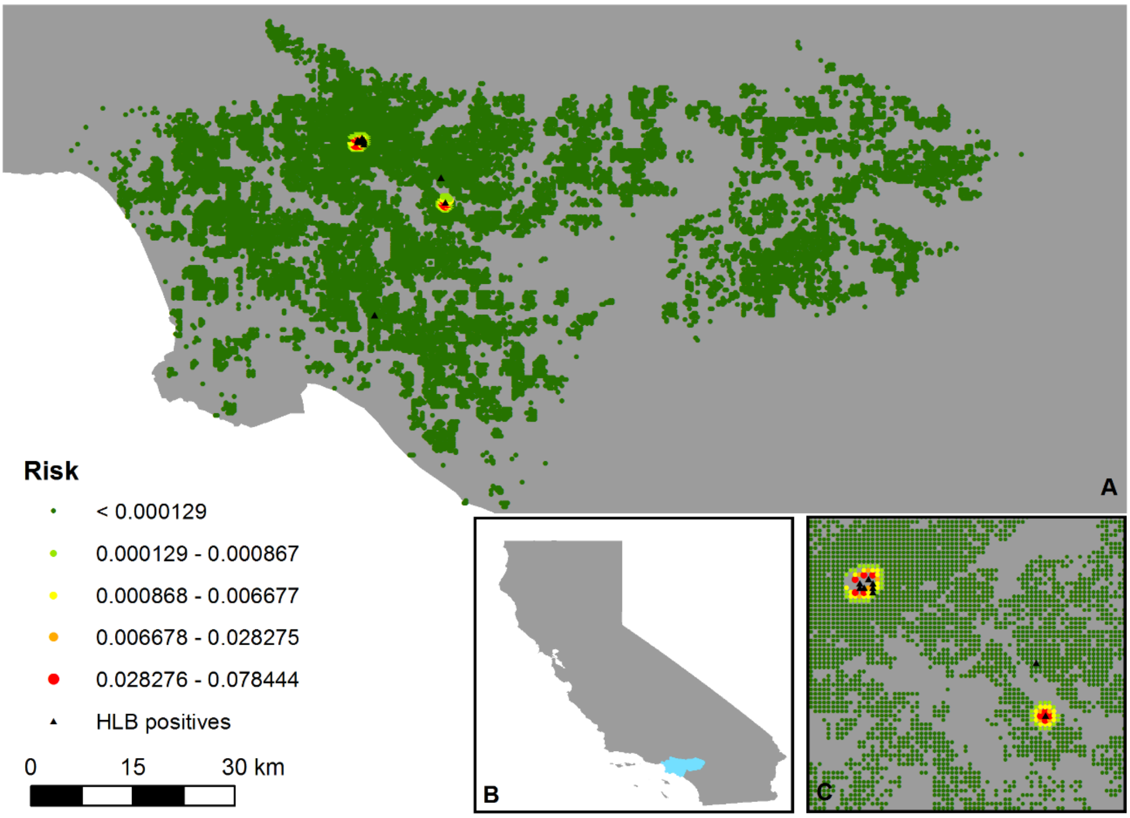


Figure 5.9 Map of risk of HLB spread in California, predicted for cycle 5, using the transferred model from Florida and a dispersal distance parameter of 250 m. A) Shows the area within the LA basin with infected trees and predicted risk. B) Position of trees sampled within the state. C) A more detailed plot of the study area within California, showing risk of infection predicted from previous cycle positive locations (coloured circles) and actual positive trees (triangles). For maps of predicted risk for cycles 4 and 6 and using other dispersal distances, see Appendix XII.

5.4 Discussion

Models were developed in Florida to predict the risk of HLB spread in the state. Three versions were trialled using different predictors: distance to an infected tree, vector density and host density. Climatic variables were also considered but were not used in the final model. The three models created all performed well in Florida, accurately predicting the spread of HLB for all data cycles using the parameterised dispersal distances. The best performing model, using only distance as a predictor, was transferred to California. However, performance dropped considerably and showed inconsistencies between cycles. Accurate predictions were made for data cycle 5 and inaccurate predictions for cycles 4 and 6. The reasons for such results are discussed in more depth in the following section:

5.4.1 Climate variables

Traditional correlative species distribution models are often created using climate variables as predictors. There has been a handful of studies using such methods to show temperature and precipitation as predictors of ACP and HLB distribution (Narouei-Khandan *et al.*, 2016; Shimwela *et al.*, 2018), hence the investigation of such variables in this study. However, as shown by Figure 5.5, there were significant differences in climate variables between Florida and California. The model would have predicted the fundamental niche of ACP, which would have little use (Randin *et al.*, 2006; Qiao *et al.*, 2015), and such differences in climates would have resulted in poor performance when the model was transferred (Sequeira *et al.*, 2018b; Yates *et al.*, 2018). Despite the differences in climate between the two regions, ACP and HLB are present in both, therefore there had to be other drivers of presence, rather than solely climate, hence the further investigation of vector and host density.

5.4.2 Vector density

The model containing vector density as a predictor offered no improvement over the distance only model. AUC values were lower, although only negligibly, therefore this version of the model was not transferred to California, as it is highly likely performance would not improve (Rödder & Lötters, 2010; Wenger & Olden, 2012). Different vector densities were examined, with the actual ACP density recorded at time of HLB surveys, proving to be the worst predictor of HLB spread (lowest AUC values). When investigating ACP movement and the lag time in development of HLB symptoms, results showed the models performed better when using ACP densities from previous cycles, and generally the earlier the better. For example, using ACP densities recorded during cycle 2 to predict HLB for cycle 6 gave the best performance; AUC = 0.973.

Studies have shown the asymptomatic period of HLB to range from ten months up to several years (Gottwald, 2010; Lee *et al.*, 2015), hence investigating ACP as a predictor at various times. Unfortunately, the time between cycle 1 and cycle 6 in Florida was only 9 months, and despite the improved AUC values using ACP densities from previous cycles, perhaps the time period investigated was not enough to truly display the trend. If data were available for two-year period, this would have allowed better investigation into using ACP density as a predictor of disease by possibly covering the time the initial infection happened, rather than when the symptoms developed and would have been represented by the real ACP density at time of infection.

Another potential reason why using ACP density as a predictor did not improve performance could be due to the movement dynamics of the psyllids. Despite their small size, the Asian Citrus Psyllid is a mobile species shown to typically disperse 50 m per day (Gottwald, 2010) and recorded by Lewis-rosenblum (2011) travelling 2 km in 12 days. Under lab conditions, the flight capabilities were tested and showed that ACP were capable of around 50 minutes of continuous flight over 1,241 m (Arakawa & Miyamoto, 2007). Studies have also shown no correlation with the abundance of ACP and wind speed, sunlight, or temperature (Hall & Hentz, 2011) and there appears to be no seasonal variation in ACP spread (Hall & Hentz, 2011; Lewis-rosenblum, 2011). Whilst the distances parameterised for the model fall within the range ACP can fly, there is a lot of variability. This combined with the asymptomatic period of HLB make it hard to accurately know whether there is a relationship between HLB and vector density.

Additionally, different life stages of ACP determine how effective as a vector they are. It has been shown that adult psyllids which only acquired LAS during the adult stage of their life were poor vectors of the pathogen (Inoue *et al.*, 2009; Pelz-Stelinski *et al.*, 2010), requiring a latent period of up to 25 days before the pathogen can be transmitted (Xu *et al.*, 1988). In contrast, adults that acquired the pathogen as nymphs were more effective at transmitting the disease, required no latent period before transmission (Xu *et al.*, 1988; Hall *et al.*, 2013) and interestingly develop faster and are more fecund (Hung *et al.*, 2004; Pelz-Stelinski *et al.*, 2010). With such variability in spread dynamics dependent upon psyllid age, this adds another layer of complexity to the data. Therefore, using vector density as a predictor of disease spread may not be the most effective way of using psyllid data within the model.

Many vector-based plant pathogen models use the vector as a predictor in some form (see; Hartemink *et al.*, 2009; Magori & Drake, 2013; Hebert & Allen, 2016; Cornara *et al.*, 2017). However, in this case, perhaps vector density was the wrong metric due to the uncertainties and variability around the psyllid’s movement dynamics and asymptomatic period of HLB, which made the true vector density at time of infection undetectable and the fact that it only takes one infected psyllid to transmit the disease. Similar studies tend to use the basic reproductive number (R0) as an estimate of risk (Hebert & Allen, 2016), but as there is no accurate estimation for ACP (Parnell *et al.*, 2014; Gottwald & McCollum, 2017), vector density was tested for use instead. Due to the complexity and variation in ACP dynamics proving hard to model for HLB spread, an alternative could be to model the vector in more detail as a proxy for allowing greater depth of parameters influencing ACP to be considered. Consequently, this could produce a model that may accurately predict ACP spread, and as a result, highlight areas at risk of becoming infected with HLB.

5.4.3 Host density

Similar to the model including vector density, using host density as a predictor offered no improvement over the distance only model. AUC values ranged from 0.863 in cycle 2, to 0.983 in cycle 6 but were consistently lower than those generated by the model using distance as the only predictor. Albeit, the values were only negligibly lower, on average 0.0018, and the model still predicted well.

Host density is recognised as key driver of disease epidemics (Otten & Gilligan, 2006; Plantegenest *et al.*, 2007). However, this was not shown in the results from the model. This may be due to the differences in susceptibility to the disease dependent upon citrus tree age; younger trees are more infectious and susceptible (Bassanezi

& Bassanezi, 2008; Gottwald, 2010). Hence when using age a key determinant of R0, Parnell *et al.*, (2014) used varying values for the differing planting ages and this was included in the initial model. But with no planting age information for California, this aspect could not be incorporated

However, what this means, is certain areas are more susceptible to the disease and more infectious than others due to the preference to younger, less waxy and softer leaves not only by ACP (Gottwald *et al.*, 2007), but other insects (Meyer & Montgomery, 1987; Ernest, 1989; Steinbauer *et al.*, 2014) and herbivores (Cerrado *et al.*, 2010). This gives no uniformity in effect of host density on HLB spread across the landscape and by simply using raw density as a predictor in the model, this is not a true reflection of how density impacts disease spread. In an ideal situation, weightings could be added to the plantings based on age, to account for the preference of ACP to the leaves of younger plantings. Saying that, results from this study show respectable AUC values when using density, despite offering no improvement over using distance as the only predictor, which is why this model was not transferred to California.

5.4.4 Distance only model

This version of the model, using distance as the only predictor, performed the best of all three versions, with the highest AUC values generated. These ranged from 0.867 in cycle 2, to 0.986 in cycle 6, and all AUC values are classed as good, with predictions of risk/spread appearing accurate when looking at new locations of infection. It is not surprising distance as a predictor performs well; if a tree is further away than the dispersal distance of ACP, the risk of spread is low. This is a simple but essential predictor, and a large number of plant disease and invasive species models incorporate dispersal distance either on its own or with other variables to predict spread (Suarez *et al.*, 2001; Thein *et al.*, 2012; Hebert & Allen, 2016; Hudgins *et al.*, 2017).

Dispersal distance was incorporated into the initial model by Parnell *et al.* (2014) and was the main predictor of spread. Whilst the actual dispersal distance of ACP is hard to quantify, research shows the maximum distance in ideal conditions (Arakawa & Miyamoto, 2007) but a varying range from other studies (Gottwald, 2010; Lewis-rosenblum, 2011), the parameterisation step during model creation, found which dispersal distance to assign, gave the most accurate results for each cycle. This eliminated the guess work of using dispersal distances outlined in other research and the dispersal distances used (250 m to 1,000 m) fall in line with typical ACP dispersal distance (Gottwald, 2010).

This simple model highlights which trees are within the distance of ACP dispersal and therefore at greatest risk. Such a model is generic and could possibly be used and tested in a variety of locations and situations provided location data and positive and negative disease status data were available. Literature shows that whilst models should be built for each unique situation, simpler models do tend to be more generic or transfer better, however there is also a trade off in predictive accuracy (Evans *et al.*, 2013; Merow *et al.*, 2014). With only one predictor variable this is a simple model able to be used in different situations, and with the excellent performance in Florida (AUC values >0.8), this version was subsequently transferred to California.

5.4.5 Transferred model

When the distance only model was transferred from Florida to California, there did not appear to be any glaringly obvious trends. Results were mixed with AUC values as low as 0.48 and as high as 0.94 depending upon which cycle, and which dispersal distance was used. This subsection explains potential reasons for such results and what should be done in future similar scenarios to ensure high predictive accuracy for similar spread models.

Where the transferred model did not perform well, was when predicting HLB spread for cycles 4 and 6 in California. This is most likely due to the number of HLB positive points and the subsequent spread of the disease to new locations ~25 km from the original HLB positive point in cycles 1 to 3. These long-distance leaps in disease spread could be true natural movement, as Lewis-rosenblum (2011) showed psyllids could travel up to 2 km in just 12 days, therefore 25 km is achievable within a year. However, as Arakawa & Miyamoto (2007) showed the maximum continuous flight of the Asian citrus psyllid to be only 1.2 km, psyllids would have most likely stopped on citrus trees between the positive locations found in cycle cycles 1 – 3 and cycle 4.

Without any additional HLB positive locations and a clustering of the 3 new positive points, it is likely that HLB was spread via other means, such as through the transportation of an infected plant or simply a psyllid unknowingly transported by hitchhiking in or on a vehicle. Such methods of disease spread are increasingly common due to continual movement of people and goods (Wilson, 1995; Kot *et al.*, 1996; Eisenberg *et al.*, 2006). Vannini *et al.* (2010) and Kauffman & Jules (2006) show there is a link between proximity to roads and the long-distance dispersal of a forest pathogens, similarly vectors of human disease such as the fleas, lice, kissing bugs, and mosquitoes have been shown to disperse through human aided transport in vehicles (Lounibos, 2002). With such a vast road network and high reliance on motor vehicles in Los Angeles (Sorensen *et al.*, 2008), it is likely human aided transport of the Asian citrus psyllid is one of the main drivers of HLB within this area.

The underlying reason for the poor transferability of models for cycles 4 and 6 may be primarily due to differences in data between Florida and California despite efforts to standardise the data into a comparable state. Sequeira *et al.* (2018) suggest that some degree of similarity in covariates is required between locations when transferring a model, however the number of long-distance jumps in HLB spread in California does not reflect the same spread dynamic of Florida where spread occurred in an outwardly fashion, hence the model was parameterised for this. Other studies with poor transferability suggest differences in habitat selection, predictors or movement dynamics in the transferred range (Torres *et al.*, 2015; Roach *et al.*, 2017), which has been further confirmed by the differences and poor performance of the transferred model in this study. However, not all transfers with this data were poor, particularly when predicting spread in cycle 5.

If only looking at predictions made for cycle 5 of the transferred model, the high predictive accuracy (AUC values of 0.90 and greater) similar to those in Florida, where the model was trained, indicate the model is transferable. These accurate predictions of HLB spread can be attributed to a couple of factors. Firstly, whilst there was new long-distance spread and foci of disease as in other cycles, there were only two points, and the majority of new infections were spread in an outward fashion from existing infected trees, as was the case in Florida. This allowed the model to perform in the way it was created and the similarity in predictor behaviour between California and Florida allowed accurate predictions and the successful transfer of the model (Sequeira *et al.*, 2018b).

Secondly, the general consensus in the literature seems to be that simple models with few predictors are expected to offer greater transferability (Wenger & Olden, 2012; Merow *et al.*, 2014; García-Callejas & Araújo, 2016). This is somewhat reflected by this study, showing that when data is in a comparable state, the simple model transferred well with high predictive accuracy. However, this is not always the case, Fordham *et al.* (2018) and Evans *et al.* (2013) have shown more complex models can perform better than simple models but this is not the typical case. Whilst there is still some ambiguity with this point, studies do show transferability can be achieved when researchers constrain the complexity of their models based on the attributes of the data and the overall objective of the study (Merow *et al.*, 2014). This was carried out during this study, using only relevant parameters and the model was developed for a specific situation with specific spread dynamics.

Finally, the mechanistic nature of the model enabled the spread dynamic to be captured. Whilst this was shown at best in Florida, the outward spread in cycle 5 of the California dataset also shows this dynamic, particularly without long distance jumps exhibited by the other Californian cycles. Researchers argue that mechanistic models are more transferable due to the predictors used to explain key factors of movement or range shift (Kearney *et al.*, 2010; Fulford *et al.*, 2013), however if the model is not trained correctly, it will not perform well, as exhibited with cycles 4 and 6. Whilst it would have been interesting to compare this mechanistic model to a similar correlative model such as those by Shimwela *et al.*, (2018) and Narouei-Khandan *et al.* (2016), the differences in data between California and Florida would not have allowed for good quality transfers using environmental data as a predictor (Sequeira *et al.*, 2018b).

5.5 Conclusion

This study has shown creating a transferable risk model of an emerging plant disease is difficult, but it is achievable. Modelling a disease, spread by a highly mobile vector presented issues which perhaps could be overcome in future studies by incorporating movement dynamics. However, one of the greatest issues with this study were the differences in data formats, which may have played a role in the poor transferability of models. This is not solely a problem for mechanistic models or those modelling plant disease, but a problem likely to be encountered in any study using different formats of data. Similarly, the low numbers of presence points contributed to the poor performance, therefore using a correlative model that can predict risk using factors other than relying upon disease presence may be worth investigating in future research.

Chapter 6 - General Conclusions

6.1 Transferable models

The use of ecological models has markedly increased in the past two decades and it is now commonplace to find models in conservation biology and ecological research (Srivastava *et al.*, 2019). The insights ecological models can provide into species-environment relationships cannot be achieved by other means, making them a vitally important tool with a wide range of applications (Zimmermann *et al.*, 2010). Ecological models are not only used to explain and predict but are increasingly used to project into novel environments, both spatially and temporally (Randin *et al.*, 2006; Werkowska *et al.*, 2017). Transferring models has been a key focus of research in recent years and can prove beneficial in situations lacking data, such as future climate scenarios (e.g. Dobrowski *et al.*, 2011; Iturbide *et al.*, 2018) or newly invaded areas (e.g. Petitpierre *et al.*, 2017). However, model transferability is a complex and evolving area of research, with little agreement between studies, and transferability seemingly determined on a case-by-case, dependant on a combination of factors (Elith & Graham, 2009). Therefore, unsurprisingly there are contrasting views and many unanswered questions surrounding both the concept and practice of transferring models (Sequeira *et al.*, 2018; Yates *et al.*, 2018).

6.2 Main findings

This research addressed aspects of transferability with little consensus or lacking answers in the literature, with the aim to fill in knowledge gaps. Overall, this thesis demonstrates model transferability can be achieved, but to what degree is dependent upon a range of factors. One such factor and perhaps one of the most studied aspects of model transferability is the long-debated question of which algorithm is “best”. Whilst there are innumerable studies focusing on this (e.g. Elith *et al.*, 2006; Peterson *et al.*, 2007; Shabani *et al.*, 2016; Norberg *et al.*, 2019), it is shown in Chapter 4 and the literature that no single algorithm is best. Instead, I found that the best performing varied depending on the species modelled. Similar findings are reported in the literature, but most notably by Qiao *et al.* (2015) and Norberg *et al.* (2019), who show that there is no single algorithm that performs well in all tasks, and performance is largely due to the characteristics of the species.

Furthermore, data here and in similar studies show particular families of models generally perform better than others. Namely, the newer machine learning based methods outperformed the regression-based and profile methods (see Figures 4.3 to 4.5 and Chapter 4). This ranking of performance by family was also recorded by Elith *et al.* (2006) and is generally agreed upon by other researchers (e.g. Rapacciuolo *et al.*, 2012; Huang & Frimpong, 2016; Shabani *et al.*, 2016). Similarly, it is regarded that an ensemble approach is the best choice, not only due to the high predictive performance and transferability, as shown here (Figures 4.3 and 4.4), but due to the reduction in uncertainty provided by this consensus method (see Araújo & New, 2007; Marmion *et al.*, 2009; Shabani *et al.*, 2016). This aspect of research, exploring how algorithm choice impacts transferability, has not provided new answers to this question, but has provided insight using a new situation, through testing 20 species and 9 algorithms over a regional scale, therefore building on and strengthening existing knowledge.

The areas of research here, offering a novel perspective and answering previously unanswered questions were Chapters 2, 3 and 5. Chapter 2 found the number of background points a model is trained and transferred with has little impact on performance and transferability above a certain threshold, typically equal numbers of background points and presences (Figures 2.1 to 2.4). When the number of background points was lower than presences, models performed poorly, which as suggested by Sequeira *et al.* (2018b), poor performance leads to poor transferability. Whilst similar research investigating the impact of pseudo-absences and background points has been carried out, models weren't transferred (e.g. Barbet-Massin *et al.*, 2012; Iturbide *et* al., 2018a; Liu *et al.*, 2019), however findings in the literature were comparable to the results here. Though results here were consistent across the twenty species modelled, it is unlikely these findings will apply to all situations due to the nature of model transferability, however, this research does provide an important and novel contribution to the transferability literature.

Similarly, the results of Chapter 3 investigated a key concept within the modelling field, examining how the spatial resolution of predictor data impacts model performance and transferability. There have been very few studies specifically investigating this as the main focus particularly in regards to transferability (see Manzoor *et al.*, 2018). However whilst the literature shows contrasting views (Guisan *et al.*, 2007), the consensus appears to be higher resolution data improves model predictive performance (Kaliontzopoulou *et al.*, 2008; Scales *et al.*, 2017). Results here were interesting as when models were used in the area they were trained, the coarse resolution data offered the best performance, however once transferred, fine resolution data provided greater predictive performance (Figure 3.4 and 3.5). The differences in best resolution between the two areas is likely attributed to differences in size of the reference and target areas, environmental gradients and niche similarity (see Baniya *et al.*, 2012; Manzoor *et al.*, 2018), which are Discussed in depth in Chapter 3. These contrasting results would not have been uncovered in a data poor scenario, resulting in the transfer of a model using coarse resolution data and in turn poorer model performance. This highlights the usefulness of studies such as this, providing insights into model transferability that would not have been revealed without such research. Therefore, based on the findings in Chapter 3, it is recommended that where applicable, models are trained and transferred over a range of resolutions to find the most appropriate for the aims of the study and the resolution which provides the greatest predictive performance.

The third novel piece of research was Chapter 5, where the transferability of a simple mechanistic model for plant pathogens was transferred and investigated for the emerging citrus disease, HLB. While model transferability was achieved here, it was not consistent across all situations (Figure 5.8). The poor transferability experienced was not due to the model itself; Kearney *et al*. (2010) and Shabani *et al.* (2016) show high transferability of mechanistic models on par with correlative models. Although the model used here, created by Parnell *et al.* (2014) had the ability to be highly transferable through the use of few but generic predictors, the data used impeded transferability through differences in format and the differences in stages of the epidemic between the two regions. Whilst the ideal results would have shown high transferability and this model could have been transferred to an emerging hotspot of HLB in Europe (Massimino *et al.*, 2017), that was not the case. However, this chapter did highlight the importance of similarities in situation and data between the target and reference areas to allow high transferability.

The research chapters here have shown user-controlled factors such as algorithm choice and data resolution do influence transferability. However, the greatest aspects determining transferability and common to the four research chapters were the species modelled, underlying idiosyncrasies in the data and niche similarity between reference and target areas. Of these, arguably the biggest and the one that is gathering much attention is whether transferability is taxon or trait specific. Chapters 2 to 4 show certain taxonomic groups transferred considerably better than others, which has been observed by other researchers (see Rapacciuolo *et al.*, 2012), however other researchers have investigated the traits of taxa and shown that to be the influence on transferability (e.g. Dobrowski *et al.*, 2011; Moran-ordonez *et al.*, 2017). Whilst this was not specifically investigated here, this research does show transferability is highly influenced by the species being modelled and further research into this is needed, as suggested by Yates *et al.* (2018).

Arguably, the differences observed between species may have been caused by idiosyncrasies in the data or ultimately data quality as described in each chapter, which has been shown to be a major driver of model performance (Aubry *et al.*, 2017). Whilst data quality is a relatively subjective measure, aspects such as the correct identification of species and positioning of occurrences can be indicators of the quality, which were addressed in the data here. Similarly, another driver of transferability and perhaps the biggest cause of poor transferability in the models here were differences in the data. Whether that was niche similarity (Chapters 2 to 5), environmental equilibrium (Chapter 2 to 4) or as previously expressed, differences in the stage of the epidemic (Chapter 5).

Overall, when transferring models, there are a lot of factors to consider; not only the aspects the modeller has control over, but unconscious choices relating to data quality that will influence transferability. Transferring models is a complex task with no clear solution in all situations, however decisions made can make the difference between great and poor model transfers. Ultimately, this research has not only shown how to improve model performance and transferability through the choice of algorithm and resolution, but it has also shown that typically overlooked aspects can impact transferability. Additionally, the insights here have shown that poor performance in the area the model was created will generally result in poor transferability, therefore only models performing well in the reference area should be transferred, which has also been suggested in other studies (e.g. Werkowska *et al.*, 2017; Sequeira *et al.*, 2018b). This research was performed using a range of species and modelling algorithms and provides robust answers and insights into knowledge gaps facing model transfers, highlighting the importance of studies such as this. Furthermore, this research shows the importance of sensitivity analysis in finding the optimum settings for transferring models. However, when this is not possible, modellers should transfer multiple models using a combination of algorithms and other factors to reduce uncertainty and increase the likelihood of finding a highly transferable solution.

6.3 Challenges and limitations

As with all studies, there were challenges and limitations here. One of the main challenges was associated with data quality and differences in data format between reference and target areas. Aubry *et al.* (2017) have shown data quality to be amongst the most important factors in determining the performance of ecological models, similarly, Engler *et al.* (2004) show data quality should be prioritised over quantity. However, to acquire the volume species occurrence data used in Chapters

2 to 4, an open access online repository was the only solution, and whilst efforts were made to remove erroneous and inaccurate records, thus improving quality, it is likely some were missed. Additionally, the occurrence data had been collected by various organisations and through different surveys, therefore methods of recording varied particularly between reference and target areas and may have had influence on the performance and transferability of models. This is most apparent in Chapter 5, with the different formats of HLB data due to differences in spread and different stages of the epidemic where the model transferred to California could not capture this as it was different from Florida where it was parameterised. Data quality and differences such as this are a reoccurring issue not only in transferability studies but for ecological modelling in general (see Randin *et al.*, 2006; Wiens *et al.*, 2009; Yates *et al.*, 2018)

The second challenge with this research were the underlying issues and challenges associated with model transferability as Yates *et al.* (2018) outline. Namely, how to account for non-stationarity, non-analogue conditions, uncertainty and whether transferability is attributed to the taxa, their traits, the choice of algorithm or data quality. Whilst in this study, the aim was to focus on fundamental aspect of modelling such as how the number of background points, predictor resolution and algorithm choice impact performance, the challenges outlined by Yates *et al.* (2018) were undoubtedly encountered. For example, models of *L. timidus* transferred poorly due to differences in niche between reference and target areas, and the choice of algorithm was clearly shown to impact performance. However, attributing the differences in performance observed in the research chapters to one particular aspect, such as data quality or the traits of a species was not possible here. Although, developing such methods, primarily to measure and account for this uncertainty and challenges could be an interesting area of research for future studies.

6.4 Future directions

Since transferability is an evolving area of research with answers needed and theories tested per situation, there will never be a one answer fits all solution. Therefore, to move the subject area forward and continue to provide applicable best practice advice, studies such as this should continue to be performed, providing insight into the limitations and successes with transferring models, particularly when new methods and techniques become available. In addition, to increase comparability between studies, standardised reporting should be carried out, such as the use of the ODMAP protocol, produced by Zurell *et al.* (2020). This comprehensive reporting protocol requires information on the data and methods of a study and the use of the protocol will no doubt increase transparency of research, thus further providing comparability and accessibility to studies.

One of the area’s most in need of research and standardisation is the assessment of model transferability. Currently a wide range of metrics are used in studies; Sequeira *et al.* (2018b) list 17 different assessment methods used in transferability research, however, which is best is a contentious topic (see Allouche *et al.*, 2006; Leroy *et al.*, 2018; Warren *et al.*, 2020) as there are benefits and downsides to all these metrics. Ultimately which is used, should be based on the suitability for the research being undertaken, the data used, the suitability for the situation and the modellers preference, hence the use of AUC here. However, such variation in assessment metrics does not allow for easy comparison between studies. Therefore, standardised assessments are needed to facilitate comparison of transferability, thereby increasing transparency and in turn provide more meaningful insights from research such as this, into the successes, issues and challenges facing model transfers.

Similarly, an area in much need of further research is how to calculate and communicate uncertainty. This is not only the uncertainty that arises from the results of a projection into the unknown, but the inherent uncertainty in methodology, such as the species recorded and sampling method, data quality, environmental equilibrium and niche similarity, predictor choice and modelling approach (Evans, 2012; Heikkinen *et al.*, 2012). Some of this uncertainty, however, can be assessed with certain programmes such as ‘usdm’ developed by Naimi (2017) which provides tools to assess positional uncertainty and multicollinearity for example and 'mopa' developed by Iturbide *et al.* (2018a), which allows the quantification of the contribution of different sources of variability in SDMs. Additionally, the package ‘dsmextra’ developed by Bouchet *et al.*, (2020), provides a tool to measure the degree of extrapolation between reference and target areas, quantifying environmental similarity thus reducing uncertainty. Whilst for this research, visualisations were created to view the degree of similarity in environmental conditions between Britain and Ireland, it would have been useful to quantify this using ‘dsmextra’.

Furthermore, uncertainty can be minimised through the use of specific modelling approaches such as the use of the ensemble approach used in Chapter 4 (see, Araújo *et al.*, 2005; Beale & Lennon, 2012; Swanson *et al.*, 2013), these methods typically only measure uncertainty for the area the model was created. Measuring uncertainty in novel environments is significantly more challenging, hence the lack of studies focusing on this area. However, a standard protocol is needed for measuring and reporting on the uncertainty surrounding model transfers which would again increase clarity of studies performed. Regardless, when transferring models in data deficient situations, there will always be a high degree of uncertainty as results will never be truly verifiable, regardless of methods for checking niche similarity (Mesgaran *et al.*, 2014) and performing cross-validation during the model training (Wenger & Olden, 2012).

There are many future directions for transferability research to take and many questions that still need answering (see Yates *et al.*, 2018). However, for research in this field to progress, the key aspects previously discussed (assessment of transferability and uncertainty) need standardising to enable the direct comparison of future studies. Whilst there is research aiming to tackle this (see Sequeira *et al.*, 2018b; Bouchet *et al.*, 2020; Zurell *et al.*, 2020), such recommendations need to be adopted by a large number of peers for the benefits to become apparent, leading to greater transparency and understanding from theoretical studies such as this, which will in turn provide greater utility to transferable models in conservation research.

6.5 Final conclusions

Transferring models is a complex concept of ecological modelling with no definitive answers; however, it has been shown here that model transferability can be achieved. Whilst studies such as this, transferring to test theories, provide insight into problems encountered, methods used and recommendations for transferability, it is highly unlikely the findings will be relevant in all situations. Therefore, when transferring models by necessity, i.e. for reasons of data deficiency, and using recommendations from theory studies such as this, caution should be taken. That being said, the findings here and consensus in the literature show specific modelling approaches i.e. machine learning methods and ensembles do provide greater performance and higher transferability. Similarly, results here show the number of background points a model is trained with has little impact on performance and transferability above a certain threshold, typically in equal number to presences. However, other factors such as resolution and model complexity should be determined by the aims of the study, as these will highly influence performance and transferability. If possible, a range of modelling approaches and resolutions should be used, providing a range of results, and decreasing uncertainty. Nevertheless, there will always be uncertainty when transferring models to novel environments, especially when there is no way of truthing results and data are gathered from separate sources and in different formats. However, by following best practice and recommendations from research such as this, high transferability may be achievable.

Bibliography

Aguirre-Gutiérrez, J., Carvalheiro, L. G., Polce, C., van Loon, E. E., Raes, N., Reemer, M. and Biesmeijer, J. C. 2013 Fit-for-Purpose: Species Distribution Model Performance Depends on Evaluation Criteria - Dutch Hoverflies as a Case Study, *PLoS ONE*, 8(5). doi: 10.1371/journal.pone.0063708.

Aho, K., Derryberry, D. and Peterson, A.T. 2014 Model selection for ecologists : the worldviews of AIC and BIC, *Ecology*, 95(3), pp. 631–636. doi: 10.2307/43495189.

Alin, A. 2010 Multicollinearity, *Wiley Interdisciplinary Reviews: Computational Statistics*, 2(3), pp. 370–374. doi: 10.1002/wics.84.

Allouche, O., Tsoar, A. and Kadmon, R. 2006 Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS), *Journal of Applied Ecology*, 43(6), pp. 1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x.

Anderson, R. M. and May, F. R. S. 1986 The invasion, persistence and spread of infectious diseases within animal and plant communities, *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 314(1167), pp. 533 LP – 570. Available at: http://rstb.royalsocietypublishing.org/content/314/1167/533.abstract.

Angelieri, C. C. S., Adams-Hosking, C., Paschoaletto, K. M., De Barros Ferraz, M., De Souza, M. P. and McAlpine, C. A. 2016 Using species distribution models to predict potential landscape restoration effects on puma conservation, *PLoS ONE*, 11(1), pp. 1–18. doi: 10.1371/journal.pone.0145232.

Arakawa, K. and Miyamoto, K. 2007 Flight ability of Asiatic citrus psyllid, Diaphorina citri Kuwayama (Homoptera; Psyllidae), measured by a flight mill, *Research Bulletin of the Plant Protection Service (Japan)*.

Araújo, M. B., Whittaker, R. J., Ladle, R. J. and Erhard, M. 2005 Reducing uncertainty in projections of extinction risk from climate change, *Global Ecology and Biogeography*, 14(6), pp. 529–538. doi: 10.1111/j.1466-822X.2005.00182.x.

Araújo, M. B. and Guisan, A. 2006 Five (or so) challenges for species distribution modelling, *Journal of Biogeography*, 33(10), pp. 1677–1688. doi: 10.1111/j.1365-2699.2006.01584.x.

Araújo, M. B. and New, M. 2007 Ensemble forecasting of species distributions, *Trends in Ecology and Evolution*, 22(1), pp. 42–47. doi: 10.1016/j.tree.2006.09.010.

Araújo, M. B. and Townsend, P. A. 2012 Uses and misuses of bioclimatic envelope modeling, *Ecology*, 93(7), pp. 1527–1539.

Asal, F. F. F. 2014 Investigating the Effects of Changing the IDW Power on the Quality of the Generated Digital Elevation Models, *International Journal of Research Studies in Science, Engineering and Technology*, 1(1), pp. 33–42.

Aubry, K. B., Raley, C. M. and Mckelvey, K. S. 2017 The importance of data quality for generating reliable distribution models for rare, elusive, and cryptic species, *PLoS ONE*, 12(6), pp. 1–17.

Austin, M. P. and Van Niel, K. P. 2011 Improving species distribution models for climate change studies: Variable selection and scale, *Journal of Biogeography*, 38(1), pp. 1–8. doi: 10.1111/j.1365-2699.2010.02416.x.

Bahar, A. and Mao, X. 2004 Stochastic delay Lotka–Volterra model, *Journal of Mathematical Analysis and Applications*, 292, pp. 364–380. doi: 10.1016/j.jmaa.2003.12.004.

Balangcod, A. K. D. 2011 Predicting distribution of Lilium philippinense (Liliaceae) over Luzon’s Cordillera Central Range, Philippines, using ArcGIS Geostatistical Analyst, 63, pp. 409–423.

Bamford, A. J., Monadjem, A., Anderson, M. D., Anthony, A., Borello, W. D., Bridgeford, M., Bridgeford, P., Hancock, P., … Hardy, I. C. W. 2009 Trade-offs between specificity and regional generality in habitat association models: a case study of two species of African vulture, *Journal of Applied Ecology*, 46, pp. 852–860. doi: 10.1111/j.1365-2664.2009.01669.x.

Baniya, C. B., Solhøy, T., Gauslaa, Y. and Palmer, M. W. 2012 Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet, *Folia Geobotanica*, 47(2), pp. 135–151. doi: 10.1007/s12224-011-9113-x.

Barbet-Massin, M., Rome, Q., Villemant, C. and Courchamp, F. 2018 Can species distribution models really predict the expansion of invasive species?, *PloS one*, pp. 1–14. doi: 10.1111/ecog.02841.We.

Barbet-Massin, M. and Jetz, W. 2014 A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling, *Diversity and Distributions*, 20(11), pp. 1285–1295. doi: 10.1111/ddi.12229.

Barbet-Massin, M., Jiguet, F., Helene Albert, C. and Thuiller, W. 2012 Selecting pseudo-absences for species distribution models: how, where and how many?, *Methods in Ecology and Evolution*, 3, pp. 327–338. doi: 10.1111/j.2041-210X.2011.00172.x.

Bassanezi, R. B. and Bassanezi, R. C. 2008 An approach to model the impact of Huanglongbing on citrus yield, *Proceedings of the International Research Conference on Huanglongbing (Orlando, Florida*, pp. 3–5.

Battini, N., Farías, N., Giachetti, C. B., Schwindt, E. and Bortolus, A. 2019 Staying ahead of invaders: Using species distribution modeling to predict alien species’ potential niche shifts, *Marine Ecology Progress Series*, (January 2020), pp. 127–140. doi: 10.3354/meps12878.

Beale, C. M. and Lennon, J. J. 2012 Incorporating uncertainty in predictive species distribution modelling, *Philosophical Transactions of the Royal Society B*, 367, pp. 247–258. doi: 10.1098/rstb.2011.0178.

Beaumont, L. J., Graham, E., Duursma, D. E., Wilson, P. D., Cabrelli, A., Baumgartner, J. B., Hallgren, W., Esperón-Rodríguez, M., … VanDerWal, J. 2016 Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges?, *Ecological Modelling*. Elsevier B.V., 342, pp. 135–146. doi: 10.1016/j.ecolmodel.2016.10.004.

Beck, K. G., Zimmerman, K., Schardt, J. D., Stone, J., Lukens, R. R., Reichard, S., Randall, J., Cangelosi, A. A., … Thompson, J. P. 2008 Invasive Species Defined in a Policy Context: Recommendations from the Federal Invasive Species Advisory Committee, *Invasive Plant Science and Management*, 1(December), pp. 414–421. doi: 10.1614/IPSM-08-089.1.

Bell, D. M. and Schlaepfer, D. R. 2016 On the dangers of model complexity without ecological justification in species distribution modeling, *Ecological Modelling*. Elsevier B.V., 330, pp. 50–59. doi: 10.1016/j.ecolmodel.2016.03.012.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M. and Courchamp, F. 2013 Will climate change promote future invasions?, *Global Change Biology*, 19(12), pp. 3740–3748. doi: 10.1111/gcb.12344.

Bhattacharya, M. 2013 Machine Learning for Bioclimatic Modelling, *International Journal of Advanced Computer Science and Applications*, 4(2), pp. 1–8. doi: 10.14569/ijacsa.2013.040201.

Bird, T. J., Bates, A. E., Lefcheck, J. S., Hill, N. A., Thomson, R. J., Edgar, G. J., Stuart-smith, R. D., Wotherspoon, S., … Frusher, S. 2014 Statistical solutions for error and bias in global citizen science datasets, *Biological Conservation*. Elsevier Ltd, 173, pp. 144–154. doi: 10.1016/j.biocon.2013.07.037.

Bogosian, V., Hellgren, E. C., Sears, M. W. and Moody, R. W. 2012 High-resolution niche models via a correlative approach: Comparing and combining correlative and process-based information, *Ecological Modelling*. Elsevier B.V., 237–238, pp. 63–73. doi: 10.1016/j.ecolmodel.2012.04.017.

Booth, T. H., Nix, H. A., Busby, J. R. and Hutchinson, M. F. 2014 Bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies, *Diversity and Distributions*, 20(1), pp. 1–9. doi: 10.1111/ddi.12144.

Bouchet, P. J., Miller, D. L., Roberts, J. J., Mannocci, L., Harris, C. M. and Thomas, L. 2020 dsmextra: Extrapolation assessment tools for density surface models, *Methods in Ecology and Evolution*, 2020(May), pp. 1–6. doi: 10.1111/2041-210X.13469.

Bouchet, P., Peterson, A.T., Zurell, D., Dormann, C., Schoeman, D., Ross, R., Snelgrove, P., Sequeira, A., Whittingham, M., Wang, L. and Rapacciuolo, G., 2019. Better model transfers require knowledge of mechanisms.

Bouzahar, F. H., Ouerdachi, L., Keblouti, M. and Seddiki, A. 2018 The contribution of remote sensing in hydraulics and hydrology, analysis and evaluation of digital terrain model for flood risk mapping, *Journal of Water and Land Development*, 39(1), pp. 17–26. doi: 10.2478/jwld-2018-0055.

Bové, J. M. 2006 Huanglongbing: A Destructive, Newly-Emerging, Century-Old Disease of Citrus, *Journal of Plant Pathology*, 88, pp. 7–37.

Boyce, M. S. 2006 Scale for resource selection functions, *Diversity and Distributions*, 12(3), pp. 269–276. doi: 10.1111/j.1366-9516.2006.00243.x.

Breiman, L. 2001 Random forests, *Machine Learning*, 45, pp. 5–32.

Brooks-Pollock, E., Roberts, G. O. and Keeling, M. J. 2014 A dynamic model of bovine tuberculosis spread and control in Great Britain, *Nature*. Nature Publishing Group, 511(7508), pp. 228–231. doi: 10.1038/nature13529.

Brotons, L., Thuiller, W., Araújo, M. B. and Hirzel, A. H. 2004 Presence absence versus presence-only modelling methods for predicting bird habitat suitability, *Ecography*, 27(4), pp. 437–448. doi: 10.1111/j.0906-7590.2004.03764.x.

Brown, J. L. and Yoder, A. D. 2015 Shifting ranges and conservation challenges for lemurs in the face of climate change, *Ecology and Evolution*, 5(6), pp. 1131–1142. doi: 10.1002/ece3.1418.

Brown, N., Vanguelova, E., Parnell, S., Broadmeadow, S. and Denman, S. 2018 Predisposition of forests to biotic disturbance: Predicting the distribution of Acute Oak Decline using environmental factors, *Forest Ecology and Management*. Elsevier, 407(October 2017), pp. 145–154. doi: 10.1016/j.foreco.2017.10.054.

Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J. and Sears, M. W. 2010 Can mechanism inform species' distribution models?, *Ecology Letters*, 13(8), pp. 1041–1054. doi: 10.1111/j.1461-0248.2010.01479.x.

Bucklin, D. N., Basille, M., Benscoter, A. M., Brandt, L. A., Mazzotti, F. J., Romañach, S. S., Speroterra, C. and Watling, J. I. 2015 Comparing species distribution models constructed with different subsets of environmental predictors, *Diversity and Distributions*, 21(1), pp. 23–35. doi: 10.1111/ddi.12247.

Byrt, T., Bishop, J. and Carlin, J. B. 1993 Bias, prevalence and kappa, *Journal of Clinical Epidemiology*, 46(5), pp. 423–429. doi: 10.1016/0895-4356(93)90018-V.

Candela, L., Castelli, D., Coro, G., Pagano, P. and Fabio, S. 2010 Species Distribution Modeling in the Cloud, *Concurrency Computation Practice and Experience*, 22(6), pp. 685–701. doi: 10.1002/cpe.

Capinha, C., Essl, F., Seebens, H., Pereira, H.M. and Kühn, I., 2018. Models of alien species richness show moderate predictive accuracy and poor transferability. *NeoBiota*, *38*, p.77.

Carboneras, C., Genovesi, P., Vilà, M., Blackburn, T. M., Carrete, M., Clavero, M., D'hondt, B., Orueta, J. F., … Wynde, R. 2017 A prioritised list of invasive alien species to assist the effective implementation of EU legislation, *Journal of Applied Ecology*, (August 2017), pp. 1–9. doi: 10.1111/1365-2664.12997.

Cerrado, D., Gonçalves-alvim, S. J. and Lana, T. C. 2010 Growth, defense and herbivory on young leaves of Qualea parvifl ora (Vochysiaceae) in three different Cerrado habitats, *Neotropical Biology and Conservation*, 5(2), pp. 86–92. doi: 10.4013/nbc.2010.52.03.

Chakraborty, S. and Newton, A. C. 2011 Climate change, plant diseases and food security: An overview, *Plant Pathology*, 60(1), pp. 2–14. doi: 10.1111/j.1365-3059.2010.02411.x.

Chefaoui, R. M. and Lobo, J. M. 2008 Assessing the effects of pseudo-absences on predictive distribution model performance, *Ecological Modelling*, 210(4), pp. 478–486. doi: 10.1016/j.ecolmodel.2007.08.010.

Chen, Y., Chen, L. and Stergiou, K. I. 2003 Impacts of data quantity on fisheries stock assessment, *Aquatic Sciences*, 65, pp. 92–98.

Christmas, S.E., Halton, W.J., Brides, K. and Sharp, S.P., 2010. Predominantly northward dispersal of Grey Herons Ardea cinerea from a heronry in Greater Manchester, UK. Ringing & Migration, 25(1), pp.52-55.

Chunco, A. J., Phimmachak, S., Sivongxay, N. and Stuart, B. L. 2013 Predicting Environmental Suitability for a Rare and Threatened Species (Lao Newt, Laotriton laoensis) Using Validated Species Distribution Models, *PLoS ONE*, 8(3). doi: 10.1371/journal.pone.0059853.

Connor, T., Hull, V., Viña, A., Shortridge, A., Tang, Y., Zhang, J., Wang, F. and Liu, J. 2018 Effects of grain size and niche breadth on species distribution modeling, *Ecography*, 41(8), pp. 1270–1282. doi: 10.1111/ecog.03416.

Copping, J. P., Stewart, B. D., McClean, C. J., Hancock, J. and Rees, R. 2018 Does bathymetry drive coastal whale shark (Rhincodon typus) aggregations?, *PeerJ*, 6, p. e4904. doi: 10.7717/peerj.4904.

Cornara, D., Saponari, M., Zeilinger, A. R., de Stradis, A., Boscia, D., Loconsole, G., Bosco, D., Martelli, G. P., … Porcelli, F. 2017 Spittlebugs as vectors of Xylella fastidiosa in olive orchards in Italy, *Journal of Pest Science*. Springer Berlin Heidelberg, 90(2), pp. 521–530. doi: 10.1007/s10340-016-0793-0.

Court, C. D., Hodges, A. W., Rahmani, M. and Spreen, T. H. 2017 *Economic Contributions of the Florida Citrus Industry in 2015-16*. Gainesville, Florida.

Craig, A. P., Cunniffe, N. J., Parry, M., Laranjeira, F. F. and Gilligan, C. A. 2018 Grower and regulator conflict in management of the citrus disease Huanglongbing in Brazil: A modelling study, *Journal of Applied Ecology*, (July 2017), pp. 1956–1965. doi: 10.1111/1365-2664.13122.

Crimmins, S. M., Dobrowski, S. Z. and Mynsberge, A. R. 2013 Evaluating ensemble forecasts of plant species distributions under climate change, *Ecological Modelling*. Elsevier B.V., 266(1), pp. 126–130. doi: 10.1016/j.ecolmodel.2013.07.006.

Dale, V. H., Gardner, R. H. and Turner, M. G. 1989 Predicting across scales: Theory development and testing, *Landscape Ecology*, 3, pp. 147–152.

Dettmers, R. and Bart, J. 1999 A GIS Modeling Method Applied to Predicting Forest Songbird Habitat, *Ecological Applications*, 9(1), pp. 152–163.

Dietze, M. C., Averill, C., Foster, J. and Wheeler, K. 2017 *Ecological Forecasting*. Princeton University Press. doi: 10.1093/OBO/9780199830060.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M. and Swanson, A. K. 2011 Modeling plant ranges over 75 years of climate change in California, USA: Relating transferability to species traits, *Ecological Monographs*, 81(2), pp. 241–257. doi: doi:10.1890/10-1325.1.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G. and Dickman, C. R. 2016 Invasive predators and global biodiversity loss, *Proceedings of the National Academy of Sciences*, 113(40), pp. 11261–11265. doi: 10.1073/pnas.1602480113.

Domisch, S., Kuemmerlen, M., Jähnig, S. C. and Haase, P. 2013 Choice of study area and predictors affect habitat suitability projections, but not the performance of species distribution models of stream biota, *Ecological Modelling*. Elsevier B.V., 257, pp. 1–10. doi: 10.1016/j.ecolmodel.2013.02.019.

Dormann, C. F. 2007 Promising the future? Global change projections of species distributions, *Basic and Applied Ecology*, 8, pp. 387–397. doi: 10.1016/j.baae.2006.11.001.

Dormann, C. F., Purschke, O., Márquez, J. R. G., Lautenbach, S. and Schröder, B. 2008 Components of Uncertainty in Species Distribution Analysis: a Case Study of the Great Grey Shrike, *Ecology*, 89(12), pp. 3371–3386.

Dullinger, S., Kleinbauer, I., Peterseil, J., Smolik, M. and Essl, F. 2009 Niche based distribution modelling of an invasive alien plant: Effects of population status, propagule pressure and invasion history, *Biological Invasions*, 11(10), pp. 2401–2414. doi: 10.1007/s10530-009-9424-5.

Duque-lazo, J., Gils, H. Van, Groen, T. A. and Navarro-cerrillo, R. M. 2016 Transferability of species distribution models: The case of Phytophthora cinnamomi in Southwest Spain and Southwest Australia, *Ecological Modelling*. Elsevier B.V., 320, pp. 62–70.

Dye, C. and Hasibeder, A. G. 1986 Population dynamics of mosquito-borne disease: effects of flies which bite some people more frequently than others, *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 80, pp. 69–77.

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D. and Blumenthal, D. M. 2016 Global threats from invasive alien species in the twenty-first century and national response capacities, *Nature Communications*, 7, p. 12465. doi: 10.1038/ncomms12485.

Efron, B. 1982 *The Jackknife, the Bootstrap and Other Resampling Plans.*, *Society for Industrial and Applied Mathematics*. doi: 10.2307/2531123.

Eisenberg, J. N. S., Cevallos, W., Ponce, K., Levy, K., Bates, S. J., Scott, J. C., Hubbard, A., Vieira, N., … Trostle, J. 2006 Environmental change and infectious disease: How new roads affect the transmission of diarrheal pathogens in rural Ecuador, *Proceedings of the National Academy of Sciences*, 103(51), pp. 19460–19465.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., … E. Zimmermann, N. 2006 Novel methods improve prediction of species' distributions from occurrence data, *Ecography*, 29(2), pp. 129–151. doi: 10.1111/j.2006.0906-7590.04596.x.

Elith, J. and Graham, C. H. 2009 Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models, *Ecography*, 32, pp. 66–77. doi: 10.1111/j.1600-0587.2008.05505.x.

Elith, J. and Leathwick, J. R. 2009 Species Distribution Models: Ecological Explanation and Prediction Across Space and Time, *Annual Review of Ecology, Evolution, and Systematics*, 40(1), pp. 677–697. doi: 10.1146/annurev.ecolsys.110308.120159.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. and Yates, C. J. 2011 A statistical explanation of MaxEnt for ecologists, *Diversity and Distributions*, 17(1), pp. 43–57. doi: 10.1111/j.1472-4642.2010.00725.x.

Elton, C. 1927 *Animal Ecology*. London: Sedgwick and Jackson.

Engler, R., Guisan, A. and Rechsteiner, L. 2004 An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data, *Journal of Applied Ecology*, 41(2), pp. 263–274. doi: 10.1111/j.0021-8901.2004.00881.x.

Environment Agency 2014 *LIDAR Composite DSM 2017 - 2m*. Available at: https://data.gov.uk/dataset/fba12e80-519f-4be2-806f-41be9e26ab96/lidar-composite-dsm-2017-2m (Accessed: 22 April 2020).

Epanchin-niell, R. S. 2017 Economics of invasive species policy and management, *Forest Invasions*. Springer International Publishing, 19(11), pp. 3333–3354. doi: 10.1007/s10530-017-1406-4.

Ernest, K. A. 1989 Biotropica-Insect herbivory on a tropical understory tree: effects of leaf age and habitat-21-3-p194.pdf, *Biotropica*, pp. 194–199.

Ervin, G. N. and Holly, D. C. 2011 Examining Local Transferability of Predictive Species Distribution Models for Invasive Plants: An Example with Cogongrass (Imperata cylindrica), *Invasive Plant Science and Management*, 4, pp. 390–401. doi: 10.1614/IPSM-D-10-00077.1.

Eschen, R., Britton, K., Brockerhoff, E., Burgess, T., Dalley, V., Epanchin-niell, R. S., Gupta, K., Hardy, G., … Kenis, M. 2015 International variation in phytosanitary legislation and regulations governing importation of plants for planting, *Environmental Science & Policy*, 51, pp. 228–237. doi: 10.1016/j.envsci.2015.04.021.

Eskildsen, A., Roux, P. C., Heikkinen, R. K., Høye, T. T., Kissling, W. D., Pöyry, J., Wisz, M. S. and Luoto, M. 2013 Testing species distribution models across space and time: high latitude butterflies and recent warming, *Global Ecology and Biogeography*, 22, pp. 1293–1303. doi: 10.1111/geb.12078.

European Comission 2015 *Copernicus - Europe’s eyes on Earth*, *Copernicus Brochure*. Brussels. doi: 10.2873/93104.

Evans, M. R. 2012 Modelling ecological systems in a changing world, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), pp. 181–190. doi: 10.1098/rstb.2011.0172.

Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., De Langhe, R., Lessells, C. M., Merz, M., Malley, M. A. O., … Benton, T. G. 2013 Do simple models lead to generality in ecology?, *Trends in Ecology & Evolution*. Elsevier Ltd, 28(10), pp. 578–583. doi: 10.1016/j.tree.2013.05.022.

Evans, M. R., Norris, K. J. and Benton, T. G. 2012 Predictive ecology: Systems approaches, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), pp. 163–169. doi: 10.1098/rstb.2011.0191.

Fajardo, J., Lessmann, J., Bonaccorso, E., Devenish, C. and Muñoz, J. 2014 Combined use of systematic conservation planning, species distribution modelling, and connectivity analysis reveals severe conservation gaps in a megadiverse country (Peru), *PLoS ONE*, 9(12), pp. 1–23. doi: 10.1371/journal.pone.0114367.

Fan, J. Y., Zhao, N. X., Li, M., Gao, W. F., Wang, M. L. and Zhu, G. P. 2018 What are the best predictors for invasive potential of weeds? Transferability evaluations of model predictions based on diverse environmental data sets for Flaveria bidentis, *Weed Research*, 58, pp. 141–149. doi: 10.1111/wre.12292.

FAO 2017 *Citrus Fruit; Fresh and Processed, Statistical Bulletin 2016*. Rome.

Farashi, A. and Alizadeh-Noughani, M. 2018 Effects of models and spatial resolutions on the species distribution model performance, *Modeling Earth Systems and Environment*. Springer International Publishing, 4(1), pp. 263–268. doi: 10.1007/s40808-018-0422-4.

Fawcett, T. 2006 An introduction to ROC analysis, *Pattern Recognition Letters*, 27(8), pp. 861–874. doi: 10.1016/j.patrec.2005.10.010.

Di Febbraro, M., Lurz, P. W. W., Genovesi, P., Maiorano, L., Girardello, M. and Bertolino, S. 2013 The Use of Climatic Niches in Screening Procedures for Introduced Species to Evaluate Risk of Spread: A Case with the American Eastern Grey Squirrel, *PLoS ONE*, 8(7), pp. 1–10. doi: 10.1371/journal.pone.0066559.

Fernández, N., Selva, N., Yuste, C., Okarma, H. and Jakubiec, Z. 2012 Brown bears at the edge: Modeling habitat constrains at the periphery of the Carpathian population, *Biological Conservation*, 153, pp. 134–142. doi: 10.1016/j.biocon.2012.04.013.

Fernández, P., Jordano, D. and Haeger, J. F. 2015 Living on the edge in species distribution models : The unexpected presence of three species of butterflies in a protected area in southern Spain, *Ecological Modelling*. Elsevier B.V., 312, pp. 335–346. doi: 10.1016/j.ecolmodel.2015.05.032.

Ferrier, S. 1984 *The Status of the Rufous Scrub-Bird’Atrichornis Rufescens’: Habitat, Geographical Variation and Abundance.* University of New England, Armidale, Australia.

Ferrier, S., Watson, G., Pearce, J. and Drielsma, M. 2002 Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling, *Biodiversity and Conservation*, 11(12), pp. 2275–2307. doi: 10.1023/A:1021302930424.

Fick, S. E. and Hijmans, R. J. 2017 Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas, *International Journal of Climatology*.

Fieberg, J. R., Forester, J. D., Street, G. M., Johnson, D. H., ArchMiller, A. A. and Matthiopoulos, J. 2018 Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models, *Ecography*, 41(5), pp. 737–752. doi: 10.1111/ecog.03123.

Fielding, A. H. and Haworth, P. F. 1995 Testing the generality of bird habitat models, *Conservation Biology*, 9(6), pp. 1466–1481.

Fischer, D., Thomas, S. M., Neteler, M., Tjaden, N. B. and Beierkuhnlein, C. 2014 Climatic suitability of aedes albopictus in europe referring to climate change projections: Comparison of mechanistic and correlative niche modelling approaches, *Eurosurveillance*, 19(6), pp. 1–13. doi: 10.2807/1560-7917.ES2014.19.6.20696.

Fisher, J. R. B., Acosta, E. A., Dennedy-Frank, P. J., Kroeger, T. and Boucher, T. M. 2018 Impact of satellite imagery spatial resolution on land use classification accuracy and modeled water quality, *Remote Sensing in Ecology and Conservation*, 4(2), pp. 137–149. doi: 10.1002/rse2.61.

Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L. and Gurr, S. J. 2013 Emerging fungal threats to animal, plant and ecosystem health, *Nature*, 484(7393), pp. 1–18. doi: 10.1038/nature10947.Emerging.

Focks, D. A., Brenner, R. J., Hayes, J. and Daniels, E. 2000 Transmission Thresholds For Dengue In Terms Of Aedes Aegypti Pupae Per Person With Discussion Of Their Utility In Source Reduction Efforts, *Am. J. Trop. Med. Hyg.*, 62(1), pp. 11–18.

Fois, M., Fenu, G., Cuena Lombraña, A., Cogoni, D. and Bacchetta, G. 2015 A practical method to speed up the discovery of unknown populations using Species Distribution Models, *Journal for Nature Conservation*, 24(C), pp. 42–48. doi: 10.1016/j.jnc.2015.02.001.

Fordham, D. A., Bertelsmeier, C., Brook, B. W., Early, R., Ara, M. B., Neto, D. and Brown, S. C. 2018 How complex should models be? Comparing correlative and mechanistic range dynamics models, *Global Change Biology*, 24, pp. 1357–1370. doi: 10.1111/gcb.13935.

Franklin, J. 2010 *Mapping Species Distributions: Spatial In- ference and Prediction*, *Oryx*. Cambridge: Cambridge University Press. Available at: https://search.proquest.com/docview/220297257?accountid=12834.

Fulford, R., Russell, M., Yoskowitz, D. and Rogers, J. 2013 *Mechanistic models as a transferable framework for projecting effects of habitat change on production and delivery of ecosystem services.* San Diego.

Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I. and Thuiller, W. 2010 Predicting potential distributions of invasive species: Where to go from here?, *Diversity and Distributions*, 16(3), pp. 331–342. doi: 10.1111/j.1472-4642.2010.00652.x.

García-Callejas, D. and Araújo, M. B. 2016 The effects of model and data complexity on predictions from species distributions models, *Ecological Modelling*. Elsevier B.V., 326, pp. 4–12. doi: 10.1016/j.ecolmodel.2015.06.002.

Garcıa-de-Lomas, J. and Montserrat, V. 2015 Lists of harmful alien organisms: Are the national regulations adapted to the global world?, *Biological Invasions*, 17, pp. 3081–3091. doi: 10.1007/s10530-015-0939-7.

Gardner, A. S., Maclean, I. M. D. and Gaston, K. J. 2019 Climatic predictors of species distributions neglect biophysiologically meaningful variables, *Diversity and Distributions*, 25(8), pp. 1318–1333. doi: 10.1111/ddi.12939.

GBIF 2020 *GBIF: The Global Biodiversity Information Facility*. Available at: www.gbif.org/what-is-gbif (Accessed: 12 December 2019).

Gilbert, L. E., Hubbell, S. P. and Foster, R. B. 1994 Density and distance to adult effect of a canker disease in trees of moist tropical forest., *Oecologia*, 1, pp. 100–108.

Gobeyn, S., Mouton, A. M., Cord, A. F., Kaim, A., Volk, M. and Goethals, P. L. M. 2019 Evolutionary algorithms for species distribution modelling: A review in the context of machine learning, *Ecological Modelling*. Elsevier, 392(November 2018), pp. 179–195. doi: 10.1016/j.ecolmodel.2018.11.013.

Godsoe, W., Murray, R. and Plank, M. J. 2014 Information on biotic interactions improves transferability of distribution models., *The American Naturalist*, 185(2), pp. 281–290.

Gomes, V. H. F., Ijff, S. D., Raes, N., Amaral, I. L., Salomão, R. P., Coelho, L. D. S., Matos, F. D. D. A., Castilho, C. V., … Ter Steege, H. 2018 Species Distribution Modelling: Contrasting presence-only models with plot abundance data, *Scientific Reports*, 8(1), pp. 1–12. doi: 10.1038/s41598-017-18927-1.

Gonçalves, L., Subtil, A., Rosário Oliveira, M. and De Zea Bermudez, P. 2014 ROC curve estimation: An overview, *Revstat Statistical Journal*, 12(1), pp. 1–20.

Gong, G., Mattevada, S. and O'Bryant, S. E. 2014 Comparison of the accuracy of kriging and IDW interpolations in estimating groundwater arsenic concentrations in Texas, *Environmental Research*. Elsevier, 130, pp. 59–69. doi: 10.1016/j.envres.2013.12.005.

Gottschalk, T. K., Aue, B., Hotes, S. and Ekschmitt, K. 2011 Influence of grain size on species-habitat models, *Ecological Modelling*. Elsevier B.V., 222(18), pp. 3403–3412. doi: 10.1016/j.ecolmodel.2011.07.008.

Gottwald, T. R. 2010 Current Epidemiological Understanding of Citrus Huanglongbing, *Annual review of phytopathology*, 48, pp. 119–139. doi: 10.1146/annurev-phyto-073009–114418.

Gottwald, T. R., Bassanezi, R. B. and Paulo, S. 2007 Citrus Huanglongbing: The Pathogen and Its Impact Plant Health Progress Plant Health Progress, *Plant Health Progress*. doi: 10.1094/PHP-2007-0906-01-RV.Introduction.

Gottwald, T. R., Luo, W. and McRoberts, N. 2014 Risk-based residential HLB/ACP survey for California, Texas and Arizona, *Journal of Citrus Pathology*, 1, pp. 121–125.

Gottwald, T. R. and McCollum, T. G. 2017 Huanglongbing solutions and the need for anti-conventional thought, *Journal of Citrus Pathology*, 4(1).

Gottwald, T. R., Irey, M. S., Gast, T. C. and Parnell, S. R. 2010 Spatio-temporal analysis of an HLB epidemic in Florida and implications for spread, *Proceedings of the 17th conference of international organization of citrus virologists*, pp. 1–13.

da Graça, J. V., Douhan, G. W., Halbert, S. E., Keremane, M. L., Lee, R. F., Vidalakis, G. and Zhao, H. 2016 Huanglongbing: An overview of a complex pathosystem ravaging the world’s citrus, *Journal of Integrative Plant Biology*, 58(4), pp. 373–387. doi: 10.1111/jipb.12437.

Grafton-cardwell, E. E., Stelinski, L. L. and Stansly, P. A. 2013 Biology and Management of Asian Citrus Psyllid , Vector of the Huanglongbing Pathogens, *Annual Review of Entomology*, 58, pp. 413–432. doi: 10.1146/annurev-ento-120811-153542.

Graham, M. H. 2003 Confronting multicollinearity in ecological multiple regression, *Ecology*, 84(11), pp. 2809–2815. doi: 10.1890/02-3114.

Grenouillet, G., Buisson, L., Casajus, N. and Lek, S. 2011 Ensemble modelling of species distribution: The effects of geographical and environmental ranges, *Ecography*, 34(1), pp. 9–17. doi: 10.1111/j.1600-0587.2010.06152.x.

Grinnell, J. 1904 The Origin and Distribution of the Chest-Nut-Backed Chickadee, *The Auk*, 21(3), pp. 364–382.

Grinnell, J. 1917 The niche-relationships of the California Thrasher, *Auk*, 34, pp. 427–434.

Gu, W. and Swihart, R. K. 2004 Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models, *Biological Conservation*, 116(2), pp. 195–203. doi: 10.1016/S0006-3207(03)00190-3.

Guillera-Arroita, G. 2017 Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities, *Ecography*, 40(2), pp. 281–295. doi: 10.1111/ecog.02445.

Guillera-Arroita, G., Lahoz-Monfort, J. J. and Elith, J. 2014 Maxent is not a presence-absence method: A comment on Thibaud et al., *Methods in Ecology and Evolution*, 5(11), pp. 1192–1197. doi: 10.1111/2041-210X.12252.

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., Mccarthy, M. A., Tingley, R. and Wintle, B. A. 2015 Is my species distribution model fit for purpose? Matching data and models to applications, *Global Ecology and Biogeography*, 24(3), pp. 276–292. doi: 10.1111/geb.12268.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., … Buckley, Y. M. 2013 Predicting species distributions for conservation decisions, *Ecology Letters*, 16(12), pp. 1424–1435. doi: 10.1111/ele.12189.

Guisan, A., Edward, T. C., Jr and Hastie, T. 2012 Generalized linear and generalized additive models in studies of species distributions: setting the scene, *Ecological Modelling*, 157(157), pp. 89–100. Available at: www.elsevier.com/locate/ecolmodel.

Guisan, A., Zimmermann, N. E., Elith, J., Graham, C. H., Phillips, S. and Peterson, A. T. 2007a What matters for predicting spatial distribution of tree occurences: techniques, data or specie's characteristics?, *Ecological Monographs*, 77(4), pp. 615–630.

Guisan, A. and Thuiller, W. 2005 Predicting species distribution: Offering more than simple habitat models, *Ecology Letters*, 8(9), pp. 993–1009. doi: 10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Thuiller, W. and Zimmermann, N. E. 2017 *Habitat suitability and distribution models: with applications in R.* Cambridge University Press.

Guisan, A. and Zimmermann, N. E. 2000 Predictive habitat distribution models in ecology, *Ecological Modelling*, 135(2–3), pp. 147–186. doi: 10.1016/S0304-3800(00)00354-9.

Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N. G., Lehmann, A. and Zimmermann, N. E. 2006 Using niche-based models to improve the sampling of rare species, *Conservation Biology*, 20(2), pp. 501–511. doi: 10.1111/j.1523-1739.2006.00354.x.

Guisan, A., Graham, C. H., Elith, J., Huettmann, F., Dudik, M., Ferrier, S., Hijmans, R., Lehmann, A., … Zimmermann, N. E. 2007b Sensitivity of predictive species distribution models to change in grain size, *Diversity and Distributions*, 13(3), pp. 332–340. doi: 10.1111/j.1472-4642.2007.00342.x.

Halbert, A. S. E. and Manjunath, K. L. 2004 Asian Citrus Psyllids (Sternorrhyncha: Psyllidae) And Greening Disease of Citrus: A Literature Review and Assessment of Risk in Florida, *Florida Entomologist*, 87(3).

Hall, D. G., Richardson, M. L., Ammar, E. and Halbert, S. E. 2013 Asian citrus psyllid, Diaphorina citri, vector of citrus huanglongbing disease, *Entomologis Experimentalis et Applicata*, 146, pp. 207–223. doi: 10.1111/eea.12025.

Hall, D. G. and Hentz, M. G. 2011 Seasonal flight activity by the Asian citrus psyllid in east central Florida, *Entomologis Experimentalis et Applicata*, pp. 75–85. doi: 10.1111/j.1570-7458.2011.01108.x.

Hampton, S. E., Strasser, C. A., Tewksbury, J. J., Gram, W. K., Budden, A. E., Batcheller, A. L., Duke, C. S. and Porter, J. H. 2013 Big data and the future of ecology, *Frontiers in Ecology and the Environment*, 11(3), pp. 156–162. doi: 10.1890/120103.

Hanley, A. J. and McNeil, J. B. 1982 The Meaning and Use of the Area under a Receiver Operating Characteristic (ROC) Curve, *Radiology*, 143, pp. 29–36. doi: 10.1148/radiology.143.1.7063747.

Hartemink, N. A., Purse, B. V., Meiswinkel, R., Brown, H. E., de Koeijer, A., Elbers, A. R. W., Boender, G. J., Rogers, D. J. and Heesterbeek, J. A. P. 2009 Mapping the basic reproduction number (R0) for vector-borne diseases: A case study on bluetongue virus, *Epidemics*. Elsevier Inc., 1(3), pp. 153–161. doi: 10.1016/j.epidem.2009.05.004.

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S. and Samuel, M. D. 2002 Climate warming and disease risks for terrestrial and marine biota, *Science*, 296(5576), pp. 2158–2162. doi: 10.1126/science.1063699.

Hastie, T. and Fithian, W. 2013 Inference from presence-only data; the ongoing controversy, *Ecography*, 36(8), pp. 864–867. doi: 10.1111/j.1600-0587.2013.00321.x.

Hebert, M. P. and Allen, L. J. 2016 Disease outbreaks in plant-vector-virus models with vector aggregation and dispersal, *Discrete & Continuous Dynamical Systems-Series B*, 21(7).

Heffernan, J. M., Smith, R. J. and Wahl, L. M. 2005 Perspectives on the basic reproductive ratio, *Journal of the Royal Society*, 2, pp. 281–293. doi: 10.1098/rsif.2005.0042.

Hefley, T. J., Tyre, A. J., Baasch, D. M. and Blankenship, E. E. 2013 Nondetection sampling bias in marked presence-only data, *Ecology and Evolution*, 3(16), pp. 5225–5236. doi: 10.1002/ece3.887.

Heikkinen, R. K., Marmion, M. and Luoto, M. 2012 Does the interpolation accuracy of species distribution models come at the expense of transferability?, *Ecography*, 35, pp. 276–288. doi: 10.1111/j.1600-0587.2011.06999.x.

Herborg, L. M., Rushton, S. P., Clare, A. S. and Bentley, M. G. 2003 Spread of the Chinese mitten crab (Eriocheir sinensis H. Milne Edwards) in Continental Europe: Analysis of a historical data set, *Hydrobiologia*, 503, pp. 21–28. doi: 10.1023/B:HYDR.0000008483.63314.3c CITATIONS.

Hernandez, P. A., Graham, C. H., Master, L. L. and Albert, D. L. 2006 The effect of sample size and species characteristics on performance of different species distribution modeling methods, *Ecography*, 29(5), pp. 773–785. doi: 10.1111/j.0906-7590.2006.04700.x.

Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., Soto, A., Swenson, J. J., … Young, B. E. 2008 Predicting species distributions in poorly-studied landscapes, *Biodiversity and Conservation*, 17(6), pp. 1353–1366. doi: 10.1007/s10531-007-9314-z.

Hijmans, R. J., Garcia, N., Kapoor, J., Rala, A., Maunahan, A. and Wieczorek, J. 2012 Global Administrative Areas (Boundaries), *Berkeley: Museum of Vertebrate Zoology and the International Rice Research Institute, University of California.*

Hirzel, A. H. and Lay, G. Le 2008 Habitat suitability modelling and niche theory, *Journal of Applied Ecology*, 45, pp. 1372–1381. doi: 10.1111/j.1365-2664.2008.01524.x.

Hjorth, J. S. U. 2017 *Computer Intense Statistical Methods: Validation, Model Selection and Bootstrap*. Routledge.

Hodges, A. W. and Spreen, T. H. 2012 Economic Impacts of Citrus Greening (HLB) in Florida, (January), pp. 7–12.

Hof, A. R., Jansson, R. and Nilsson, C. 2012 How biotic interactions may alter future predictions of species distributions: Future threats to the persistence of the arctic fox in Fennoscandia, *Diversity and Distributions*, 18(6), pp. 554–562. doi: 10.1111/j.1472-4642.2011.00876.x.

Holt, R. D. 1990 The Microevolutionary Consequences of Climate Change, *Trends in Ecology & Evolution*, 5(9).

Houlahan, J. E., Mckinney, S. T., Anderson, T. M. and Mcgill, B. J. 2017 The priority of prediction in ecological understanding, *Oikos*, 126, pp. 1–7. doi: 10.1111/oik.03726.

Huang, J. and Frimpong, E. A. 2016 Limited transferability of stream-fish distribution models among river catchments: reasons and implications, *Freshwater Biology*, 61, pp. 729–744. doi: 10.1111/fwb.12743.

Hudgins, E. J., Liebhold, A. M. and Leung, B. 2017 Predicting the spread of all invasive forest pests in the United States, *Ecology Letters*, 20, pp. 426–435. doi: 10.1111/ele.12741.

Hulme, P. E. 2009 Trade, transport and trouble: Managing invasive species pathways in an era of globalization, *Journal of Applied Ecology*, 46(1), pp. 10–18. doi: 10.1111/j.1365-2664.2008.01600.x.

Hulme, P. E. 2015 Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions, *Journal of Applied Ecology*, 52, pp. 1418–1424. doi: 10.1111/1365-2664.12470.

Hung, T. H., Hung, S. C., Chen, C. N., Hsu, M. H. and Su, H. J. 2004 Detection by PCR of Candidatus Liberibacter asiaticus, the bacterium causing citrus huanglongbing in vector psyllids: application to the study of vector-pathogen relationships, *Plant Pathology*, 53, pp. 96–102. doi: 10.1046/j.1365-3059.2003.00948.x.

Husain, M. A. and Nath, D. 1927 The citrus psylla (Diaphorina citri, Kuw.) [Psyllidae: Homoptera], *Mem. Dept. Agric. India Entomol. Ser.*, 10(2), pp. 1–27.

Hutchinson, G. E. 1957 Concluding Remarks, *Cold Spring Harbor Symposia on Quantitative Biology*, 22(0), pp. 415–427. doi: 10.1101/SQB.1957.022.01.039.

Hutchinson, G. E. 1978 *An introduction to population ecology*.

Hyatt-Twynam, S. R., Parnell, S., Stutt, R. O. J. H., Gottwald, T. R., Gilligan, C. A. and Cunniffe, N. J. 2017 Risk-based management of invading plant disease, *New Phytologist*, 214(3), pp. 1317–1329. doi: 10.1111/nph.14488.

Inoue, H., Ohnishi, J., Ito, T., Tomimura, K., Miyata, S., Iwanami, T. and Ashihara, W. 2009 Enhanced proliferation and efficient transmission of Candidatus Liberibacter asiaticus by adult Diaphorina citri after acquisition feeding in the nymphal stage, *Annals of Applied Biology*, 155, pp. 29–36. doi: 10.1111/j.1744-7348.2009.00317.x.

Iturbide, M., Bedia, J. and Gutiérrez, J. M. 2018a Tackling uncertainties of Species Distribution Model projections with package mopa, *R Journal*, 10(1), pp. 122–139. doi: 10.32614/rj-2018-019.

Iturbide, M., Bedia, J. and Manuel, J. 2018b Background sampling and transferability of species distribution model ensembles under climate change, *Global and Planetary Change*. Elsevier, 166(March), pp. 19–29. doi: 10.1016/j.gloplacha.2018.03.008.

Iturbide, M., Bedia, J., Herrera, S., del Hierro, O., Pinto, M. and Gutiérrez, J. M. 2015 A framework for species distribution modelling with improved pseudo-absence generation, *Ecological Modelling*. Elsevier B.V., 312, pp. 166–174. doi: 10.1016/j.ecolmodel.2015.05.018.

Jackson, L. J., Trebitz, A. S. and Cottingham, K. L. 2000 An introduction to the practice of ecological modeling, *BioScience*, 50(8), pp. 694–706. doi: 10.1641/0006-3568(2000)050[0694:AITTPO]2.0.CO;2.

Jarnevich, C. S., Stohlgren, T. J., Kumar, S., Morisette, J. T. and Holcombe, T. R. 2015 Caveats for correlative species distribution modeling, *Ecological Informatics*. Elsevier B.V., 29(P1), pp. 6–15. doi: 10.1016/j.ecoinf.2015.06.007.

Jesse, M., Ezanno, P., Davis, S. and Heesterbeek, J. A. P. 2008 A fully coupled, mechanistic model for infectious disease dynamics in a metapopulation: Movement and epidemic duration, *Journal of Theoretical Biology*, 254(2), pp. 331–338. doi: 10.1016/j.jtbi.2008.05.038.

Jiménez-Valverde, A. 2012 Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling, *Global Ecology and Biogeography*, 21(4), pp. 498–507. doi: 10.1111/j.1466-8238.2011.00683.x.

Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P. and Lobo, J. M. 2011 Use of niche models in invasive species risk assessments, *Biological Invasions*, 13(12), pp. 2785–2797. doi: 10.1007/s10530-011-9963-4.

Jiménez-Valverde, A., Lobo, J. M. and Hortal, J. 2008 Not as good as they seem: The importance of concepts in species distribution modelling, *Diversity and Distributions*, 14(6), pp. 885–890. doi: 10.1111/j.1472-4642.2008.00496.x.

Jones, M. C. and Cheung, W. W. L. 2015 Multi-model ensemble projections of climate change effects on global marine biodiversity, *ICES Journal of Marine Science*, 72(3), pp. 741–752.

Jopp, F., Reuter, H. and Breckling, B. 2011 *Historical background of ecological modelling and its importance for modern ecology*, *Modelling Complex Ecological Dynamics*. Berlin: Springer. doi: 10.1007/978-3-642-05029-9.

Jorgensen, S. E. 2017 *The Handbook of Environemntal and Ecological Modelling*. CRC Press.

Kaliontzopoulou, A., Brito, J. C., Carretero, M. A., Larbes, S. and Harris, D. J. 2008 Modelling the partially unknown distribution of wall lizards (Podarcis) in North Africa: Ecological affinities, potential areas of occurrence, and methodological constraints, *Canadian Journal of Zoology*, 86(9), pp. 992–1001. doi: 10.1139/Z08-078.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppakoski, E., Cinar, M. E., Ozturk, B., Grabowski, M., Golani, D. and Cardoso, A. C. 2014 Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review, *Aquat. Invas.*, 9(4), pp. 391–423.

Kauffman, M. J. and Jules, E. S. 2006 Heterogeneity shapes invasion: host size and environment influence susceptibility to a nonnative pathogen, *Ecological Applications*, 16(1), pp. 166–175.

Kearney, M. and Porter, W. 2009 Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges, *Ecology Letters*, 12(4), pp. 334–350. doi: 10.1111/j.1461-0248.2008.01277.x.

Kearney, M. R., Wintle, B. A. and Porter, W. P. 2010 Correlative and mechanistic models of species distribution provide congruent forecasts under climate change, *Conservation Letters*, 3(3), pp. 203–213. doi: 10.1111/j.1755-263X.2010.00097.x.

Keller, R. P., Frang, K. and Lodge, D. M. 2008 Preventing the spread of invasive species: Economic benefits of intervention guided by ecological predictions, *Conservation Biology*, 22(1), pp. 80–88. doi: 10.1111/j.1523-1739.2007.00811.x.

Keller, R. P., Geist, J., Jeschke, J. M. and Kühn, L. 2011 Invasive species in Europe: Ecology, status, and policy, *Environmental Sciences Europe*, 23(1), pp. 8–11. doi: 10.1186/2190-4715-23-23.

Kharouba, H. M., Algar, A. C. and Kerr, J. T. 2009 Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment, *Ecology*, 90(8), pp. 2213–2222.

Khatibi, M. and Sheikholeslami, R. 2016 Ecological Niche Theory: A Brief Review, *The International Journal of Indian Psycology*, 3(2), pp. 1–4.

Kot, M., Lewis, A. M. and van den Driessche, P. 1996 Dispersal Data and the Spread of Invading Organisms, *Ecology*, 77(7), pp. 2027–2042.

Kumagai, L. B., LeVesque, C. S., Blomquist, C. L., Madishetty, K., Guo, Y., Woods, P. W., Rooney-Latham, S., Rascoe, J., … Polek, M. 2013 First report of Candidatus Liberibacter asiaticus associated with citrus Huanglongbing in California., *Plant Disease*, 97(2), p. 283.

Lauzeral, C., Grenouillet, G. and Brosse, S. 2013 Spatial range shape drives the grain size effects in species distribution models, *Ecography*, 36(7), pp. 778–787. doi: 10.1111/j.1600-0587.2013.07696.x.

Lawler, J. J., White, D., Neilson, R. P. and Blaustein, A. R. 2006 Predicting climate-induced range shifts: Model differences and model reliability, *Global Change Biology*, 12(8), pp. 1568–1584. doi: 10.1111/j.1365-2486.2006.01191.x.

Lee, J. A., Halbert, S. E., Dawson, W. O., Robertson, C. J., Keesling, J. E. and Singer, B. H. 2015 Asymptomatic spread of huanglongbing and implications for disease control, *Proceedings of the National Academy of Sciences*, 112(24), pp. 7605–7610. doi: 10.1073/pnas.1508253112.

Leibold, M. A., Ecology, S. and Jul, N. 1995 The Niche Concept Revisited: Mechanistic Models and Community Context, *Ecology*, 76(5), pp. 1371–1382. doi: 10.1007/s.

Leroy, B., Delsol, R., Hugueny, B., Meynard, C. N., Barhoumi, C., Barbet-Massin, M. and Bellard, C. 2018 Without quality presence–absence data, discrimination metrics such as TSS can be misleading measures of model performance, *Journal of Biogeography*, 45(9), pp. 1994–2002. doi: 10.1111/jbi.13402.

Lewis-rosenblum, H. 2011 *Seasonal and long-range movement of asian citrus psyllid,*. University of Floria.

Liu, C., Newell, G. and White, M. 2019 The effect of sample size on the accuracy of species distribution models: considering both presences and pseudo-absences or background sites, *Ecography*, 42(3), pp. 535–548. doi: 10.1111/ecog.03188.

Liu, C., White, M. and Newell, G. 2011 Measuring and comparing the accuracy of species distribution models with presence-absence data, *Ecography*, 34(2), pp. 232–243. doi: 10.1111/j.1600-0587.2010.06354.x.

Lobo, J.M., Jiménez-Valverde, A. and Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global ecology and Biogeography*, 17(2), pp.145-151.

Lobo, J. M., Jiménez-Valverde, A. and Hortal, J. 2010 The uncertain nature of absences and their importance in species distribution modelling, *Ecography*, 33(1), pp. 103–114. doi: 10.1111/j.1600-0587.2009.06039.x.

Lobo, J. M., Verdú, J. R. and Numa, C. 2006 Environmental and geographical factors affecting the Iberian distribution of flightless Jekelius species (Coleoptera: Geotrupidae), *Diversity and Distributions*, 12(2), pp. 179–188. doi: 10.1111/j.1366-9516.2005.00214.x.

Lotka, A. J. 1925 Elements of Physical Biology, *Williams and Wilkins Company*, p. 435. doi: 10.2105/AJPH.15.9.812-b.

Lounibos, L. P. 2002 Invasions by Insect Vectors of Human Disease, *Annual Review of Entomology*, 47, pp. 233–266. doi: 10.1146/annurev.ento.47.091201.145206.

Lowen, J. B., McKindsey, C. W., Therriault, T. W. and DiBacco, C. 2016 Effects of spatial resolution on predicting the distribution of aquatic invasive species in nearshore marine environments, *Marine Ecology Progress Series*, 556, pp. 17–30.

Luan, J., Zhang, C., Xu, B., Xue, Y. and Ren, Y. 2020 The predictive performances of random forest models with limited sample size and different species traits, *Fisheries Research*. Elsevier, 227(August 2019), p. 105534. doi: 10.1016/j.fishres.2020.105534.

MacArthur, R. H. 1972 *Geographical Ecology*. New York: Harper & Row.

Maddock, M. and Geering, D., 1994. Range expansion and migration of the cattle egret. Ostrich, 65(2), pp.191-203.

Magori, K. and Drake, J. M. 2013 The Population Dynamics of Vector-borne Diseases, *Nature Education Knowledge*, 14(4).

Mainali, K. P., Warren, D. A. N. L. and Dhileepan, K. 2015 Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling, *Global Change Biology*, 21, pp. 4464–4480. doi: 10.1111/gcb.13038.

Mainka, S. A. and Howard, G. W. 2010 Climate change and invasive species: Double jeopardy, *Integrative Zoology*, 5(2), pp. 102–111. doi: 10.1111/j.1749-4877.2010.00193.x.

Manel, S., Williams, H. C. and Ormerod, S. J. 2001 Evaluating presence absence models in ecology; the need to count for prevalence, *Journal of Applied ecology*, 38, pp. 921–931. doi: 10.1046/j.1365-2664.2001.00647.x.

Mannocci, L., Roberts, J. J., Miller, D. L. and Halpin, P. N. 2017 Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas, *Conservation Biology*, 31(3), pp. 601–614. doi: 10.1111/cobi.12856.

Mannocci, L., Roberts, J.J., Pedersen, E.J. and Halpin, P.N., 2020. Geographical differences in habitat relationships of cetaceans across an ocean basin. *Ecography*, *43*(8), pp.1250-1259.

Manzoor, S. A., Griffiths, G. and Lukac, M. 2018 Species distribution model transferability and model grain size-finer may not always be better, *Scientific Reports*. Springer US, 8(1), pp. 1–9. doi: 10.1038/s41598-018-25437-1.

Marini, M., Barbet-Massin, M., Lopes, L. E. and Jiguet, F. 2010 Predicting the occurrence of rare Brazilian birds with species distribution models, *Journal of Ornithology*, 151(4), pp. 857–866. doi: 10.1007/s10336-010-0523-y.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K. and Thuiller, W. 2009 Evaluation of consensus methods in predictive species distribution modelling, *Diversity and Distributions*, 15(1), pp. 59–69. doi: 10.1111/j.1472-4642.2008.00491.x.

Massimino, G. E., Urbaneja, C., Estrella, A., Siverio, F., Di, S., Alejandro, S. and Rapisarda, T. 2017 A review on Trioza erytreae (African citrus psyllid), now in mainland Europe, and its potential risk as vector of huanglongbing (HLB) in citrus, *Journal of Pest Science*, 90, pp. 1–17. doi: 10.1007/s10340-016-0804-1.

Mateo, R. G., Croat, T. B., Felicísimo, Á. M. and Muñoz, J. 2010 Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections, *Diversity and Distributions*, 16(1), pp. 84–94. doi: 10.1111/j.1472-4642.2009.00617.x.

Matthiopoulos, J., Hebblewhite, M., Aarts, G. and Fieberg, J. R. 2011 Generalized functional responses for species distributions, *Ecology*, 92(3), pp. 583–589. doi: 10.1890/10-0751.1.

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E. and Contasti, A. L. 2010 Considering ecological dynamics in resource selection functions, *Journal of Animal Ecology*, 79, pp. 4–12. doi: 10.1111/j.1365-2656.2009.01613.x.

McNeely, J. A. 2006 As the world gets smaller, the chances of invasion grow, *Euphytica*, 148(1–2), pp. 5–15. doi: 10.1007/s10681-006-5937-5.

Medley, K. A. 2010 Niche shifts during the global invasion of the Asian tiger mosquito, Aedes albopictus Skuse (Culicidae), revealed by reciprocal distribution models, *Global Ecology and Biogeography*, 19(1), pp. 122–133. doi: 10.1111/j.1466-8238.2009.00497.x.

Meineri, E., Deville, A. S., Grémillet, D., Gauthier-Clerc, M. and Béchet, A. 2015 Combining correlative and mechanistic habitat suitability models to improve ecological compensation, *Biological Reviews*, 90(1), pp. 314–329. doi: 10.1111/brv.12111.

Mellin, C., Mengersen, K., Bradshaw, C. J. A. and Caley, M. J. 2014 Generalizing the use of geographical weights in biodiversity modelling, *Global Ecology and Biogeography*, 23(11), pp. 1314–1323. doi: 10.1111/geb.12203.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., Mcmahon, S. M., Normand, S., Thuiller, W., Wüest, R. O., … Elith, J. 2014 What do we gain from simplicity versus complexity in species distribution models?, *Ecography*, 37(12), pp. 1267–1281. doi: 10.1111/ecog.00845.

Merow, C., Smith, M. J. and Silander, J. A. 2013 A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter, *Ecography*, 36(10), pp. 1058–1069. doi: 10.1111/j.1600-0587.2013.07872.x.

Mesgaran, M. B., Cousens, R. D. and Webber, B. L. 2014 Here be dragons: A tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models, *Diversity and Distributions*, 20(10), pp. 1147–1159. doi: 10.1111/ddi.12209.

Messina, J. P., Kraemer, M. U. G., Brady, O. J., Pigott, D. M., Shearer, F. M., Weiss, D. J., Golding, N., Ruktanonchai, C. W., … Hay, S. I. 2016 Mapping global environmental suitability for Zika virus, *eLife*, 5(APRIL2016), pp. 1–19. doi: 10.7554/eLife.15272.

Meyer, G. A. and Montgomery, M. E. 1987 Oecologia Relationships between leaf age and the food quality of cottonwood foliage for the gypsy moth, Lymantria dispar, *Oecologia*, 72, pp. 527–532.

Meynard, C. N. and Quinn, J. F. 2007 Predicting species distributions: a critical comparison of the most common statistical models using artificial species, *Journal of Biogeography*, 34, pp. 1455–1469. doi: 10.1111/j.1365-2699.2007.01720.x.

Mi, C., Huettmann, F., Guo, Y., Han, X. and Wen, L. 2017 Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence, *PeerJ*, 2017(1). doi: 10.7717/peerj.2849.

Millar, C. S. and Blouin-Demers, G. 2012 Habitat suitability modelling for species at risk is sensitive to algorithm and scale: A case study of Blanding's turtle, Emydoidea blandingii, in Ontario, Canada, *Journal for Nature Conservation*. Elsevier GmbH., 20(1), pp. 18–29. doi: 10.1016/j.jnc.2011.07.004.

Monzo, C., Arevalo, H. A., Jones, M. M., Vanaclocha, P., Croxton, S. D., Qureshi, J. A. and Stansly, P. A. 2015 Sampling Methods for Detection and Monitoring of the Asian Citrus Psyllid (Hemiptera: Psyllidae), *Environmental Entomology*, 44(3), pp. 780–788. doi: 10.1093/ee/nvv032.

Moon, J. B., Dewitt, T. H., Errend, M. N., Bruins, R. J. F., Kentula, M. E., Chamberlain, S. J., Fennessy, S. M. and Naithani, K. J. 2017 Model application niche analysis: assessing the transferability and generalizability of ecological models, *Ecosphere*, 8(10). doi: 10.1002/ecs2.1974.

Morales, N. S., Fernández, I. C. and Baca-González, V. 2017 MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review, *PeerJ*, 5, p. e3093. doi: 10.7717/peerj.3093.

Moran-ordonez, A., Lahoz-Monfort, J. J., Elith, J. and Wintle, B. A. 2017 Evaluating 318 continental-scale species distribution models over a 60-year prediction horizon: what factors influence the reliability of predictions?, *Global Ecology and Biogeography*, 26, pp. 371–384. doi: 10.1111/geb.12545.

Moreno-amat, E., Mateo, R. G., Nieto-lugilde, D., Morueta-holme, N., Svenning, J. and García-amorena, I. 2015 Impact of model complexity on cross-temporal transferability in Maxent species distribution models: An assessment using paleobotanical data, *Ecological Modelling*. Elsevier B.V., 312, pp. 308–317. doi: 10.1016/j.ecolmodel.2015.05.035.

Moudrý, V. and Šímová, P. 2012 Influence of positional accuracy, sample size and scale on modelling species distributions: A review, *International Journal of Geographical Information Science*, 26(11), pp. 2083–2095. doi: 10.1080/13658816.2012.721553.

Nabout, J. C., Caetano, J. M., Ferreira, R. B., Teixeira, I. R. and Alves, S. M. de F. 2012 Using correlative, mechanistic and hybrid niche models to predict the productivity and impact of global climate change on maize crop in Brazil, *Natureza a Conservacao*, 10(2), pp. 177–183. doi: 10.4322/natcon.2012.034.

Naimi, B. 2017 Uncertainty Analysis for Species Distribution Models.

Naimi, B. and Araújo, M. B. 2016 Sdm: A reproducible and extensible R platform for species distribution modelling, *Ecography*, 39(4), pp. 368–375. doi: 10.1111/ecog.01881.

Narouei-Khandan, H. A., Halbert, S. E., Worner, S. P. and van Bruggen, A. H. C. 2016 Global climate suitability of citrus huanglongbing and its vector, the Asian citrus psyllid, using two correlative species distribution modeling approaches, with emphasis on the USA, *European Journal of Plant Pathology*, 144(3), pp. 655–670. doi: 10.1007/s10658-015-0804-7.

Neubert, M. G. and Parker, I. M. 2004 Projecting rates of spread for invasive species, *Risk Analysis*, 24(4), pp. 817–831. doi: 10.1111/j.0272-4332.2004.00481.x.

Nix, H. A. 1986 No A biogeographic analysis of Australian elapid snakes., *Atlas of elapid snakes of Australia*, 7, pp. 4–15.

Nogués-Bravo, D. and Araújo, M. B. 2006 Species richness, area and climate correlates, *Global Ecology and Biogeography*, 15(5), pp. 452–460. doi: 10.1111/j.1466-822X.2006.00240.x.

Norberg, A., Abrego, N., Blanchet, F. G., Adler, F. R., Anderson, B. J., Anttila, J., Araújo, M. B., Dallas, T., … Ovaskainen, O. 2019 A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels, *Ecological Monographs*, 89(3). doi: 10.1002/ecm.1370.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., Connell, A. F. O., Miller, P. I. and Louzao, M. 2012 Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds, *Biological Conservation*. Elsevier Ltd, 156, pp. 94–104. doi: 10.1016/j.biocon.2011.11.013.

Otten, W. and Gilligan, C. A. 2006 Soil structure and soil-borne diseases: Using epidemiological concepts to scale from fungal spread to plant epidemics, *European Journal of Soil Science*, 57(1), pp. 26–37. doi: 10.1111/j.1365-2389.2006.00766.x.

Ouma, Y. O. 2016 Advancements in medium and high resolution Earth observation for land-surface imaging: Evolutions, future trends and contributions to sustainable development, *Advances in Space Research*. COSPAR, 57(1), pp. 110–126. doi: 10.1016/j.asr.2015.10.038.

Paini, D. R., Sheppard, A. W., Cook, D. C., De Barro, P. J., Worner, S. P. and Thomas, M. B. 2016 Global threat to agriculture from invasive species, *Proceedings of the National Academy of Sciences*, (20). doi: 10.1073/pnas.1602205113.

Pan, X., Geng, Y., Zhang, W., Li, B. and Chen, J. 2006 The influence of abiotic stress and phenotypic plasticity on the distribution of invasive Alternanthera philoxeroides along a riparian zone, *Acta Oecologica*, 30(3), pp. 333–341. doi: 10.1016/j.actao.2006.03.003.

Park, R., Fetch, T., Hodson, D., Jin, Y., Nazari, K., Prashar, M. and Pretorius, Z. 2011 International surveillance of wheat rust pathogens: Progress and challenges, *Euphytica*, 179(1), pp. 109–117. doi: 10.1007/s10681-011-0375-4.

Parnell, S., Gottwald, T. R., Cunniffe, N. J., Chavez, V. A. and van den Bosch, F. 2015 Early-detection surveillance for an emerging plant pathogen: a rule of thumb to predict incidence at first discovery, *Proceedings B*. doi: 10.1098/rspb.2015.1478.

Parnell, S., Gottwald, T. R., Riley, T. and Van Den Bosch, F. 2014 A generic risk-based surveying method for invading plant pathogens, *Ecological Applications*, 24(4), pp. 779–790. doi: 10.1890/13-0704.1.

Paton, R. S. and Matthiopoulos, J. 2015 Defining the scale of habitat availability for models of habitat selection, *Ecology*, 97, pp. 1113–1122. doi: 10.1890/14-2241.

Pautasso, M., Dehnen-Schmutz, K., Holdenrieder, O., Pietravalle, S., Salama, N., Jeger, M. J., Lange, E. and Hehl-Lange, S. 2010 Plant health and global change - Some implications for landscape management, *Biological Reviews*, 85(4), pp. 729–755. doi: 10.1111/j.1469-185X.2010.00123.x.

Pearce, J. L. and Boyce, M. S. 2006 Modelling distribution and abundance with presence-only data, *Journal of Applied Ecology*, 43(3), pp. 405–412. doi: 10.1111/j.1365-2664.2005.01112.x.

Pearman, P. B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N. E. and Thuiller, W. 2014 Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage, *Global Ecology and Biogeography*, 23(4), pp. 414–424. doi: 10.1111/geb.12127.

Pearson, R. G. and Dawson, T. P. 2003 Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful?, *Global Ecology and Biogeography*, 12(5), pp. 361–371. doi: 10.1046/j.1466-822X.2003.00042.x.

Pelz-Stelinski, K. S., Brlansky, R. H., Ebert, T. A. and Rogers, M. E. 2010 Transmission Parameters for Candidatus Liberibacter asiaticus by Asian Citrus Psyllid (Hemiptera: Psyllidae), *Journal of Economic Entomology*, 103(5), pp. 1531–1541. doi: 10.1603/EC10123.

Perrin, E. 1904 On some Dangers of Extrapolation., *Biometrika*, 3, pp. 99–103.

Peterson, A.T., Papeş, M. and Eaton, M. 2007 Transferability and model evaluation in ecological niche modeling: A comparison of GARP and Maxent, *Ecography*, 30(4), pp. 550–560. doi: 10.1111/j.2007.0906-7590.05102.x.

Peterson, A.T. , Papeş, M. and Soberón, J. 2008 Rethinking receiver operating characteristic analysis applications in ecological niche modeling, *Ecological Modelling*, 213(1), pp. 63–72. doi: 10.1016/j.ecolmodel.2007.11.008.

Peterson, A. T., Papeş, M. and Soberón, J. 2015 Mechanistic and correlative models of ecological niches, *European Journal of Ecology*, 1(2), pp. 28–38. doi: 10.1515/eje-2015-0014.

Peterson, A. T. and Robins, C. R. 2003 Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation, *Conservation Biology*, 17(4), pp. 1161–1165. doi: 10.1046/j.1523-1739.2003.02206.x.

Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C. and Guisan, A. 2017 Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plant invasions, *Global Ecology and Biogeography*, 26(3), pp. 275–287. doi: 10.1111/geb.12530.

Phillips, S. J., Anderson, R. P. and Schapire, R. E. 2006 Maximum entropy modeling of species geographic distributions, *Ecological Modelling*, 190, pp. 231–259. doi: 10.1016/j.ecolmodel.2005.03.026.

Phillips, S. J. and Dudik, M. 2008 Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation, *Ecography*, 31, pp. 161–175. doi: 10.1111/j.2007.0906-7590.05203.x.

Phillips, S. J., Dudík, M. and Schapire, R. E. 2004 A maximum entropy approach to species distribution modeling, *21st International Conference on Machine Learning, Banff, Canada*, pp. 655–662. doi: 10.1145/1015330.1015412.

Phillips, S. J., Dudik, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J. and Ferrier, S. 2009 Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data, *Ecological Applications*, 19(1), pp. 181–197.

Piero, G., Carles, C., Montserrat, V. and Walton, P. 2015 EU adopts innovative legislation on invasive species: a step towards a global response to biological invasions?, *Biological Invasions*, 17, pp. 1307–1311. doi: 10.1007/s10530-014-0817-8.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., … Tsomondo, T. 2001 Economic and environmental threats of alien plant, animal, and microbe invasions, *Agriculture, Ecosystems and Environment*, 84(1), pp. 1–20. doi: 10.1016/S0167-8809(00)00178-X.

Pimentel, D., Zuniga, R. and Morrison, D. 2005 Update on the environmental and economic costs associated with alien-invasive species in the United States, *Ecological Economics*, 52(3 SPEC. ISS.), pp. 273–288. doi: 10.1016/j.ecolecon.2004.10.002.

Plantegenest, M., Le May, C. and Fabre, F. 2007 Landscape epidemiology of plant diseases, *Journal of the Royal Society Interface*, 4(16), pp. 963–972. doi: 10.1098/rsif.2007.1114.

Polechova, J. and Storch, D. 2019 *Encyclopdia of Ecology*. 3rd edn. Edited by S. E. Jorgensen. Academic Press.

Préau, C., Isselin-Nondedeu, F., Sellier, Y., Bertrand, R. and Grandjean, F. 2019 Predicting suitable habitats of four range margin amphibians under climate and land-use changes in southwestern France, *Regional Environmental Change*. Regional Environmental Change, 19(1), pp. 27–38. doi: 10.1007/s10113-018-1381-z.

Préau, C., Grandjean, F., Sellier, Y., Gailledrat, M., Bertrand, R. and Isselin-nondedeu, F. 2020 Habitat patches for newts in the face of climate change: local scale assessment combining niche modelling and graph theory, *Scientific Reports*, 10(3570), pp. 1–13. doi: 10.1038/s41598-020-60479-4.

Pyšek, P. and Richardson, D. M. 2010 Invasive Species, Environmental Change and Management, and Health, *Annual Review of Environment and Resources*, 35(1), pp. 25–55. doi: 10.1146/annurev-environ-033009-095548.

Qiao, H., Soberón, J. and Peterson, A. T. 2015 No silver bullets in correlative ecological niche modelling: Insights from testing among many potential algorithms for niche estimation, *Methods in Ecology and Evolution*, 6(10), pp. 1126–1136. doi: 10.1111/2041-210X.12397.

Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M. and Guisan, A. 2006 Are niche-based species distribution models transferable in space?, *Journal of Biogeography*, 33(10), pp. 1689–1703. doi: 10.1111/j.1365-2699.2006.01466.x.

Ranjitkar, S., Xu, J., Shrestha, K. K. and Kindt, R. 2014 Ensemble forecast of climate suitability for the Trans-Himalayan Nyctaginaceae species, *Ecological Modelling*. Elsevier B.V., 282, pp. 18–24. doi: 10.1016/j.ecolmodel.2014.03.003.

Rapacciuolo, G. 2019 Strengthening the contribution of macroecological models to conservation practice, *Global Ecology and Biogeography*, 28(1), pp. 54–60. doi: 10.1111/geb.12848.

Rapacciuolo, G., Roy, D. B., Gillings, S., Fox, R., Walker, K. and Purvis, A. 2012 Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change, *PLoS ONE*, 7(7). doi: 10.1371/journal.pone.0040212.

Refsgaard, J. C. and Henriksen, H. J. 2004 Modelling guidelines - Terminology and guiding principles, *Advances in Water Resources*, 27(1), pp. 71–82. doi: 10.1016/j.advwatres.2003.08.006.

Reichenbach, T., Mobilia, M. and Frey, E. 2006 Coexistence versus extinction in the stochastic cyclic Lotka-Volterra model, *Phsyical Review*, 74, pp. 1–11. doi: 10.1103/PhysRevE.74.051907.

Reid, W. V., Mooney, H. A., Cropper, A., Capistrano, D., Carpenter, S. R., Chopra, K., Dasgupta, P., Dietz, T., … Zurek, M. B. 2005 *Ecosystems and Human Well-being: Synthesis / Millenium Ecosystem Assessment*, *Island Press*. Washington, DC. doi: 10.1196/annals.1439.003.

Reiss, H., Cunze, H., König, K., Neumann, K. and Kröncke, I. 2011 Species distribution modelling of marine benthos: A North Sea case study, *Marine Ecology Progress Series*, 442, pp. 71–86. doi: 10.3354/meps09391.

Ren-Yan, D., Xiao-Quan, K., Min-Yi, H., Wei-Yi, F. and Zhi-Gao, W. 2014 The predictive performance and stability of six species distribution models, *PLoS ONE*, 9(11). doi: 10.1371/journal.pone.0112764.

Renner, I. W. and Warton, D. I. 2013 Equivalence of MAXENT and Poisson Point Process Models for Species Distribution Modeling in Ecology, *Biometrics*, 69(1), pp. 274–281. doi: 10.1111/j.1541-0420.2012.01824.x.

Roach, N. S., Hnter, E. A., Nibbelink, N. P. and Barrett, K. 2017 Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States, *Ecosphere*, 8(3). doi: 10.1002/ecs2.1715.

Robertson, M. P., Peter, C. I., Villet, M. H. and Ripley, B. S. 2003 Comparing models for predicting species’ potential distributions: A case study using correlative and mechanistic predictive modelling techniques, *Ecological Modelling*, 164(2–3), pp. 153–167. doi: 10.1016/S0304-3800(03)00028-0.

Rödder, D. and Lötters, S. 2010 Explanative power of variables used in species distribution modelling: An issue of general model transferability or niche shift in the invasive Greenhouse frog (Eleutherodactylus planirostris), *Naturwissenschaften*, 97(9), pp. 781–796. doi: 10.1007/s00114-010-0694-7.

Rodríguez-Rey, M., Jiménez-Valverde, A. and Acevedo, P. 2013 Species distribution models predict range expansion better than chance but not better than a simple dispersal model, *Ecological Modelling*. Elsevier B.V., 256, pp. 1–5. doi: 10.1016/j.ecolmodel.2013.01.024.

Rondinini, C., Wilson, K. A., Boitani, L., Grantham, H. and Possingham, H. P. 2006 Tradeoffs of different types of species occurrence data for use in systematic conservation planning, *Ecology Letters*, 9(10), pp. 1136–1145. doi: 10.1111/j.1461-0248.2006.00970.x.

Ross, L. K., Ross, R. E., Stewart, H. A. and Howell, K. L. 2015 The influence of data resolution on predicted distribution and estimates of extent of current protection of three ‘listed’ deep-sea habitats, *PLoS ONE*, 10(10), pp. 1–19. doi: 10.1371/journal.pone.0140061.

Rougier, T., Lassalle, G., Drouineau, H., Dumoulin, N., Faure, T., Deffuant, G., Rochard, E. and Lambert, P. 2015 The combined use of correlative and mechanistic species distribution models benefits low conservation status species, *PLoS ONE*, 10(10), pp. 1–21. doi: 10.1371/journal.pone.0139194.

Ruete, A. and Leynaud, G.C., 2015. Goal-oriented evaluation of species distribution models' accuracy and precision: True Skill Statistic profile and uncertainty maps. *PeerJ PrePrints,* 3, p.e1208v1.

Le Roux, M., Redon, M., Archaux, F., Long, J., Vincent, S. and Luque, S. 2017 Conservation planning with spatially explicit models: a case for horseshoe bats in complex mountain landscapes, *Landscape Ecology*, 32(5), pp. 1005–1021. doi: 10.1007/s10980-017-0505-z.

Santika, T., 2011. Assessing the effect of prevalence on the predictive performance of species distribution models using simulated data. *Global Ecology and Biogeography*, 20(1), pp.181-192.

Sarquis, J. A., Cristaldi, M. A., Arzamendia, V., Bellini, G. and Giraudo, A. R. 2018 Species distribution models and empirical test: Comparing predictions with well-understood geographical distribution of Bothrops alternatus in Argentina, *Ecology and Evolution*, 8(21), pp. 10497–10509. doi: 10.1002/ece3.4517.

Scales, K. L., Hazen, E. L., Jacox, M. G., Edwards, C. A., Boustany, A. M., Oliver, M. J. and Bograd, S. J. 2017 Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data, *Ecography*, 40(1), pp. 210–220. doi: 10.1111/ecog.02272.

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., … Trepl, L. 2002 Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx, *Journal of Applied Ecology*, 39(2), p. 203.

Segurado, P. and Araújo, M. B. 2004 An evaluation of methods for modelling species distributions, *Journal of Biogeography*, 31(10), pp. 1555–1568. doi: 10.1111/j.1365-2699.2004.01076.x.

Senay, S. D., Worner, S. P. and Ikeda, T. 2013 Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling, *PLoS ONE*, 8(8). doi: 10.1371/journal.pone.0071218.

Seo, C., Thorne, J. H., Hannah, L. and Thuiller, W. 2009 Scale effects in species distribution models: Implications for conservation planning under climate change, *Biology Letters*, 5(1), pp. 39–43. doi: 10.1098/rsbl.2008.0476.

Seoane, J., Carrascal, L.M., Alonso, C.L. and Palomino, D., 2005. Species-specific traits associated to prediction errors in bird habitat suitability modelling. Ecological Modelling, 185(2-4), pp.299-308.

Sequeira, A. M. M., Mellin, C., Lozano-montes, H. M., Mathew, A., Babcock, R. C., Haywood, M. D. E., Meeuwig, J. J. and Caley, M. J. 2016 Transferability of predictive models of coral reef fish species richness, *Journal of Applied Ecology*, 53, pp. 64–72. doi: 10.1111/1365-2664.12578.

Sequeira, A. M. M., Mellin, C., Lozano-montes, H. M., Meeuwig, J. J., Vanderklift, M. A., Haywood, M. D. E., Babcock, R. C. and Caley, M. J. 2018a Challenges of transferring models of fish abundance between coral reefs, *PeerJ*, 6, p. e4566. doi: 10.7717/peerj.4566.

Sequeira, A. M. M., Bouchet, P. J., Yates, K. L., Mengersen, K. and Caley, M. J. 2018b Transferring biodiversity models for conservation: Opportunities and challenges, *Methods in Ecology and Evolution*, 9(5), pp. 1250–1264. doi: 10.1111/2041-210X.12998.

Shabani, F., Kumar, L. and Ahmadi, M. 2016 A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area, *Ecology and Evolution*, 6(16), pp. 5973–5986. doi: 10.1002/ece3.2332.

Shabani, F., Kumar, L. and Ahmadi, M. 2018 Assessing accuracy methods of species distribution models: AUC, Specificity, Sensitivity and the True Skill Statistic, *Global Journal of Human Social Science*, 18(1), pp. 6–18.

Shepard, D. 1968 A two-dimensional interpolation function for irregularly-spaced data, *Proceedings of the 1968 23rd ACM national conference*, pp. 517–524.

Shimwela, M., Schubert, T., Albritton, M., Halbert, S., Jones, D., Sun, X., Roberts, P., Singer, B., … van Bruggen, A. 2018 Regional Spatial-Temporal Spread of Citrus Huanglongbing Is Affected by Rain in Florida, *Phytopathology*. doi: 10.1094/PHYTO-03-18-0088-R.

Sillero, N. 2011 What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods, *Ecological Modelling*, 222(8), pp. 1343–1346. doi: 10.1016/j.ecolmodel.2011.01.018.

Singerman, A. and Useche, P. 2015 Impact of Citrus Greening on Citrus Operations in Florida, *University of Florida*, pp. 1–6.

Soberón, J. 2007 Grinnellian and Eltonian niches and geographic distributions of species, *Ecology Letters*, 10(12), pp. 1115–1123. doi: 10.1111/j.1461-0248.2007.01107.x.

Soberón, J. and Peterson, T. A. 2005 Interpretation of models of fundamental ecologicalniches and species' distributional areas, *Biodiversity Informatics*, 2, pp. 1–10.

Soininen, J. and Luoto, M. 2014 Predictability in species distributions: a global analysis across organisms, *Global Change Biology*, 23, pp. 1264–1274. doi: 10.1111/geb.12204.

Sorensen, P., Wachs, M., Min, E. Y., Kofner, A. and Ecola, L. 2008 *Moving Los Angeles: Short-term policy options for improving transportation*. Rand Corporation.

Spreen, T. H., Baldwin, J. and Futch, S. H. 2014 An Economic Assessment of the Impact of Huanglongbing on Citrus Tree Plantings in Florida, *Horticultural Science*, 49(8), pp. 1052–1055.

Srivastava, V., Lafond, V. and Griess, V. C. 2019 Species distribution models (SDM): Applications, benefits and challenges in invasive species management, *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 14(December). doi: 10.1079/PAVSNNR201914020.

Steinbauer, M. J., Burns, A. E., Hall, A., Riegler, M. and Taylor, G. S. 2014 Nutritional enhancement of leaves by a psyllid through senescence-like processes: insect manipulation or plant defence ?, *Oecologia*, 176, pp. 1061–1074. doi: 10.1007/s00442-014-3087-3.

Stewart, J. A. E., Perrine, J. D., Nichols, L. B., Thorne, J. H., Millar, C. I., Goehring, K. E., Massing, C. P. and Wright, D. H. 2015 Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California, *Journal of Biogeography*, 42(5), pp. 880–890. doi: 10.1111/jbi.12466.

Stokland, J. N., Halvorsen, R. and Støa, B. 2011 Species distribution modelling-Effect of design and sample size of pseudo-absence observations, *Ecological Modelling*. Elsevier B.V., 222(11), pp. 1800–1809. doi: 10.1016/j.ecolmodel.2011.02.025.

Strauss, B. and Biedermann, R. 2007 Evaluating temporal and spatial generality: How valid are species-habitat relationship models?, *Ecological Modelling*, 204(1–2), pp. 104–114. doi: 10.1016/j.ecolmodel.2006.12.027.

Suárez-Seoane, S., Virgós, E., Terroba, O., Pardavila, X. and Barea-Azcón, J. M. 2014 Scaling of species distribution models across spatial resolutions and extents along a biogeographic gradient. The case of the Iberian mole Talpa occidentalis, *Ecography*, 37(3), pp. 279–292. doi: 10.1111/j.1600-0587.2013.00077.x.

Suarez, A. V., Holway, D. A. and Case, T. J. 2001 Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants, *Proceedings of the National Academy of Sciences*, 98(3), pp. 1095–1100. doi: 10.1073/pnas.98.3.1095.

Swanson, A. K., Dobrowski, S. Z., Finley, A. O., Thorne, J. H. and Schwartz, M. K. 2013 Spatial regression methods capture prediction uncertainty in species distribution model projections through time, *Global Ecology and Biogeography*, 22(2), pp. 242–251. doi: 10.1111/j.1466-8238.2012.00794.x.

Syfert, M. M., Smith, M. J. and Coomes, D. A. 2013 The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models, *PLoS ONE*, 8(2). doi: 10.1371/journal.pone.0055158.

Syphard, A. D. and Franklin, J. 2009 Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors, *Ecography*, 32(6), pp. 907–918. doi: 10.1111/j.1600-0587.2009.05883.x.

Tang, L. and Shao, G. 2015 Drone remote sensing for forestry research and practices, *Journal of Forestry Research*. Northeast Forestry University, 26(4), pp. 791–797. doi: 10.1007/s11676-015-0088-y.

Thein, M. M., Jamjanya, T., Kobori, Y. and Hanboonsong, Y. 2012 Dispersal of the leafhoppers Matsumuratettix hiroglyphicus and Yamatotettix flavovittatus (Homoptera: Cicadellidae), vectors of sugarcane white leaf disease, *Appl. Entomol. Zool*, pp. 255–262. doi: 10.1007/s13355-012-0117-7.

Thuiller, W., Brotons, L., Araújo, M. B. and Lavorel, S. 2004 Effects of restricting environmental range of data to project current and future species distributions, *Ecography*, 2(September 2003).

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T. and Prentice, I. C. 2005a Climate change threats to plant diversity in Europe, *Proceedings of the National Academy of Sciences*, 102(23), pp. 8245–8250.

Thuiller, W., Richardson, D. M., Py Ek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. 2005b Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale, *Global Change Biology*, 11(12), pp. 2234–2250. doi: 10.1111/j.1365-2486.2005.01018.x.

Tobalske, C. 2002 *Effects of spatial scale on the predictive ability of habitat models for the green woodpecker in Switzerland.* Covelo: Island Press.

Torres, L. G., Sutton, P. J. H., Thompson, D. R., Delord, K., Weimerskirch, H., Sagar, P. M., Sommer, E., Dilley, B. J., … Phillips, R. A. 2015 Poor Transferability of Species Distribution Models for a Pelagic Predator, the Grey Petrel, Indicates Contrasting Habitat Preferences across Ocean Basins, *PLoS ONE*, 10(3), pp. 1–18. doi: 10.1371/journal.pone.0120014.

Tran, D. X., Pla, F., Latorre-Carmona, P., Myint, S. W., Caetano, M. and Kieu, H. V. 2017 Characterizing the relationship between land use land cover change and land surface temperature, *ISPRS Journal of Photogrammetry and Remote Sensing*. International Society for Photogrammetry and Remote Sensing, Inc. (ISPRS), 124, pp. 119–132. doi: 10.1016/j.isprsjprs.2017.01.001.

Trivedi, M. R., Berry, P. M., Morecroft, M. D. and Dawson, T. P. 2008 Spatial scale affects bioclimate model projections of climate change impacts on mountain plants, *Global Change Biology*, 14(5), pp. 1089–1103. doi: 10.1111/j.1365-2486.2008.01553.x.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. and Kadmon, R. 2007 A comparative evaluation of presence-only methods for modelling species distribution, *Diversity and Distributions*, 13(4), pp. 397–405. doi: 10.1111/j.1472-4642.2007.00346.x.

Tuanmu, M. N., Viña, A., Roloff, G. J., Liu, W., Ouyang, Z., Zhang, H. and Liu, J. 2011 Temporal transferability of wildlife habitat models: Implications for habitat monitoring, *Journal of Biogeography*, 38(8), pp. 1510–1523. doi: 10.1111/j.1365-2699.2011.02479.x.

USDA 2012 *Florida Citrus Statistics 2010-2011*. Florida.

Václavík, T. and Meentemeyer, R. K. 2009 Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions?, *Ecological Modelling*, 220(23), pp. 3248–3258. doi: 10.1016/j.ecolmodel.2009.08.013.

Václavík, T., Kanaskie, A., Hansen, E. M., Ohmann, J. L. and Meenterneyer, R. K. 2010 Predicting potential and actual distribution of sudden oak death in Oregon: Prioritizing landscape contexts for early detection and eradication of disease outbreaks, *Forest Ecology and Management*, 260, pp. 1026–1035.

Vannini, A., Natili, G., Anselmi, N., Montaghi, A. and Vettraino, A. M. 2010 Distribution and gradient analysis of Ink disease in chestnut forests, *Forest Pathology*, 40, pp. 73–86. doi: 10.1111/j.1439-0329.2009.00609.x.

Vanreusel, W., Maes, D. and Van Dyck, H. 2007 Transferability of species distribution models: A functional habitat approach for two regionally threatened butterflies, *Conservation Biology*, 21(1), pp. 201–212. doi: 10.1111/j.1523-1739.2006.00577.x.

Varela, S., Anderson, R. P., García-valdés, R. and Fernández-gonzález, F. 2014 Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models, *Ecography*, 37, pp. 1084–1091. doi: 10.1111/j.1600-0587.2013.00441.x.

Varela, S., Rodriguez, J. and Lobo, J. M. 2009 Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena, *Journal of Biogeography*, 36, pp. 1645–1655. doi: 10.1111/j.1365-2699.2009.02125.x.

Vaughan, I. P. and Ormerod, S. J. 2003 Improving the Quality of Distribution Models for Conservation by Addressing Shortcomings in the Field Collection of Training Data, *Conservation Biology*, 17(6), pp. 1601–1611. doi: 10.1111/j.1523-1739.2003.00359.x.

Verbruggen, H., Tyberghein, L., Belton, G. S., Mineur, F., Jueterbock, A., Hoarau, G., Gurgel, C. F. D. and De Clerck, O. 2013 Improving Transferability of Introduced Species' Distribution Models: New Tools to Forecast the Spread of a Highly Invasive Seaweed, *PLoS ONE*, 8(6), pp. 1–13. doi: 10.1371/journal.pone.0068337.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., … Pyšek, P. 2011 Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems, *Ecology Letters*, 14(7), pp. 702–708. doi: 10.1111/j.1461-0248.2011.01628.x.

Volterra, V. 1926 Fluctuations in the abundance of a species considered mathematically, *Nature*, 118(2972), pp. 558–560. doi: 10.1038/118558a0.

Vurro, M., Bonciani, B. and Vannacci, G. 2010 Emerging infectious diseases of crop plants in developing countries: impact on agriculture and socio-economic consequences, *Food Security*, 2, pp. 113–132. doi: 10.1007/s12571-010-0062-7.

Wallinga, J. and Lipsitch, M. 2007 How generation intervals shape the relationship between growth rates and reproductive numbers, *Proceedings of the Royal Society B: Biological Sciences*, 274(1609), pp. 599–604. doi: 10.1098/rspb.2006.3754.

Wang, L. and Jackson, D. A. 2014 Shaping up model transferability and generality of species distribution modeling for predicting invasions: implications from a study on Bythotrephes longimanus, *Biological Invasions*, 16(10), pp. 2079–2103. doi: 10.1007/s10530-014-0649-6.

Warren, D. L., Matzke, N. J. and Iglesias, T. L. 2020 Evaluating presence-only species distribution models with discrimination accuracy is uninformative for many applications, *Journal of Biogeography*, 47(1), pp. 167–180. doi: 10.1111/jbi.13705.

Watson, A. and Wilson, J. D. 2018 Seven decades of mountain hare counts show severe declines where high-yield recreational game bird hunting is practised, *Journal of Applied Ecology*, 55(6), pp. 2663–2672. doi: 10.1111/1365-2664.13235.

Watson, D. F. and Philip, G. M. 1985 A refinement of inverse distance weighted interpolation., *Geoprocessing*, 2, pp. 315–327.

Webber, B. L., Yates, C. J., Le Maitre, D. C., Scott, J. K., Kriticos, D. J., Ota, N., Mcneill, A., Le Roux, J. J. and Midgley, G. F. 2011 Modelling horses for novel climate courses: Insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models, *Diversity and Distributions*, 17(5), pp. 978–1000. doi: 10.1111/j.1472-4642.2011.00811.x.

Wenger, S. J. and Olden, J. D. 2012 Assessing transferability of ecological models: An underappreciated aspect of statistical validation, *Methods in Ecology and Evolution*, 3(2), pp. 260–267. doi: 10.1111/j.2041-210X.2011.00170.x.

Werkowska, W., Ana, L., Real, R. and Acevedo, P. 2017 A practical overview of Transferability in species distribution modelling, *Environmental Reviews*, 25(1), pp. 127–133.

Whelan, J. 1985 The population and distribution of the mountain hare (Lepus timidus L.) on farmland., *Irish Naturalists' Journal*, 21(12), pp. 532–534.

Wiens, J. A. 1977 On competition and variable environments, *American Scientist*, 65, pp. 590–597.

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A. and Snyder, M. A. 2009 Niches, models, and climate change: Assessing the assumptions and uncertainties, *Proceedings of the National Academy of Sciences*, 106(Supplement_2), pp. 19729–19736. doi: 10.1073/pnas.0901639106.

Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. and Davis, C. C. 2008 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change, *Proceedings of the National Academy of Sciences of the United States of America*, 105(44), pp. 17029–17033. doi: 10.1073/pnas.0806446105.

Willis, K. J. and Whittaker, R. J. 2002 Species diversity--scale matters, *Science*, pp. 1245–1248.

Wilson, C. D., Roberts, D. and Reid, N. 2011 Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using Margaritifera margaritifera (L.), *Biological Conservation*. Elsevier Ltd, 144(2), pp. 821–829. doi: 10.1016/j.biocon.2010.11.014.

Wilson, M. E. 1995 Travel and the Emergence of Infectious Diseases, *Emerging Infectious Diseases*, 1(2), pp. 39–46.

Wisz, M. S. and Guisan, A. 2009 Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data, *BMC Ecology*, 9, pp. 1–13. doi: 10.1186/1472-6785-9-8.

Wogan, G. O. U. 2016 Life History Traits and Niche Instability Impact Accuracy and Temporal Transferability for Historically Calibrated Distribution Models of North American Birds, *PLoS ONE*, 11(3), p. e0151024. doi: 10.1371/journal.pone.0151024.

WorldClim 2020 *WorldClim Data Format*. Available at: https://worldclim.org/data/v1.4/formats.html (Accessed: 17 April 2020).

Xu, C. F., Xia, Y. H., Li, K. B. and Ke, C. 1988 Further Study of the Transmission of Citrus Huanglungbin by a Psyllid, Diaphorina citri Kuwayama, *International Organization of Citrus Virologists Conference Proceedings (1957-2010)*, 10(10).

Yackulic, C. B., Chandler, R. B., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H. and Veran, S. 2013 Presence-only modelling using MAXENT: When can we trust the inferences?, *Methods in Ecology and Evolution*, 4(3), pp. 236–243. doi: 10.1111/2041-210x.12004.

Yates, D. N., Kittel, T. G. F. and Cannon, R. F. 2000 Comparing the Correlative Holdridgemodel to Mechanistic Biogeographicalmodels for Assessing Vegetation Distribution Response to Climatic Change, *Climatic change*, 44, pp. 59–87.

Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., Fielding, A. H., Bamford, A. J., … Sequeira, A. M. M. 2018 Outstanding Challenges in the Transferability of Ecological Models, *Trends in Ecology and Evolution*. Elsevier Ltd, 33(10), pp. 790–802. doi: 10.1016/j.tree.2018.08.001.

Yee, T. W. and Dirnböck, T. 2009 Models for analysing species' presence/absence data at two time points, *Journal of Theoretical Biology*, 259(4), pp. 684–694. doi: 10.1016/j.jtbi.2009.05.004.

Youcefi, A., Baaloudj, A., Zebsa, R., Mahdjoub, H., Bensakhri, Z., Bensouilah, S., Amari, H., Si Bachir, A. and Khelifa, R., 2019. Weather conditions affect the collective roosting behaviour of the Cattle Egret Bubulcus ibis. Bird Study, 66(3), pp.413-419.

Zanini, F., Pellet, J. and Schmidt, B. R. 2009 The transferability of distribution models across regions: An amphibian case study, *Diversity and Distributions*, 15(3), pp. 469–480. doi: 10.1111/j.1472-4642.2008.00556.x.

Zhu, C. and Yin, G. 2009 Journal of Mathematical Analysis and Applications On competitive Lotka–Volterra model in random environments, *Journal of Mathematical Analysis and Applications*. Elsevier Inc., 357(1), pp. 154–170. doi: 10.1016/j.jmaa.2009.03.066.

Zimmermann, N. E., Edwards, T. C., Graham, C. H., Pearman, P. B. and Svenning, J. C. 2010 New trends in species distribution modelling, *Ecography*, 33(6), pp. 985–989. doi: 10.1111/j.1600-0587.2010.06953.x.

Zuckerberg, B., Fink, D., La Sorte, F. A., Hochachka, W. M. and Kelling, S. 2016 Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling, *Diversity and Distributions*, 22(6), pp. 717–730. doi: 10.1111/ddi.12428.

Zurell, D., Elith, J. and Schro, B. 2012 Predicting to new environments: tools for visualizing model behaviour and impacts on mapped distributions, *Diversity and Distributions*, 18, pp. 628–634. doi: 10.1111/j.1472-4642.2012.00887.x.

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., … Merow, C. 2020 A standard protocol for reporting species distribution models, *Ecography*, pp. 1–17. doi: 10.1111/ecog.04960.

Zurell, D., Jeltsch, F., Dormann, C. F. and Schro, B. 2009 Static species distribution models in dynamically changing systems: how good can predictions really be?, *Ecography*, 32, pp. 733–744. doi: 10.1111/j.1600-0587.2009.05810.x.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., … Zimmermann, N. E. 2016 Benchmarking novel approaches for modelling species range dynamics, *Global change biology*, 22(8), pp. 2651–2664. doi: 10.1111/gcb.13251.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. 2009 GLM and GAM for count data, in *Mixed effects models and extensions in ecology with R*. New York, NY: Springer, pp. 209–243.

Appendices

Appendix I: Search details for Figure 1.5

The ISI Web of Science (webofknowledge.com) was searched for peer-reviewed journal articles written in English within the following research areas: Biodiversity and Conservation, Environmental Sciences and Ecology, Fisheries, Marine and Freshwater Biology, Plant Sciences, and Zoology. Ecological models were defined as per Elith & Leathwick (2009), using the following keywords as search terms: “SDM*”, "Species distribution model*", "bioclimatic model*", "climat* envelope", "ecological niche model*", "habitat model*", "resource selection function*", "range map*". Journal articles addressing transferability were identified by refining the search query, using the following additional search terms: “transferab*”, “extrapol*”, "cross-applicabil*", “generalit*”, “generalizability”, “transference”, "hindcast*","backcast*", "project*" and "forecast*". * denotes wildcard characters enabling additional letters to be added to the word with a length of 0 to unlimited characters, for example: Transferab* will return transferable and transferability. Results shown in Figure 1.5 are valid as of 3rd of August 2020.

Appendix II: Additional details and references for Figure 1.6

List of peer-reviewed publications used to build Figure 1.6, sorted according to corresponding number in the figure. In addition, how the level of transferability was determined for building the figure is outlined.

1. Butterflies (multiple species; pictured: green hairstreak, *Callophrys rubi*)
    - **Reference:** Vanreusel, W., Maes, D. and Van Dyck, H., 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation biology,* 21(1), pp.201-212.
    - **Number of species:** 2 species of butterfly
    - **Transferred between:** 3 nature reserves in Northern Belgium
    - **Transferability:** Good
    - **Justification:** "[…] our resource-based models showed high levels of transferability among areas. The AUC values of among-area transferred models were typically lower than for internal tests but were still good-to-excellent […]"

2. Invasive seaweed, *Caulerpa cylindracea*
    - **Reference:** Verbruggen, H. *et al.* (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLoS One 8, e68337.
    - **Number of species:** 1
    - **Transferred between**: Native range (Australia) and invaded range (Mediterranean)
    - **Transferability:** Good
    - **Justification:** "We presented an SDM of *Caulerpa cylindracea* that achieves very high predictive power […]. Reducing the set of predictors to those anticipated to be of global significance resulted in a strong improvement of SDM transferability."

3. Coral reef fishes (multiple species; pictured: bluestripe snapper, *Lutjanus kasmira*)
    - **Reference:** Sequeira, A.M. *et al.* (2016) Transferability of predictive models of coral reef fish species richness. J. Appl. Ecol. 53, 64-72.
    - **Number of species:** Reef fish species from 46 families
    - **Transferred between:** Great Barrier Reef, Queensland and Ningaloo Reef, Western Australia, Australia.
    - **Transferability:** Good
    - **Justification:** "Our results suggest that both data and models developed for a well- studied reef ecosystem (e.g. GBR) can provide useful information for understanding other coral reefs."

4. Barred owl, *Strix varia*
   - **Reference:** Peterson, A.T. and Robins, C.R., 2003. Using ecological-niche modeling to predict barred owl invasions with implications for spotted owl conservation. *Conservation Biology,* 17(4), pp.1161-1165.
   - **Number of species:** 1
   - **Transferred between:** Eastern USA and the Pacific Northwest, USA
   - **Transferability:** Good
   - **Justification:** "[…] the ecological niche model developed on the native range of the Barred Owl had highly significant predictive ability even on the invaded range of the species in the Pacific Northwest."

5. Smooth crotalaria, *Crotalaria pallida*
   - **Reference:** Fonseca, R.L. *et al.* (2006) Predicting invasive potential of smooth crotalaria (*Crotalaria pallida*) in Brazilian national parks based on African records. Weed Sci. 54, 458-463.
   - **Number of species:** 1
   - **Transferred between:** Africa and Brazil
   - **Transferability:** Good
   - **Justification:** "Models for the native range and their projections to South America showed good predictive ability when challenged with independent occurrence data."

6. Eurasian badger, *Meles meles*
   - **Reference:** Acevedo, P. *et al.*, 2014. Generalizing and transferring spatial models: a case study to predict Eurasian badger abundance in Atlantic Spain. *Ecological modelling,* 275, 1-8.
   - **Number of species:** 1
   - **Transferred between:** the UK and Spain
   - **Transferability:** Good
   - **Justification:** "The new model […] accurately predicted badger abundance in Atlantic Spain."

7. Blue whale, *Balaenoptera musculus*
   - **Reference:** Redfern, J.V. et al. (2017) Predicting cetacean distributions in data-poor marine ecosystems. Divers. Distrib. 23, 394-408.
   - **Number of species:** 1
   - **Transferred between:** Eastern Pacific in the California Current and Eastern Tropical Pacific areas
   - **Transferability:** Mixed - varied across space
   - **Justification:** "Ecosystem-specific blue whale models performed well in their respective ecosystems but were not transferable. […] However, […] predictions of blue whale habitat in the NIO from the models built with

combined CC and ETP data compare favourably to hypotheses about NIO blue whale distributions."

8. Butterflies (multiple species; pictured: Black-veined white, *Aporia crataegi*)
    - **Reference:** Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J., Wisz, M.S. and Luoto, M., 2013. Testing species distribution models across space and time: high latitude butterflies and recent warming. *Global Ecology and Biogeography*, 22(12), pp.1293-1303.
    - **Number of species:** 77 species of butterfly found in Finland
    - **Transferred between:** Finland
    - **Transferability:** Mixed - varied by species/mobility
    - **Justification:** "SDMs showed fair to good model fits when modelling butterfly distributions under climate change […] SDMs performed less well for highly mobile species and for species with long flight seasons and large ranges."

9. Holarctic invasive plants (multiple species; pictured: Common Vetch, *Vicia sativa*)
    - **Reference:** Petitpierre, B. *et al.*, 2017. Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plants invasions. *Global Ecol. Biogeogr*. 26: 275-287
    - **Number of species:** 50
    - **Transferred between:** North America, Europe and Australia
    - **Transferability:** Mixed - varied by species
    - **Justification:** "We found 45 species with a transferable […] and five species with bad or poor predictive SDMs in the invaded range".

10. Birds (multiple species; pictured: Mourning dove, *Zenaida macroura*)
    - **Reference:** Peterson, A.T. *et al.* (2007) Transferability and model evaluation in ecological niche modeling: A comparison of GARP and MaxEnt. Ecography 30, 550-560.
    - **Number of species:** 3
    - **Transferred between:** USA
    - **Transferability:** Mixed - varied by modelling technique.
    - **Reference: "**Challenging the two algorithms with predicting into unsampled regions […] changed the picture considerably. GARP models continued to reconstruct much of the species' known distributions. MaxEnt models, on the other hand, produced an odd pattern […] MaxEnt models failed to make general predictions unless very low probability value thresholds were considered."

11. Fish (multiple species; pictured: Blacknose dace, Rhinichthys atratulus)
    - **Reference:** Huang, J. and Frimpong, E.A., 2016. Limited transferability of stream-fish distribution models among river catchments: reasons and implications. *Freshwater biology,* 61(5), pp.729-744.

- **Number of species:** 21
- **Transferred between:** Rivers in the USA
- **Transferability:** Mixed - varied by modelling technique.
- **Reference: “**[…] SDMs showed moderate to limited transferability among river catchments. Model transferability varied by species, and by pair of training and prediction catchments. Good transferability was achieved for Macrhybopsis hyostoma, Etheostoma gracile and Aphredoderus sayanus when SDMs were transferred between Brazos River and Colorado River, and for Rhinichthys atratulus when the SDM was transferred from Illinois River to New River”

12. Grey petrel, *Procellaria cinerea*
    - **Reference:** Torres, L.G. et al., 2015. Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. PLoS One 10, e0120014.
    - **Number of species:** 1
    - **Transferred between:** 3 colonies in the Southern Hemisphere, on Antipodes Island, Kerguelen Island and Marion Island.
    - **Transferability:** Poor
    - **Justification:** “[…] All model validation tests, including of the combined model, determined strong interpolation but weak extrapolation capabilities […] when the population models were extrapolated between regions, the models demonstrated poor predictive capacity and calibration.”

13. Clapper rail, *Rallus crepitans*
    - **Reference:** Roach, N.S., Hunter, E.A., Nibbelink, N.P. and Barrett, K., 2017. Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States. *Ecosphere* 8(3).
    - **Number of species:** 1
    - **Transferred between:** Marshland in the states of South Carolina and Georgia
    - **Transferability:** Poor
    - **Justification:** “Models did not transfer well from one state to another.”

14. Asian tiger mosquito, *Stegomyia albopicta*
    - **Reference:** Medley, K.A. 2010., Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecol. Biogeogr.* 19, 122-133.
    - **Number of species:** 1
    - **Transferred between:** Native range (Southeast Asia) and Europe, North America and South America.
    - **Transferability:** Poor

- **Justification:** “The native model failed to predict an entire region of occurrences in South America, approximately 20% of occurrences in North America and nearly all Italian occurrences of *A. albopictus*.”

15. Amphibians (multiple species; pictured: common toad, *Bufo bufo*)
    - **Reference:** Zanini, F. *et al.* 2009. The transferability of distribution models across regions: An amphibian case study. *Divers. Distrib*. 15, 469–480.
    - **Number of species:** 6
    - **Transferred between:** Ponds throughout Switzerland
    - **Transferability:** Poor
    - **Justification:** “Different species are affected by different landscape variables at different spatial scales and these effects may vary geographically, resulting in a generally low transferability of distribution models across regions. […] Region-by-landscape interactions suggest that models are specific to a region and cannot be generalized to other regions.”

16. Plants (multiple species; pictured: Spotted St. John’s-wort, *Hypericum maculatum*)
    - **Reference:** Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. and Guisan, A., 2006. Are niche-based species distribution models transferable in space?. *Journal of biogeography*, 33(10), pp.1689-1703.
    - **Number of species:** 54
    - **Transferred between:** Austria and Switzerland
    - **Transferability:** Poor
    - **Justification:** “Overall, we observed a weak geographical transferability for the 54 SDMs […]”

Appendix III: ODMAP Protocols for Chapters 2 to 4

Table A1 ODMAP reporting for Chapter 2

ODMAP element	**Contents**
OVERVIEW	
Authorship	• **Author:** Joshua Copping • **Title:** Does the number of background points impact species distribution model performance and transferability?
Model objective	• **Objective:** Forecast/Transfer • **Main target output:** Probability of species presence
Taxon	20 British and Irish plant and animal species
Location	The British Isles: mainland Great Britain and the Island of Ireland
Scale of analysis	• **Spatial extent:** Longitude 10.8° W – 1.8° E, Latitude 49.8° N – 61.5° N • **Spatial resolution:** 30 arc-seconds • **Temporal resolution**: Data contained occurrences between 1970 and 2010 • **Type of extent boundary**: Natural
Biodiversity data overview	• **Observation type:** Citizen science, field survey, standardised monitoring data • **Response/Data type:** Presence-only
Type of predictors	Climatic
Conceptual model / Hypotheses	I tested whether the number of background points a model is trained with affects predictive performance and spatial transferability using three commonly-used SDM algorithms.
Assumptions	I assumed that species were at pseudo-equilibrium with the environment, that the predictors used were drivers of the species' distribution.
SDM algorithms	• **Algorithms**: SDMs were built using 3 popular modelling algorithms; boosted regression trees, BRT; generalised linear models, GLM; maximum entropy, Maxent. • **Complexity**: Models were simple, with no temporal or stochastic aspects and no biological relationships. The data determined the model complexity in BRT and Maxent. • **Model averaging**: No ensembles were used; however, results were expressed as the average of the 1,000 bootstrapped runs per model algorithm.
Model workflow	Variables were checked for multicollinearity using Spearman's rank correlation coefficient and the variance inflation factor, with any colinear variables removed. Models were fit to the 20 species in the reference area using the three algorithms (BRT, GLM and Maxent), and run with 1,000 bootstrapped iterations. This was performed using 15 different quantities of background points (10,000 background and prevalence values ranging from 0.06 to 0.9). Model performance was assessed with AUC. Models were then transferred to the target area for each of the combinations of background point quantities/prevalence levels and then assessed using AUC.
Software	• **Software**: Analyses were performed in R version 3.6.1 (R Core Team, 2016), using the 'sdm' R package version 1.0-81 (Naimi & Araújo, 2016) • **Data availability**: The raw data are available at: www.gbif.org/occurrence/download/0021091-200613084148143

DATA	
Biodiversity data	• **Taxon names:** *Acrocephalus scirpaceus, Asplenium scolopendrium, Bombus jonellus, Bubulcus ibis, Chorthippus brunneus, Drosera rotundifolia, Gonepteryx rhamni, Lagopus lagopus, Lasiommata megera, Lepus timidus, Linaria flavirostris, Lissotriton vulgaris, Martes martes, Narthecium ossifragum, Quercus petraea, Rhinolophus hipposideros, Taxus baccata, Tyria jacobaeae, Tyto alba, Zootoca vivipara* • **Ecological level:** Individuals • **Data source**: DOI 10.15468/dl.hxbdp6 • **Sampling design**: Data were from an online repository, with occurrences collected using a range of survey methods. • **Sample size per taxon:** Species, reference area, target area: *Acrocephalus scirpaceus*, 2184, 74; *Asplenium scolopendrium*, 4505, 297; *Bombus jonellus*, 936, 532; *Bubulcus ibis*, 137, 81; *Chorthippus brunneus*, 7865, 203; *Drosera rotundifolia*, 6243, 97; *Gonepteryx rhamni*, 5073, 466; *Lagopus lagopus*, 2731, 858; *Lasiommata megera*, 3080, 106; *Lepus timidus*, 3774, 5495; *Linaria flavirostris*, 2319, 83; *Lissotriton vulgaris*, 2790, 162; *Martes martes*, 2056, 1622; *Narthecium ossifragum*, 8667, 101; *Quercus petraea*, 3811, 105; *Rhinolophus hipposideros*, 1202, 554; *Taxus baccata*, 6764, 95; *Tyria jacobaeae*, 4902, 112; *Tyto alba*, 7533, 786; *Zootoca vivipara*, 3883, 151. • **Data cleaning/filtering**: Data were initially filtered before downloading on the GBIF website. Records only included verified occurrences within the countries and timeframe of interest and collected through human observation. • **Background data**: Background points were generated in random geographic space within the study area. 10,000 points were initially use, testing the following range of prevalence values for each species. Prevalence values tested = 0.06, 0.09, 0.1, 0.11, 0.13, 0.14, 0.17, 0.2, 0.25, 0.33, 0.5, 0.66, 0.75, 0.9.
Data partitioning	Data was partitioned into 70% training and 30% test. Model performance was assessed using bootstrapping with 1,000 replicates.
Predictor variables	• **Predictor variables:** Isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of warmest quarter. • **Data sources:** Predictors were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data had a resolution of 30 arc-seconds and covered the area of England, Scotland and Wales: Longitude 7.4° W – 1.8° E, Latitude 49.8° N – 61.5° N. • **Geographic projection:** WGS84 • **Temporal extent:** 1970 – 2000
Transfer data	• **Data sources:** The predictors used were the same as in the reference area and were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data had a resolution of 30 arc-seconds and covered the area of Ireland and Northern Ireland: Longitude 10.8° W – 5.4° E, Latitude 51.2° N – 55.5° N. • **Temporal extent:** 1970 – 2000 • **Models and scenarios used:** Spatial transfers were carried out, using models trained in mainland Great Britain and transferred across the Irish Sea to the Island of Ireland.

MODEL	
Variable pre-selection	Variables were chosen based on the assumption that climate was the main constraint in the distribution of the 20 species chosen. In addition, the ease of freely available bioclimate data, similarity between the reference and target area and the suitability of climate as a predictor at this scale (Pearson & Dawson, 2003) were also reasons for predictor choice.
Multicollinearity	Multicollinearity between climatic predictors was assessed using the Spearman's rank correlation coefficient and variance inflation factor. Variables that were strongly correlated ($\|rs\| > 0.5$ and/or $VIF > 7$) were removed using stepwise reduction, until the 12 listed in the "data" section remained.
Model settings	Generalised Linear Models (GLM) with linear terms using a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature classes available for automatic selection based on best fit for the data; Boosted Regression Trees (BRT) with family = bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01. All models were trained with 70% and tested with 30% of the data. 1,000 iterations were performed with bootstrapping.
Model estimates	Bootstrapping was used with 1,000 iterations to generate performance statistics and ensure no over reliance upon a single occurrence point.
Non-independence analysis	None
Threshold selection	Outputs were kept as continuous predictions, rather than a binary presence/absence.
ASSESSMENT	
Performance statistics	Model performance was assessed using the average of the Receiver Operator Characteristic and Area Under the Curve from 1,000 bootstrap runs.
Plausibility checks	Maps of modelled predictions were compared to the IUCN known distribution.
PREDICTION	
Prediction output	Predictions of presence probability, scaled from 0 to 1.
Uncertainty quantification	Model outputs were compared to assess algorithmic uncertainty.

Table A2 ODMAP reporting for Chapter 3

ODMAP element	Contents
OVERVIEW	
Authorship	• **Author:** Joshua Copping • **Title:** Does predictor resolution influence model transferability?
Model objective	• **Objective:** Forecast/Transfer • **Main target output:** Probability of species presence
Taxon	20 British and Irish plant and animal species
Location	The British Isles: mainland Great Britain and the Island of Ireland
Scale of analysis	• **Spatial extent:** Longitude 10.8° W – 1.8° E, Latitude 49.8° N – 61.5° N • **Spatial resolution:** 30 arc-seconds, 2.5 arc-minutes, 5 arc-minutes & 10 arc-minutes. • **Temporal resolution**: Data contained occurrences between 1970 and 2010 • **Type of extent boundary**: Natural
Biodiversity data overview	• **Observation type:** Citizen science, field survey, standardised monitoring data • **Response/Data type:** Presence-only
Type of predictors	Climatic
Conceptual model / Hypotheses	I examined how the spatial resolution of predictor data influences predictive performance and spatial transferability using three commonly used SDM algorithms.
Assumptions	I assumed that species were at pseudo-equilibrium with the environment, that the predictors used were drivers of the species' distribution.
SDM algorithms	• **Algorithms**: SDMs were built using 3 popular modelling algorithms; boosted regression trees, BRT; generalised linear models, GLM; maximum entropy, Maxent. • **Complexity**: Models were simple, with no temporal or stochastic aspects and no biological relationships. The data determined the model complexity in BRT and Maxent. • **Model averaging**: No ensembles were used; however, results were expressed as the average of the 1,000 bootstrapped runs per model algorithm.
Model workflow	Variables were checked for multicollinearity using Spearman's rank correlation coefficient and the variance inflation factor, with any colinear variables removed. Models were fit to the 20 species in the reference area using the three algorithms (BRT, GLM and Maxent), and run with 1,000 bootstrapped iterations. Models were trained using data in 4 different resolutions and the performance was assessed with AUC. Models were then transferred to the target area for each combination of the 4 resolutions and again assessed using AUC.
Software	• **Software**: Analyses were performed in R version 3.6.1 (R Core Team, 2016), using the 'sdm' R package version 1.0-81 (Naimi & Araújo, 2016) • **Data availability**: The raw data are available at: www.gbif.org/occurrence/download/0021091-200613084148143

DATA	
Biodiversity data	• **Taxon names:** *Acrocephalus scirpaceus, Asplenium scolopendrium, Bombus jonellus, Bubulcus ibis, Chorthippus brunneus, Drosera rotundifolia, Gonepteryx rhamni, Lagopus lagopus, Lasiommata megera, Lepus timidus, Linaria flavirostris, Lissotriton vulgaris, Martes martes, Narthecium ossifragum, Quercus petraea, Rhinolophus hipposideros, Taxus baccata, Tyria jacobaeae, Tyto alba, Zootoca vivipara* • **Ecological level:** Individuals • **Data source**: DOI 10.15468/dl.hxbdp6 • **Sampling design**: Data were from an online repository, with occurrences collected using a range of survey methods. • **Sample size per taxon:** Species, reference area, target area: *Acrocephalus scirpaceus*, 2184, 74; *Asplenium scolopendrium*, 4505, 297; *Bombus jonellus*, 936, 532; *Bubulcus ibis*, 137, 81; *Chorthippus brunneus*, 7865, 203; *Drosera rotundifolia*, 6243, 97; *Gonepteryx rhamni*, 5073, 466; *Lagopus lagopus*, 2731, 858; *Lasiommata megera*, 3080, 106; *Lepus timidus*, 3774, 5495; *Linaria flavirostris*, 2319, 83; *Lissotriton vulgaris*, 2790, 162; *Martes martes*, 2056, 1622; *Narthecium ossifragum*, 8667, 101; *Quercus petraea*, 3811, 105; *Rhinolophus hipposideros*, 1202, 554; *Taxus baccata*, 6764, 95; *Tyria jacobaeae*, 4902, 112; *Tyto alba*, 7533, 786; *Zootoca vivipara*, 3883, 151. • **Data cleaning/filtering**: Data were initially filtered before downloading on the GBIF website. Records only included verified occurrences within the countries and timeframe of interest and collected through human observation. • **Background data**: Background points were generated in random geographic space with an equal number to the number of presences per species (prevalence = 0.5).
Data partitioning	Data was partitioned into 70% training and 30% test. Model performance was assessed using bootstrapping with 1,000 replicates.
Predictor variables	• **Predictor variables:** Isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of warmest quarter. • **Data sources:** Predictors were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data were used in 4 resolutions: 30 arc-seconds, 2.5 arc-minutes, 5 arc-minutes & 10 arc-minutes, and covered the area of England, Scotland and Wales: Longitude 7.4° W – 1.8° E, Latitude 49.8° N – 61.5° N. • **Geographic projection:** WGS84 • **Temporal extent:** 1970 – 2000
Transfer data	• **Data sources:** The predictors used were the same as in the reference area and were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data were used in 4 resolutions: 30 arc-seconds, 2.5 arc-minutes, 5 arc-minutes & 10 arc-minutes, and covered the area of Ireland and Northern Ireland: Longitude 10.8° W – 5.4° E, Latitude 51.2° N – 55.5° N. • **Temporal extent:** 1970 – 2000 • **Models and scenarios used:** Spatial transfers were carried out, using models trained in mainland Great Britain and transferred across the Irish Sea to the Island of Ireland.

MODEL	
Variable pre-selection	Variables were chosen based on the assumption that climate was the main constraint in the distribution of the 20 species chosen. In addition, the ease of freely available bioclimate data, similarity between the reference and target area and the suitability of climate as a predictor at this scale (Pearson & Dawson, 2003) were also reasons for predictor choice.
Multicollinearity	Multicollinearity between climatic predictors was assessed using the Spearman's rank correlation coefficient and variance inflation factor. Variables that were strongly correlated (|rs| > 0.5 and/or VIF > 7) were removed using stepwise reduction, until the 12 listed in the "data" section remained.
Model settings	Generalised Linear Models (GLM) with linear terms using a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature classes available for automatic selection based on best fit for the data; Boosted Regression Trees (BRT) with family = bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01. All models were trained with 70% and tested with 30% of the data. 1,000 iterations were performed with bootstrapping.
Model estimates	Bootstrapping was used with 1,000 iterations to generate performance statistics and ensure no over reliance upon a single occurrence point.
Non-independence analysis	None
Threshold selection	Outputs were kept as continuous predictions, rather than a binary presence/absence.
ASSESSMENT	
Performance statistics	Model performance was assessed using the average of the Receiver Operator Characteristic and Area Under the Curve from 1,000 bootstrap runs.
Plausibility checks	Maps of modelled predictions were compared to the IUCN known distribution.
PREDICTION	
Prediction output	Predictions of presence probability, scaled from 0 to 1.
Uncertainty quantification	Model outputs were compared to assess algorithmic uncertainty.

Table A3 ODMAP reporting for Chapter 4

ODMAP element	Contents
OVERVIEW	
Authorship	• **Author:** Joshua Copping • **Title:** The impact of modelling approach on transferability
Model objective	• **Objective:** Forecast/Transfer • **Main target output:** Probability of species presence
Taxon	20 British and Irish plant and animal species
Location	The British Isles: mainland Great Britain and the Island of Ireland
Scale of analysis	• **Spatial extent:** Longitude 10.8° W – 1.8° E, Latitude 49.8° N – 61.5° N • **Spatial resolution:** 30 arc-seconds • **Temporal resolution**: Data contained occurrences between 1970 and 2010 • **Type of extent boundary**: Natural
Biodiversity data overview	• **Observation type:** Citizen science, field survey, standardised monitoring data • **Response/Data type:** Presence-only
Type of predictors	Climatic
Conceptual model / Hypotheses	I examined how the modelling approach influences predictive performance and spatial transferability using 8 SDM algorithms in the profile, regression and machine learning families, and an ensemble of these methods.
Assumptions	I assumed that species were at pseudo-equilibrium with the environment, that the predictors used were drivers of the species' distribution.
SDM algorithms	• **Algorithms**: SDMs were built using 8 popular modelling algorithms; Bioclim; boosted regression trees, BRT; Domain; generalised additive model, GAM; generalised linear model, GLM; maximum entropy, Maxent; random forests, RF; support vector machine, SVM. • **Complexity**: Models were simple, with no temporal or stochastic aspects and no biological relationships. The data determined the model complexity of machine learning based methods. • **Model averaging**: The ensemble approach used weighted means of the previous 8 algorithms, based on their performance (AUC value) in each iteration. Additionally, results were expressed as the average of the 1,000 bootstrapped runs per model algorithm.
Model workflow	Variables were checked for multicollinearity using Spearman's rank correlation coefficient and the variance inflation factor, with any colinear variables removed. Models were fitted for the 20 species in the reference area using 8 algorithms, followed by an average weighted ensemble and performance was assessed. Models were then transferred to the target area and performance was again assessed using AUC. This was performed using 1,000 bootstrapped iterations.
Software	• **Software**: Analyses were performed in R version 3.6.1 (R Core Team, 2016), using the 'sdm' R package version 1.0-81 (Naimi & Araújo, 2016) • **Data availability**: The raw data are available at: www.gbif.org/occurrence/download/0021091-200613084148143

DATA	
Biodiversity data	• **Taxon names:** *Acrocephalus scirpaceus, Asplenium scolopendrium, Bombus jonellus, Bubulcus ibis, Chorthippus brunneus, Drosera rotundifolia, Gonepteryx rhamni, Lagopus lagopus, Lasiommata megera, Lepus timidus, Linaria flavirostris, Lissotriton vulgaris, Martes martes, Narthecium ossifragum, Quercus petraea, Rhinolophus hipposideros, Taxus baccata, Tyria jacobaeae, Tyto alba, Zootoca vivipara* • **Ecological level:** Individuals • **Data source**: DOI 10.15468/dl.hxbdp6 • **Sampling design**: Data were from an online repository, with occurrences collected using a range of survey methods. • **Sample size per taxon:** Species, reference area, target area: *Acrocephalus scirpaceus*, 2184, 74; *Asplenium scolopendrium*, 4505, 297; *Bombus jonellus*, 936, 532; *Bubulcus ibis*, 137, 81; *Chorthippus brunneus*, 7865, 203; *Drosera rotundifolia*, 6243, 97; *Gonepteryx rhamni*, 5073, 466; *Lagopus lagopus*, 2731, 858; *Lasiommata megera*, 3080, 106; *Lepus timidus*, 3774, 5495; *Linaria flavirostris*, 2319, 83; *Lissotriton vulgaris*, 2790, 162; *Martes martes*, 2056, 1622; *Narthecium ossifragum*, 8667, 101; *Quercus petraea*, 3811, 105; *Rhinolophus hipposideros*, 1202, 554; *Taxus baccata*, 6764, 95; *Tyria jacobaeae*, 4902, 112; *Tyto alba*, 7533, 786; *Zootoca vivipara*, 3883, 151. • **Data cleaning/filtering**: Data were initially filtered before downloading on the GBIF website. Records only included verified occurrences within the countries and timeframe of interest and collected through human observation. • **Background data**: Background points were generated in random geographic space with an equal number to the number of presences per species (prevalence = 0.5).
Data partitioning	Data was partitioned into 70% training and 30% test. Model performance was assessed using bootstrapping with 1,000 replicates.
Predictor variables	• **Predictor variables:** Isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of coldest quarter, precipitation seasonality and precipitation of warmest quarter. • **Data sources:** Predictors were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data were used in a 30 arc-second resolution and covered the area of England, Scotland and Wales: Longitude 7.4° W – 1.8° E, Latitude 49.8° N – 61.5° N. • **Geographic projection:** WGS84 • **Temporal extent:** 1970 – 2000
Transfer data	• **Data sources:** The predictors used were the same as in the reference area and were freely available from: www.worldclim.org/data/worldclim21.html • **Spatial resolution and extant data:** The climate data were used in a 30 arc-second resolution and covered the area of Ireland and Northern Ireland: Longitude 10.8° W – 5.4° E, Latitude 51.2° N – 55.5° N. • **Temporal extent:** 1970 – 2000 • **Models and scenarios used:** Spatial transfers were carried out, using models trained in mainland Great Britain and transferred across the Irish Sea to the Island of Ireland.

MODEL	
Variable pre-selection	Variables were chosen based on the assumption that climate was the main constraint in the distribution of the 20 species chosen. In addition, the ease of freely available bioclimate data, similarity between the reference and target area and the suitability of climate as a predictor at this scale (Pearson & Dawson, 2003) were also reasons for predictor choice.
Multicollinearity	Multicollinearity between climatic predictors was assessed using the Spearman's rank correlation coefficient and variance inflation factor. Variables that were strongly correlated (|rs| > 0.5 and/or VIF > 7) were removed using stepwise reduction, until the 12 listed in the "data" section remained.
Model settings	Models were typically used with the default settings, specifically: Bioclim with default settings; Boosted Regression Trees (BRT) with family = bernoulli, bag fraction = 0.75, tree complexity = 5, and learning rate = 0.01; Domain using default settings; Generalised Additive Models (GAM) with a logit link function and smoothing λ = 0.6; Generalised Linear Models (GLM) with linear terms and a logit link function; Maximum Entropy Modelling (Maxent) with all 6 feature types available for automatic selection based on best fit of the data; Random Forests (RF) with the number of trees set to a maximum of 500, with the complexity automatically defined by model, according to the data; Support Vector Machine (SVM) set as a classification machine; Ensemble approach used weighted means of the previous 8 algorithms, based on their performance (AUC value) in each iteration, with greater weighting given to the better performing models. All models were trained with 70% and tested with 30% of the data, with 1,000 bootstrapped iterations performed.
Model estimates	Bootstrapping was used with 1,000 iterations to generate performance statistics and ensure no over reliance upon a single occurrence point.
Non-independence analysis	None
Threshold selection	Outputs were kept as continuous predictions, rather than a binary presence/absence.
ASSESSMENT	
Performance statistics	Model performance was assessed using the average of the Receiver Operator Characteristic and Area Under the Curve from 1,000 bootstrap runs.
Plausibility checks	Maps of modelled predictions were compared to the IUCN known distribution.
PREDICTION	
Prediction output	Predictions of presence probability, scaled from 0 to 1.
Uncertainty quantification	Model outputs were compared to assess algorithmic uncertainty.

Appendix IV: List of WorldClim bioclimatic variables

BIO1 - Annual Mean Temperature
BIO2 - Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 - Isothermality (BIO2/BIO7) (* 100)
BIO4 - Temperature Seasonality (standard deviation *100)
BIO5 - Max Temperature of Warmest Month
BIO6 - Min Temperature of Coldest Month
BIO7 - Temperature Annual Range (BIO5-BIO6)
BIO8 - Mean Temperature of Wettest Quarter
BIO9 - Mean Temperature of Driest Quarter
BIO10 - Mean Temperature of Warmest Quarter
BIO11 - Mean Temperature of Coldest Quarter
BIO12 - Annual Precipitation
BIO13 - Precipitation of Wettest Month
BIO14 - Precipitation of Driest Month
BIO15 - Precipitation Seasonality (Coefficient of Variation)
BIO16 - Precipitation of Wettest Quarter
BIO17 - Precipitation of Driest Quarter
BIO18 - Precipitation of Warmest Quarter
BIO19 - Precipitation of Coldest Quarter

Appendix V: Chapter 2 prevalence values

Table A4 Prevalence values when 10,000 background points were used, displayed per species and in the reference and target areas.

Species	**Prevalence with 10,000 points**	
	Britain	**Ireland**
Acrocephalus scirpaceus	0.179	0.007
Asplenium scolopendrium	0.311	0.029
Bombus jonellus	0.086	0.051
Bubulcus ibis	0.014	0.008
Chorthippus brunneus	0.440	0.020
Drosera rotundifolia	0.384	0.010
Gonepteryx rhamni	0.337	0.045
Lagopus lagopus	0.215	0.079
Lasiommata megera	0.235	0.010
Lepus timidus	0.274	0.355
Linaria flavirostris	0.188	0.008
Lissotriton vulgaris	0.218	0.016
Martes martes	0.171	0.140
Narthecium ossifragum	0.464	0.010
Quercus petraea	0.276	0.010
Rhinolophus hipposideros	0.107	0.052
Taxus baccata	0.403	0.009
Tyria jacobaeae	0.329	0.011
Tyto alba	0.430	0.073
Zootoca vivipara	0.280	0.015

Appendix VI: Chapter 2 results tables

Table A5 Results from the BRT models in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.837	0.872	0.855	0.870	0.867	0.872	0.866	0.867	0.865	0.862	0.867	0.860	0.861	0.858	0.860
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.787	0.814	0.801	0.787	0.793	0.784	0.784	0.784	0.779	0.777	0.774	0.769	0.774	0.775	0.770
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. jonellus	Mean	0.814	0.832	0.816	0.803	0.822	0.821	0.828	0.823	0.820	0.814	0.816	0.808	0.815	0.811	0.821
	95% CI	±0.001	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.845	0.921	0.895	0.906	0.871	0.870	0.861	0.871	0.881	0.915	0.904	0.917	0.914	0.864	0.905
	95% CI	±0.003	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002
C. brunneus	Mean	0.772	0.799	0.816	0.814	0.819	0.818	0.819	0.818	0.819	0.821	0.819	0.817	0.821	0.821	0.817
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.789	0.834	0.833	0.835	0.832	0.841	0.847	0.841	0.842	0.843	0.842	0.843	0.839	0.840	0.839
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.823	0.846	0.850	0.854	0.852	0.854	0.848	0.854	0.849	0.848	0.846	0.847	0.848	0.845	0.844
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.897	0.910	0.894	0.899	0.897	0.900	0.900	0.900	0.897	0.896	0.893	0.891	0.888	0.891	0.886
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.001	±0.000	±0.001
L. megera	Mean	0.807	0.773	0.802	0.801	0.807	0.807	0.811	0.805	0.803	0.805	0.806	0.804	0.803	0.804	0.802
	95% CI	±0.001	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.914	0.945	0.953	0.952	0.952	0.952	0.951	0.942	0.941	0.938	0.937	0.936	0.938	0.935	0.934
	95% CI	±0.000	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.864	0.857	0.843	0.867	0.857	0.864	0.860	0.863	0.864	0.861	0.858	0.858	0.856	0.858	0.852
	95% CI	±0.000	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.826	0.814	0.827	0.835	0.828	0.826	0.829	0.828	0.828	0.830	0.830	0.827	0.828	0.831	0.831
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001
M. martes	Mean	0.776	0.844	0.871	0.868	0.872	0.874	0.875	0.877	0.883	0.884	0.879	0.878	0.877	0.878	0.878
	95% CI	±0.001	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.000
N. ossifragum	Mean	0.798	0.824	0.829	0.829	0.838	0.832	0.833	0.836	0.836	0.834	0.837	0.835	0.835	0.837	0.837
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.782	0.784	0.788	0.787	0.785	0.781	0.785	0.774	0.781	0.778	0.770	0.774	0.772	0.772	0.772
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.837	0.899	0.901	0.916	0.913	0.902	0.893	0.889	0.888	0.886	0.881	0.887	0.885	0.878	0.882
	95% CI	±0.001	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
T.baccata	Mean	0.796	0.813	0.838	0.836	0.784	0.793	0.829	0.836	0.830	0.827	0.829	0.826	0.826	0.823	0.819
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.799	0.787	0.797	0.803	0.801	0.801	0.800	0.796	0.797	0.795	0.797	0.794	0.793	0.795	0.790
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. alba	Mean	0.701	0.706	0.698	0.711	0.709	0.700	0.701	0.692	0.697	0.692	0.693	0.689	0.685	0.690	0.687
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000
Z.vivipara	Mean	0.689	0.729	0.710	0.707	0.697	0.695	0.689	0.688	0.688	0.687	0.683	0.686	0.681	0.681	0.676
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.808	0.830	0.831	0.834	0.830	0.829	0.830	0.829	0.829	0.830	0.828	0.827	0.827	0.824	0.825
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001

Table A6 Results from the GLMs in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.842	0.847	0.829	0.857	0.845	0.850	0.849	0.848	0.845	0.846	0.851	0.843	0.844	0.845	0.842
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.689	0.687	0.695	0.676	0.690	0.687	0.684	0.683	0.685	0.686	0.684	0.684	0.684	0.685	0.680
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. jonellus	Mean	0.761	0.787	0.768	0.733	0.774	0.756	0.775	0.764	0.770	0.763	0.758	0.751	0.760	0.767	0.765
	95% CI	±0.001	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.879	0.851	0.828	0.870	0.881	0.881	0.865	0.875	0.892	0.888	0.874	0.891	0.880	0.890	0.880
	95% CI	±0.002	±0.005	±0.005	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.002	±0.001
C. brunneus	Mean	0.796	0.781	0.789	0.795	0.795	0.795	0.793	0.794	0.795	0.797	0.795	0.793	0.797	0.797	0.793
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.796	0.795	0.800	0.807	0.800	0.800	0.800	0.796	0.800	0.797	0.800	0.800	0.797	0.797	0.798
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.820	0.809	0.813	0.825	0.818	0.823	0.820	0.824	0.817	0.820	0.820	0.820	0.821	0.819	0.820
	95% CI	±0.000	±0.002	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.861	0.876	0.857	0.863	0.860	0.859	0.861	0.863	0.859	0.864	0.861	0.863	0.859	0.859	0.861
	95% CI	±0.000	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.001	±0.000	±0.001	±0.000
L. megera	Mean	0.725	0.702	0.718	0.718	0.723	0.727	0.722	0.727	0.724	0.726	0.726	0.723	0.721	0.719	0.722
	95% CI	±0.001	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.944	0.934	0.934	0.936	0.940	0.942	0.942	0.940	0.939	0.939	0.939	0.940	0.940	0.941	0.935
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.840	0.838	0.830	0.840	0.833	0.844	0.843	0.843	0.844	0.839	0.833	0.838	0.837	0.837	0.835
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.717	0.718	0.740	0.722	0.727	0.716	0.714	0.724	0.724	0.722	0.718	0.722	0.722	0.723	0.724
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000
M. martes	Mean	0.802	0.784	0.795	0.789	0.801	0.801	0.799	0.792	0.805	0.795	0.798	0.795	0.790	0.797	0.794
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000
N. ossifragum	Mean	0.802	0.800	0.808	0.806	0.811	0.803	0.805	0.808	0.809	0.806	0.806	0.801	0.807	0.804	0.806
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.643	0.646	0.654	0.652	0.647	0.642	0.641	0.650	0.644	0.650	0.644	0.647	0.644	0.640	0.643
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.873	0.839	0.867	0.885	0.884	0.876	0.874	0.882	0.876	0.877	0.878	0.878	0.877	0.879	0.875
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001
T.baccata	Mean	0.748	0.744	0.739	0.743	0.743	0.749	0.743	0.748	0.747	0.745	0.748	0.746	0.745	0.746	0.744
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.778	0.772	0.774	0.785	0.778	0.782	0.780	0.777	0.779	0.779	0.783	0.776	0.776	0.776	0.778
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. alba	Mean	0.649	0.645	0.639	0.656	0.651	0.651	0.654	0.653	0.653	0.654	0.648	0.651	0.647	0.649	0.652
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.000	±0.000
Z.vivipara	Mean	0.604	0.596	0.591	0.609	0.608	0.605	0.602	0.609	0.608	0.607	0.604	0.607	0.599	0.604	0.608
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.778	0.773	0.773	0.778	0.781	0.779	0.778	0.780	0.781	0.780	0.778	0.778	0.777	0.779	0.778
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001

Table A7 Results from the Maxent models in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.866	0.861	0.853	0.867	0.867	0.871	0.876	0.874	0.872	0.871	0.877	0.871	0.873	0.871	0.869
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001
A. scolopendrium	Mean	0.799	0.785	0.790	0.778	0.793	0.793	0.796	0.796	0.796	0.795	0.794	0.793	0.793	0.795	0.794
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.001	±0.001	±0.000
B. jonellus	Mean	0.818	0.798	0.783	0.777	0.804	0.805	0.821	0.815	0.812	0.817	0.813	0.813	0.811	0.811	0.822
	95% CI	±0.001	±0.003	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.905	0.896	0.890	0.901	0.907	0.897	0.897	0.908	0.923	0.913	0.899	0.915	0.913	0.914	0.906
	95% CI	±0.002	±0.003	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002
C. brunneus	Mean	0.821	0.789	0.809	0.810	0.817	0.824	0.823	0.823	0.826	0.828	0.825	0.824	0.826	0.826	0.825
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.828	0.803	0.810	0.823	0.825	0.834	0.843	0.837	0.840	0.839	0.843	0.844	0.839	0.840	0.839
	95% CI	±0.000	±0.002	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.859	0.834	0.855	0.859	0.861	0.862	0.859	0.865	0.859	0.863	0.861	0.862	0.862	0.859	0.861
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.908	0.901	0.889	0.899	0.899	0.906	0.907	0.910	0.909	0.907	0.906	0.905	0.904	0.907	0.911
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. megera	Mean	0.798	0.752	0.768	0.775	0.792	0.796	0.801	0.797	0.800	0.803	0.799	0.801	0.797	0.800	0.795
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
L. timidus	Mean	0.959	0.932	0.952	0.954	0.957	0.958	0.960	0.958	0.960	0.958	0.957	0.960	0.960	0.960	0.959
	95% CI	±0.000	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.863	0.833	0.834	0.850	0.849	0.859	0.862	0.862	0.871	0.867	0.863	0.868	0.862	0.866	0.862
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.840	0.776	0.826	0.833	0.830	0.840	0.842	0.842	0.840	0.845	0.843	0.843	0.845	0.845	0.844
	95% CI	±0.001	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000
M. martes	Mean	0.896	0.800	0.881	0.887	0.886	0.892	0.894	0.893	0.899	0.897	0.895	0.897	0.895	0.897	0.898
	95% CI	±0.000	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
N. ossifragum	Mean	0.815	0.798	0.807	0.809	0.823	0.819	0.823	0.824	0.827	0.826	0.827	0.823	0.828	0.828	0.826
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.794	0.762	0.780	0.781	0.784	0.789	0.796	0.794	0.796	0.798	0.796	0.797	0.794	0.791	0.795
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.914	0.891	0.903	0.917	0.913	0.912	0.911	0.914	0.919	0.916	0.919	0.914	0.918	0.916	0.916
	95% CI	±0.001	±0.003	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.000	±0.001	±0.000	±0.000	±0.001
T.baccata	Mean	0.851	0.801	0.833	0.833	0.841	0.850	0.847	0.853	0.849	0.849	0.853	0.851	0.851	0.851	0.851
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.801	0.778	0.794	0.809	0.805	0.805	0.807	0.804	0.804	0.802	0.805	0.803	0.803	0.801	0.804
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. alba	Mean	0.712	0.675	0.703	0.714	0.713	0.714	0.716	0.715	0.715	0.717	0.714	0.718	0.711	0.713	0.718
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000	±0.001	±0.000	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000
Z.vivipara	Mean	0.692	0.664	0.663	0.673	0.686	0.693	0.691	0.698	0.697	0.698	0.697	0.693	0.697	0.691	0.695
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.837	0.806	0.821	0.827	0.833	0.836	0.839	0.839	0.841	0.840	0.839	0.840	0.839	0.839	0.839
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001

Table A8 Results from BRT models transferred to the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.765	0.687	0.739	0.765	0.823	0.798	0.809	0.788	0.780	0.781	0.750	0.723	0.729	0.742	0.732
	95% CI	±0.002	±0.009	±0.004	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.002
A. scolopendrium	Mean	0.443	0.470	0.479	0.439	0.440	0.454	0.439	0.441	0.436	0.433	0.461	0.444	0.440	0.429	0.458
	95% CI	±0.002	±0.005	±0.004	±0.003	±0.003	±0.004	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001
B. jonellus	Mean	0.524	0.470	0.526	0.529	0.504	0.514	0.502	0.513	0.507	0.508	0.504	0.513	0.517	0.513	0.513
	95% CI	±0.001	±0.004	±0.004	±0.004	±0.002	±0.003	±0.002	±0.001	±0.002	±0.001	±0.002	±0.001	±0.001	±0.002	±0.001
B. ibis	Mean	0.666	0.635	0.562	0.562	0.682	0.698	0.701	0.701	0.715	0.798	0.796	0.754	0.702	0.723	0.624
	95% CI	±0.004	±0.009	±0.01	±0.01	±0.004	±0.005	±0.005	±0.004	±0.004	±0.004	±0.004	±0.005	±0.005	±0.005	±0.009
C. brunneus	Mean	0.625	0.606	0.636	0.624	0.663	0.726	0.724	0.734	0.733	0.731	0.727	0.716	0.728	0.724	0.717
	95% CI	±0.001	±0.005	±0.003	±0.003	±0.003	±0.002	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
D. rotundifolia	Mean	0.623	0.560	0.515	0.582	0.590	0.623	0.630	0.632	0.648	0.635	0.646	0.630	0.634	0.635	0.637
	95% CI	±0.001	±0.007	±0.005	±0.004	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001
G. rhamni	Mean	0.606	0.643	0.652	0.650	0.662	0.657	0.640	0.640	0.646	0.593	0.568	0.595	0.556	0.562	0.540
	95% CI	±0.002	±0.005	±0.003	±0.003	±0.003	±0.002	±0.002	±0.002	±0.002	±0.004	±0.004	±0.003	±0.004	±0.005	±0.004
L. lagopus	Mean	0.648	0.712	0.712	0.715	0.715	0.722	0.706	0.707	0.611	0.612	0.586	0.591	0.574	0.599	0.572
	95% CI	±0.004	±0.003	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.005	±0.005	±0.006	±0.006	±0.005	±0.005	±0.005
L. megera	Mean	0.641	0.543	0.640	0.582	0.605	0.628	0.611	0.607	0.638	0.649	0.639	0.646	0.623	0.644	0.651
	95% CI	±0.003	±0.007	±0.006	±0.005	±0.002	±0.003	±0.003	±0.003	±0.002	±0.003	±0.002	±0.003	±0.002	±0.002	±0.002
L. timidus	Mean	0.493	0.523	0.528	0.512	0.393	0.385	0.437	0.489	0.481	0.482	0.488	0.488	0.490	0.485	0.480
	95% CI	±0.001	±0.004	±0.003	±0.003	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.001
L. flavirostris	Mean	0.737	0.776	0.786	0.764	0.755	0.737	0.748	0.746	0.744	0.742	0.761	0.742	0.748	0.751	0.753
	95% CI	±0.002	±0.007	±0.004	±0.003	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
L. vulgaris	Mean	0.526	0.492	0.532	0.551	0.555	0.541	0.535	0.535	0.526	0.532	0.531	0.533	0.521	0.525	0.524
	95% CI	±0.002	±0.006	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002
M. martes	Mean	0.489	0.479	0.486	0.478	0.441	0.435	0.450	0.445	0.449	0.461	0.453	0.461	0.467	0.454	0.453
	95% CI	±0.002	±0.003	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
N. ossifragum	Mean	0.607	0.596	0.609	0.609	0.606	0.631	0.635	0.646	0.647	0.642	0.644	0.641	0.639	0.639	0.635
	95% CI	±0.001	±0.008	±0.005	±0.004	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Q. petraea	Mean	0.377	0.484	0.433	0.450	0.376	0.378	0.357	0.393	0.365	0.365	0.384	0.368	0.390	0.387	0.374
	95% CI	±0.002	±0.009	±0.006	±0.005	±0.003	±0.003	±0.002	±0.003	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002
R. hipposideros	Mean	0.868	0.555	0.560	0.604	0.598	0.650	0.737	0.706	0.684	0.717	0.725	0.719	0.723	0.754	0.745
	95% CI	±0.000	±0.006	±0.005	±0.005	±0.005	±0.004	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.002
T.baccata	Mean	0.662	0.600	0.624	0.654	0.687	0.674	0.686	0.687	0.696	0.678	0.680	0.679	0.677	0.676	0.674
	95% CI	±0.002	±0.007	±0.006	±0.003	±0.002	±0.002	±0.001	±0.002	±0.001	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001
T. jacobaeae	Mean	0.483	0.587	0.576	0.491	0.524	0.469	0.437	0.454	0.455	0.435	0.447	0.451	0.453	0.458	0.478
	95% CI	±0.003	±0.011	±0.006	±0.006	±0.004	±0.004	±0.003	±0.004	±0.004	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003
T. alba	Mean	0.488	0.472	0.478	0.476	0.491	0.498	0.509	0.522	0.518	0.533	0.522	0.524	0.535	0.530	0.535
	95% CI	±0.002	±0.004	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.548	0.451	0.476	0.453	0.472	0.500	0.517	0.559	0.532	0.544	0.531	0.547	0.548	0.549	0.525
	95% CI	±0.004	±0.006	±0.004	±0.004	±0.003	±0.004	±0.004	±0.004	±0.004	±0.003	±0.004	±0.004	±0.004	±0.004	±0.003
Mean	Mean	0.591	0.567	0.577	0.575	0.579	0.586	0.590	0.597	0.591	0.594	0.592	0.588	0.585	0.589	0.581
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002

Table A9 Results from GLMs transferred to the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.882	0.817	0.872	0.871	0.866	0.885	0.871	0.882	0.872	0.882	0.883	0.892	0.887	0.885	0.887
	95% CI	±0.001	±0.006	±0.003	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.541	0.630	0.621	0.581	0.560	0.531	0.532	0.523	0.523	0.521	0.520	0.524	0.516	0.513	0.515
	95% CI	±0.001	±0.005	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. jonellus	Mean	0.465	0.505	0.502	0.500	0.497	0.462	0.474	0.471	0.468	0.465	0.468	0.465	0.462	0.466	0.455
	95% CI	±0.001	±0.004	±0.003	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.835	0.822	0.706	0.734	0.749	0.822	0.826	0.858	0.870	0.851	0.848	0.853	0.844	0.864	0.825
	95% CI	±0.002	±0.003	±0.01	±0.008	±0.007	±0.005	±0.004	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
C. brunneus	Mean	0.673	0.642	0.643	0.667	0.673	0.661	0.682	0.675	0.674	0.682	0.672	0.675	0.677	0.678	0.676
	95% CI	±0.001	±0.004	±0.003	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
D. rotundifolia	Mean	0.637	0.616	0.613	0.638	0.641	0.626	0.629	0.635	0.632	0.629	0.638	0.627	0.630	0.633	0.632
	95% CI	±0.001	±0.007	±0.005	±0.004	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
G. rhamni	Mean	0.653	0.640	0.664	0.649	0.666	0.658	0.649	0.663	0.655	0.652	0.648	0.646	0.650	0.649	0.651
	95% CI	±0.001	±0.004	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. lagopus	Mean	0.627	0.709	0.663	0.673	0.662	0.650	0.644	0.620	0.625	0.619	0.611	0.619	0.602	0.610	0.597
	95% CI	±0.001	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. megera	Mean	0.728	0.674	0.709	0.691	0.705	0.736	0.725	0.729	0.719	0.736	0.720	0.733	0.740	0.731	0.729
	95% CI	±0.002	±0.007	±0.005	±0.004	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.642	0.582	0.627	0.625	0.639	0.642	0.641	0.641	0.643	0.644	0.645	0.642	0.647	0.645	0.644
	95% CI	±0.000	±0.002	±0.001	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.869	0.816	0.857	0.850	0.853	0.869	0.864	0.862	0.865	0.867	0.860	0.863	0.863	0.860	0.849
	95% CI	±0.001	±0.006	±0.003	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.544	0.579	0.562	0.544	0.548	0.545	0.547	0.548	0.538	0.547	0.545	0.543	0.544	0.553	0.548
	95% CI	±0.001	±0.006	±0.004	±0.003	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
M. martes	Mean	0.463	0.432	0.426	0.428	0.441	0.446	0.449	0.462	0.464	0.466	0.470	0.469	0.472	0.469	0.480
	95% CI	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
N. ossifragum	Mean	0.623	0.596	0.596	0.610	0.615	0.632	0.643	0.620	0.622	0.625	0.624	0.620	0.631	0.625	0.628
	95% CI	±0.001	±0.008	±0.006	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001
Q. petraea	Mean	0.631	0.647	0.605	0.631	0.656	0.627	0.641	0.633	0.648	0.634	0.618	0.638	0.630	0.635	0.648
	95% CI	±0.001	±0.008	±0.005	±0.003	±0.003	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001
R. hipposideros	Mean	0.739	0.754	0.762	0.775	0.770	0.735	0.750	0.745	0.740	0.739	0.741	0.739	0.737	0.746	0.739
	95% CI	±0.001	±0.004	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
T.baccata	Mean	0.679	0.675	0.682	0.680	0.684	0.690	0.690	0.675	0.676	0.673	0.671	0.663	0.670	0.668	0.668
	95% CI	±0.001	±0.009	±0.004	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.002
T. jacobaeae	Mean	0.586	0.639	0.535	0.584	0.568	0.563	0.576	0.568	0.588	0.601	0.603	0.593	0.601	0.591	0.591
	95% CI	±0.002	±0.007	±0.006	±0.005	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. alba	Mean	0.563	0.551	0.562	0.576	0.562	0.575	0.565	0.576	0.572	0.570	0.569	0.575	0.573	0.570	0.569
	95% CI	±0.001	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.446	0.428	0.455	0.442	0.448	0.432	0.451	0.441	0.446	0.449	0.446	0.443	0.444	0.449	0.455
	95% CI	±0.002	±0.007	±0.004	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.641	0.638	0.633	0.637	0.640	0.639	0.642	0.641	0.642	0.643	0.640	0.641	0.641	0.642	0.639
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002

Table A10 Results from the Maxent models transferred to the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each background point prevalence and when using 10,000 points.

		10k	**0.90**	**0.75**	**0.66**	**0.50**	**0.33**	**0.25**	**0.20**	**0.17**	**0.14**	**0.13**	**0.11**	**0.10**	**0.09**	**0.06**
A.scirpaceus	Mean	0.777	0.745	0.768	0.766	0.794	0.800	0.794	0.751	0.765	0.757	0.749	0.771	0.766	0.781	0.777
	95% CI	±0.002	±0.007	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002
A. scolopendrium	Mean	0.476	0.479	0.472	0.464	0.462	0.467	0.444	0.457	0.445	0.436	0.437	0.436	0.448	0.434	0.438
	95% CI	±0.002	±0.005	±0.004	±0.003	±0.003	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
B. jonellus	Mean	0.451	0.494	0.480	0.473	0.447	0.443	0.441	0.448	0.450	0.454	0.439	0.443	0.445	0.445	0.436
	95% CI	±0.001	±0.004	±0.003	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001
B. ibis	Mean	0.751	0.820	0.686	0.697	0.742	0.755	0.732	0.762	0.781	0.796	0.785	0.789	0.773	0.796	0.765
	95% CI	±0.004	±0.006	±0.006	±0.006	±0.006	±0.006	±0.005	±0.005	±0.005	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003
C. brunneus	Mean	0.683	0.637	0.647	0.660	0.694	0.690	0.709	0.709	0.704	0.708	0.698	0.703	0.706	0.702	0.701
	95% CI	±0.001	±0.004	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
D. rotundifolia	Mean	0.578	0.585	0.502	0.583	0.567	0.577	0.602	0.586	0.611	0.599	0.619	0.607	0.603	0.615	0.614
	95% CI	±0.001	±0.008	±0.005	±0.005	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001
G. rhamni	Mean	0.592	0.628	0.624	0.624	0.603	0.588	0.612	0.586	0.560	0.569	0.570	0.575	0.568	0.554	0.553
	95% CI	±0.002	±0.005	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
L. lagopus	Mean	0.691	0.685	0.704	0.679	0.692	0.690	0.695	0.684	0.685	0.698	0.672	0.683	0.674	0.669	0.678
	95% CI	±0.001	±0.003	±0.001	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. megera	Mean	0.624	0.565	0.619	0.578	0.617	0.633	0.623	0.638	0.627	0.625	0.623	0.634	0.627	0.642	0.635
	95% CI	±0.002	±0.006	±0.004	±0.005	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001
L. timidus	Mean	0.631	0.620	0.619	0.628	0.639	0.633	0.632	0.621	0.622	0.613	0.619	0.628	0.612	0.623	0.622
	95% CI	±0.001	±0.001	±0.002	±0.001	±0.000	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. flavirostris	Mean	0.711	0.709	0.717	0.717	0.738	0.747	0.790	0.762	0.752	0.760	0.744	0.728	0.745	0.743	0.764
	95% CI	±0.003	±0.009	±0.007	±0.006	±0.005	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003
L. vulgaris	Mean	0.474	0.494	0.479	0.496	0.481	0.475	0.472	0.473	0.477	0.475	0.475	0.473	0.475	0.466	0.473
	95% CI	±0.001	±0.007	±0.005	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
M. martes	Mean	0.481	0.528	0.509	0.486	0.478	0.481	0.488	0.482	0.482	0.480	0.482	0.483	0.482	0.472	0.470
	95% CI	±0.001	±0.003	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
N. ossifragum	Mean	0.607	0.591	0.587	0.589	0.600	0.630	0.632	0.639	0.636	0.636	0.641	0.633	0.638	0.632	0.642
	95% CI	±0.002	±0.008	±0.005	±0.004	±0.003	±0.002	±0.002	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001
Q. petraea	Mean	0.472	0.478	0.450	0.502	0.456	0.459	0.488	0.473	0.468	0.461	0.468	0.470	0.481	0.470	0.485
	95% CI	±0.001	±0.01	±0.005	±0.005	±0.003	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
R. hipposideros	Mean	0.606	0.575	0.572	0.648	0.600	0.587	0.638	0.604	0.581	0.577	0.615	0.595	0.604	0.597	0.581
	95% CI	±0.002	±0.007	±0.005	±0.003	±0.004	±0.003	±0.002	±0.003	±0.002	±0.003	±0.002	±0.003	±0.003	±0.002	±0.003
T.baccata	Mean	0.654	0.667	0.625	0.646	0.656	0.629	0.665	0.649	0.647	0.652	0.655	0.656	0.658	0.652	0.663
	95% CI	±0.001	±0.006	±0.005	±0.003	±0.004	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.002	±0.001
T. jacobaeae	Mean	0.715	0.718	0.701	0.682	0.698	0.715	0.695	0.713	0.726	0.724	0.728	0.720	0.738	0.731	0.716
	95% CI	±0.002	±0.009	±0.005	±0.005	±0.003	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. alba	Mean	0.510	0.520	0.525	0.513	0.508	0.519	0.521	0.528	0.519	0.524	0.517	0.515	0.522	0.515	0.525
	95% CI	±0.001	±0.003	±0.002	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.467	0.384	0.389	0.412	0.425	0.428	0.472	0.451	0.468	0.468	0.475	0.496	0.480	0.478	0.487
	95% CI	±0.002	±0.006	±0.005	±0.003	±0.002	±0.003	±0.003	±0.003	±0.002	±0.002	±0.002	±0.003	±0.002	±0.003	±0.002
Mean	Mean	0.598	0.596	0.584	0.592	0.595	0.597	0.607	0.601	0.600	0.601	0.601	0.602	0.602	0.601	0.601
	95% CI	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002

Appendix VII: Chapter 3 results tables

Table A11 Results from BRT models in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for the four resolutions of predictor data.

		30 seconds	**2.5 minutes**	**5 minutes**	**10 minutes**
A.scirpaceus	Mean	0.870	0.881	0.898	0.940
	95% CI	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.792	0.816	0.844	0.887
	95% CI	±0.001	±0.001	±0.001	±0.001
B. jonellus	Mean	0.822	0.831	0.870	0.896
	95% CI	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.913	0.923	0.898	0.929
	95% CI	±0.002	±0.002	±0.002	±0.002
C. brunneus	Mean	0.822	0.866	0.910	0.910
	95% CI	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.830	0.874	0.923	0.958
	95% CI	±0.000	±0.000	±0.000	±0.001
G. rhamni	Mean	0.849	0.892	0.931	0.975
	95% CI	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.901	0.924	0.940	0.960
	95% CI	±0.000	±0.000	±0.000	±0.000
L. megera	Mean	0.809	0.825	0.859	0.905
	95% CI	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.955	0.969	0.975	0.982
	95% CI	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.867	0.874	0.897	0.930
	95% CI	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.829	0.853	0.887	0.930
	95% CI	±0.001	±0.001	±0.001	±0.001
M. martes	Mean	0.872	0.900	0.918	0.947
	95% CI	±0.001	±0.001	±0.001	±0.001
N. ossifragum	Mean	0.831	0.886	0.935	0.935
	95% CI	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.786	0.804	0.833	0.881
	95% CI	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.911	0.924	0.941	0.969
	95% CI	±0.001	±0.001	±0.001	±0.000
T.baccata	Mean	0.844	0.868	0.888	0.888
	95% CI	±0.000	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.802	0.841	0.901	0.954
	95% CI	±0.000	±0.000	±0.000	±0.001
T. alba	Mean	0.707	0.746	0.778	0.778
	95% CI	±0.000	±0.000	±0.001	±0.001
Z.vivipara	Mean	0.697	0.719	0.747	0.814
	95% CI	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.836	0.861	0.889	0.918
	95% CI	±0.001	±0.001	±0.001	±0.001

Table A12 Results from GLM models in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for the four resolutions of predictor data.

		30 seconds	**2.5 minutes**	**5 minutes**	**10 minutes**
A.scirpaceus	Mean	0.846	0.851	0.866	0.914
	95% CI	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.694	0.706	0.707	0.719
	95% CI	±0.001	±0.001	±0.001	±0.001
B. jonellus	Mean	0.774	0.783	0.836	0.854
	95% CI	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.874	0.889	0.860	0.900
	95% CI	±0.002	±0.002	±0.003	±0.002
C. brunneus	Mean	0.798	0.841	0.890	0.890
	95% CI	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.794	0.846	0.909	0.962
	95% CI	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.818	0.864	0.905	0.968
	95% CI	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.866	0.881	0.893	0.917
	95% CI	±0.001	±0.000	±0.000	±0.001
L. megera	Mean	0.730	0.744	0.774	0.840
	95% CI	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.944	0.956	0.963	0.977
	95% CI	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.844	0.854	0.883	0.912
	95% CI	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.719	0.753	0.783	0.833
	95% CI	±0.001	±0.001	±0.001	±0.001
M. martes	Mean	0.789	0.813	0.860	0.904
	95% CI	±0.001	±0.001	±0.001	±0.001
N. ossifragum	Mean	0.805	0.863	0.927	0.927
	95% CI	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.642	0.658	0.658	0.683
	95% CI	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.886	0.892	0.912	0.945
	95% CI	±0.001	±0.001	±0.001	±0.000
T.baccata	Mean	0.750	0.762	0.772	0.773
	95% CI	±0.000	±0.000	±0.001	±0.001
T. jacobaeae	Mean	0.782	0.822	0.881	0.957
	95% CI	±0.000	±0.000	±0.000	±0.001
T. alba	Mean	0.654	0.675	0.689	0.689
	95% CI	±0.000	±0.000	±0.001	±0.001
Z.vivipara	Mean	0.596	0.618	0.637	0.718
	95% CI	±0.001	±0.001	±0.001	±0.002
Mean	Mean	0.780	0.804	0.830	0.864
	95% CI	±0.001	±0.001	±0.001	±0.001

Table A13 Results from Maxent models in the reference area of Britain. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for the four resolutions of predictor data.

		30 seconds	**2.5 minutes**	**5 minutes**	**10 minutes**
A.scirpaceus	Mean	0.867	0.876	0.893	0.931
	95% CI	±0.001	±0.001	±0.001	±0.001
A. scolopendrium	Mean	0.795	0.817	0.839	0.858
	95% CI	±0.000	±0.000	±0.000	±0.001
B. jonellus	Mean	0.809	0.815	0.854	0.874
	95% CI	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.903	0.911	0.888	0.923
	95% CI	±0.002	±0.002	±0.002	±0.002
C. brunneus	Mean	0.820	0.866	0.908	0.908
	95% CI	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.824	0.865	0.914	0.958
	95% CI	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.855	0.897	0.931	0.975
	95% CI	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.905	0.927	0.939	0.953
	95% CI	±0.000	±0.000	±0.000	±0.001
L. megera	Mean	0.793	0.806	0.843	0.887
	95% CI	±0.001	±0.001	±0.001	±0.001
L. timidus	Mean	0.958	0.970	0.975	0.979
	95% CI	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.859	0.865	0.889	0.918
	95% CI	±0.001	±0.001	±0.001	±0.001
L. vulgaris	Mean	0.831	0.856	0.889	0.916
	95% CI	±0.001	±0.001	±0.000	±0.001
M. martes	Mean	0.877	0.911	0.928	0.964
	95% CI	±0.001	±0.001	±0.000	±0.000
N. ossifragum	Mean	0.817	0.873	0.926	0.925
	95% CI	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.786	0.807	0.835	0.858
	95% CI	±0.001	±0.001	±0.001	±0.001
R. hipposideros	Mean	0.916	0.931	0.950	0.981
	95% CI	±0.001	±0.001	±0.000	±0.000
T.baccata	Mean	0.847	0.876	0.895	0.895
	95% CI	±0.000	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.803	0.843	0.904	0.960
	95% CI	±0.000	±0.000	±0.000	±0.001
T. alba	Mean	0.713	0.751	0.786	0.786
	95% CI	±0.000	±0.000	±0.001	±0.001
Z.vivipara	Mean	0.684	0.710	0.734	0.768
	95% CI	±0.001	±0.001	±0.001	±0.001
Mean	Mean	0.833	0.859	0.886	0.911
	95% CI	±0.001	±0.001	±0.001	±0.001

Table A14 Results from BRT models in the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each combination of transfers for the four resolutions of predictor data.

		30 to 30	**30 to 2.5**	**30 to 5**	**30 to 10**	**2.5 to 30**	**2.5 to 2.5**	**2.5 to 5**	**2.5 to 10**	**5 to 30**	**5 to 2.5**	**5 to 5**	**5 to 10**	**10 to 30**	**10 to 2.5**	**10 to 5**	**10 to 10**
A.scirpaceus	Mean	0.823	0.785	0.698	0.637	0.837	0.822	0.746	0.650	0.810	0.791	0.708	0.637	0.765	0.732	0.633	0.557
	95% CI	±0.003	±0.003	±0.004	±0.004	±0.003	±0.003	±0.004	±0.004	±0.003	±0.003	±0.004	±0.004	±0.004	±0.005	±0.006	±0.005
A. scolopendrium	Mean	0.440	0.451	0.438	0.483	0.409	0.410	0.394	0.457	0.407	0.399	0.383	0.410	0.473	0.472	0.449	0.462
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001
B. jonellus	Mean	0.504	0.488	0.482	0.373	0.528	0.498	0.496	0.406	0.530	0.512	0.503	0.444	0.489	0.482	0.472	0.461
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.003	±0.003	±0.003	±0.003
B. ibis	Mean	0.682	0.675	0.623	0.565	0.696	0.622	0.545	0.489	0.727	0.677	0.608	0.522	0.699	0.668	0.595	0.523
	95% CI	±0.004	±0.006	±0.007	±0.007	±0.004	±0.005	±0.006	±0.007	±0.005	±0.006	±0.007	±0.007	±0.005	±0.005	±0.006	±0.006
C. brunneus	Mean	0.663	0.647	0.615	0.561	0.711	0.688	0.649	0.599	0.698	0.695	0.640	0.581	0.699	0.695	0.639	0.580
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
D. rotundifolia	Mean	0.590	0.566	0.550	0.485	0.590	0.554	0.549	0.479	0.552	0.514	0.495	0.446	0.516	0.467	0.446	0.430
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.003	±0.003	±0.003
G. rhamni	Mean	0.662	0.629	0.613	0.510	0.658	0.634	0.617	0.513	0.638	0.621	0.619	0.526	0.603	0.596	0.568	0.490
	95% CI	±0.003	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002	±0.003	±0.003	±0.003	±0.003
L. lagopus	Mean	0.715	0.715	0.709	0.702	0.699	0.672	0.660	0.658	0.684	0.646	0.616	0.613	0.678	0.648	0.616	0.595
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003
L. megera	Mean	0.605	0.649	0.591	0.565	0.628	0.651	0.582	0.569	0.577	0.600	0.496	0.482	0.570	0.592	0.489	0.464
	95% CI	±0.002	±0.003	±0.003	±0.002	±0.002	±0.002	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002	±0.003	±0.003
L. timidus	Mean	0.393	0.352	0.343	0.561	0.401	0.351	0.339	0.611	0.410	0.346	0.369	0.575	0.464	0.402	0.434	0.537
	95% CI	±0.001	±0.001	±0.001	±0.005	±0.001	±0.001	±0.001	±0.007	±0.002	±0.001	±0.002	±0.004	±0.003	±0.002	±0.003	±0.005
L. flavirostris	Mean	0.755	0.683	0.642	0.663	0.752	0.680	0.655	0.673	0.731	0.647	0.633	0.702	0.734	0.631	0.622	0.686
	95% CI	±0.002	±0.003	±0.004	±0.003	±0.002	±0.003	±0.003	±0.003	±0.003	±0.003	±0.004	±0.003	±0.002	±0.003	±0.003	±0.003
L. vulgaris	Mean	0.555	0.536	0.539	0.512	0.560	0.539	0.541	0.514	0.549	0.527	0.532	0.522	0.494	0.474	0.474	0.489
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003
M. martes	Mean	0.441	0.451	0.458	0.479	0.458	0.459	0.466	0.505	0.436	0.410	0.460	0.442	0.452	0.451	0.459	0.525
	95% CI	±0.002	±0.001	±0.002	±0.003	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.003
N. ossifragum	Mean	0.606	0.576	0.588	0.483	0.623	0.588	0.593	0.483	0.563	0.528	0.538	0.483	0.565	0.531	0.535	0.482
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.003	±0.002
Q. petraea	Mean	0.376	0.386	0.376	0.388	0.349	0.363	0.355	0.370	0.361	0.376	0.373	0.372	0.468	0.450	0.424	0.391
	95% CI	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002
R. hipposideros	Mean	0.598	0.638	0.628	0.653	0.583	0.562	0.558	0.568	0.572	0.534	0.512	0.498	0.595	0.574	0.563	0.558
	95% CI	±0.005	±0.005	±0.005	±0.005	±0.003	±0.004	±0.004	±0.004	±0.003	±0.003	±0.003	±0.004	±0.003	±0.004	±0.004	±0.004
T.baccata	Mean	0.687	0.663	0.637	0.636	0.682	0.651	0.625	0.646	0.660	0.636	0.623	0.651	0.661	0.638	0.623	0.652
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. jacobaeae	Mean	0.524	0.513	0.479	0.444	0.466	0.459	0.435	0.348	0.490	0.484	0.464	0.360	0.575	0.558	0.585	0.518
	95% CI	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.004	±0.004	±0.004	±0.004	±0.004	±0.004	±0.004	±0.005	±0.005	±0.005
T. alba	Mean	0.491	0.505	0.500	0.555	0.480	0.489	0.479	0.507	0.449	0.454	0.452	0.471	0.448	0.454	0.451	0.470
	95% CI	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.472	0.481	0.448	0.386	0.451	0.448	0.424	0.366	0.467	0.476	0.457	0.374	0.436	0.436	0.390	0.335
	95% CI	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002	±0.003	±0.002	±0.003	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002
Mean	Mean	0.579	0.569	0.548	0.532	0.578	0.557	0.535	0.521	0.566	0.544	0.524	0.506	0.569	0.548	0.523	0.510
	95% CI	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001

Table A15 Results from GLM models in the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each combination of transfers for the four resolutions of predictor data.

		30 to 30	30 to 2.5	30 to 5	30 to 10	2.5 to 30	2.5 to 2.5	2.5 to 5	2.5 to 10	5 to 30	5 to 2.5	5 to 5	5 to 10	10 to 30	10 to 2.5	10 to 5	10 to 10
A.scirpaceus	Mean	0.866	0.852	0.740	0.583	0.868	0.843	0.726	0.572	0.885	0.868	0.758	0.613	0.831	0.806	0.680	0.565
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.003	±0.003	±0.003
A. scolopendrium	Mean	0.560	0.532	0.531	0.480	0.527	0.514	0.509	0.461	0.509	0.502	0.503	0.463	0.547	0.535	0.537	0.491
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002
B. jonellus	Mean	0.497	0.456	0.445	0.357	0.476	0.460	0.453	0.364	0.465	0.449	0.443	0.354	0.438	0.424	0.420	0.350
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.749	0.765	0.692	0.523	0.776	0.696	0.609	0.457	0.836	0.764	0.689	0.495	0.779	0.704	0.622	0.485
	95% CI	±0.007	±0.004	±0.004	±0.005	±0.004	±0.004	±0.005	±0.005	±0.004	±0.004	±0.005	±0.006	±0.006	±0.006	±0.006	±0.006
C. brunneus	Mean	0.673	0.626	0.601	0.558	0.670	0.633	0.607	0.575	0.674	0.651	0.621	0.612	0.674	0.650	0.620	0.612
	95% CI	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.002	±0.002
D. rotundifolia	Mean	0.641	0.599	0.556	0.515	0.640	0.594	0.556	0.517	0.636	0.583	0.556	0.511	0.622	0.555	0.536	0.490
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
G. rhamni	Mean	0.666	0.636	0.590	0.421	0.676	0.643	0.600	0.444	0.686	0.655	0.609	0.489	0.697	0.671	0.629	0.502
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. lagopus	Mean	0.662	0.609	0.578	0.520	0.643	0.584	0.550	0.439	0.636	0.578	0.544	0.450	0.625	0.579	0.545	0.468
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002
L. megera	Mean	0.705	0.734	0.658	0.657	0.707	0.724	0.654	0.651	0.691	0.715	0.636	0.655	0.685	0.711	0.638	0.666
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002
L. timidus	Mean	0.639	0.635	0.648	0.383	0.638	0.638	0.652	0.371	0.640	0.637	0.658	0.389	0.624	0.613	0.635	0.406
	95% CI	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.001	±0.000	±0.001	±0.000	±0.000	±0.000	±0.001	±0.001	±0.001
L. flavirostris	Mean	0.853	0.799	0.810	0.785	0.857	0.797	0.810	0.782	0.843	0.787	0.805	0.776	0.819	0.761	0.799	0.776
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
L. vulgaris	Mean	0.548	0.520	0.501	0.499	0.535	0.506	0.486	0.487	0.528	0.503	0.481	0.490	0.530	0.500	0.480	0.489
	95% CI	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.002	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002
M. martes	Mean	0.441	0.434	0.412	0.318	0.432	0.434	0.416	0.320	0.439	0.449	0.435	0.378	0.444	0.447	0.434	0.409
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002
N. ossifragum	Mean	0.615	0.581	0.560	0.458	0.637	0.579	0.562	0.463	0.621	0.551	0.549	0.457	0.623	0.553	0.547	0.456
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
Q. petraea	Mean	0.656	0.617	0.584	0.481	0.601	0.600	0.581	0.480	0.569	0.592	0.558	0.468	0.513	0.560	0.535	0.446
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.003	±0.003	±0.002
R. hipposideros	Mean	0.770	0.796	0.803	0.809	0.762	0.804	0.813	0.814	0.758	0.803	0.814	0.817	0.767	0.814	0.824	0.827
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.000
T.baccata	Mean	0.684	0.637	0.597	0.629	0.668	0.630	0.587	0.629	0.650	0.611	0.570	0.615	0.651	0.613	0.571	0.613
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. jacobaeae	Mean	0.568	0.564	0.531	0.418	0.532	0.530	0.502	0.397	0.463	0.457	0.448	0.363	0.423	0.415	0.412	0.353
	95% CI	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.004	±0.003
T. alba	Mean	0.562	0.577	0.573	0.580	0.556	0.559	0.551	0.556	0.541	0.544	0.534	0.537	0.541	0.544	0.535	0.539
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.448	0.445	0.392	0.322	0.390	0.389	0.342	0.304	0.400	0.402	0.353	0.317	0.358	0.360	0.325	0.306
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.002
Mean	Mean	0.640	0.621	0.590	0.515	0.629	0.608	0.578	0.504	0.624	0.605	0.578	0.512	0.610	0.591	0.566	0.512
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002

Table A16 Results from Maxent models in the target area of Ireland. Showing the mean AUC for each of the 20 species and the mean across the whole dataset, with 95% confidence intervals for each combination of transfers for the four resolutions of predictor data.

		30 to 30	**30 to 2.5**	**30 to 5**	**30 to 10**	**2.5 to 30**	**2.5 to 2.5**	**2.5 to 5**	**2.5 to 10**	**5 to 30**	**5 to 2.5**	**5 to 5**	**5 to 10**	**10 to 30**	**10 to 2.5**	**10 to 5**	**10 to 10**
A.scirpaceus	Mean	0.794	0.739	0.616	0.544	0.778	0.733	0.593	0.511	0.769	0.715	0.583	0.507	0.786	0.745	0.606	0.523
	95% CI	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.004	±0.004	±0.004	±0.003
A. scolopendrium	Mean	0.462	0.456	0.454	0.473	0.447	0.445	0.437	0.459	0.451	0.443	0.442	0.484	0.490	0.473	0.471	0.483
	95% CI	±0.003	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001
B. jonellus	Mean	0.447	0.439	0.429	0.335	0.467	0.454	0.448	0.354	0.471	0.468	0.454	0.369	0.481	0.473	0.459	0.385
	95% CI	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
B. ibis	Mean	0.742	0.693	0.613	0.465	0.768	0.685	0.596	0.383	0.807	0.721	0.637	0.372	0.772	0.693	0.597	0.401
	95% CI	±0.006	±0.004	±0.004	±0.006	±0.003	±0.003	±0.004	±0.005	±0.003	±0.004	±0.004	±0.005	±0.004	±0.005	±0.005	±0.006
C. brunneus	Mean	0.694	0.638	0.598	0.538	0.693	0.640	0.600	0.546	0.676	0.623	0.587	0.523	0.676	0.622	0.586	0.523
	95% CI	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002
D. rotundifolia	Mean	0.567	0.535	0.514	0.474	0.569	0.516	0.492	0.450	0.544	0.476	0.442	0.395	0.525	0.462	0.440	0.388
	95% CI	±0.003	±0.003	±0.003	±0.003	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.003	±0.003	±0.002	±0.003
G. rhamni	Mean	0.603	0.572	0.551	0.435	0.606	0.561	0.542	0.439	0.639	0.592	0.563	0.470	0.658	0.608	0.571	0.461
	95% CI	±0.002	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
L. lagopus	Mean	0.692	0.693	0.669	0.627	0.642	0.639	0.612	0.565	0.660	0.640	0.575	0.525	0.619	0.608	0.576	0.497
	95% CI	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.002
L. megera	Mean	0.617	0.618	0.554	0.548	0.619	0.629	0.570	0.553	0.609	0.615	0.539	0.521	0.570	0.579	0.502	0.488
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003
L. timidus	Mean	0.639	0.632	0.664	0.423	0.641	0.643	0.664	0.382	0.640	0.636	0.667	0.405	0.642	0.644	0.661	0.384
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.738	0.686	0.716	0.720	0.731	0.661	0.711	0.734	0.676	0.619	0.699	0.728	0.644	0.596	0.682	0.723
	95% CI	±0.005	±0.003	±0.003	±0.002	±0.003	±0.003	±0.003	±0.002	±0.003	±0.003	±0.003	±0.002	±0.004	±0.003	±0.003	±0.002
L. vulgaris	Mean	0.481	0.458	0.436	0.466	0.471	0.447	0.427	0.460	0.483	0.459	0.433	0.468	0.489	0.463	0.440	0.464
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
M. martes	Mean	0.478	0.495	0.506	0.506	0.489	0.485	0.493	0.528	0.507	0.507	0.524	0.582	0.512	0.513	0.523	0.608
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
N. ossifragum	Mean	0.600	0.563	0.560	0.480	0.618	0.551	0.549	0.470	0.599	0.533	0.536	0.448	0.600	0.535	0.534	0.447
	95% CI	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
Q. petraea	Mean	0.456	0.470	0.431	0.443	0.459	0.457	0.420	0.426	0.444	0.448	0.417	0.425	0.479	0.459	0.429	0.420
	95% CI	±0.003	±0.003	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002
R. hipposideros	Mean	0.600	0.564	0.506	0.557	0.577	0.507	0.448	0.382	0.609	0.525	0.450	0.408	0.639	0.570	0.513	0.498
	95% CI	±0.004	±0.003	±0.003	±0.006	±0.003	±0.003	±0.002	±0.004	±0.002	±0.002	±0.002	±0.005	±0.002	±0.003	±0.003	±0.005
T.baccata	Mean	0.656	0.620	0.609	0.667	0.642	0.615	0.603	0.665	0.627	0.597	0.586	0.655	0.628	0.599	0.588	0.656
	95% CI	±0.004	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. jacobaeae	Mean	0.698	0.711	0.721	0.698	0.659	0.666	0.683	0.655	0.668	0.677	0.716	0.715	0.713	0.720	0.755	0.765
	95% CI	±0.003	±0.003	±0.003	±0.004	±0.003	±0.003	±0.004	±0.004	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003	±0.003
T. alba	Mean	0.508	0.522	0.515	0.537	0.501	0.501	0.493	0.509	0.472	0.472	0.460	0.478	0.472	0.473	0.461	0.479
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.425	0.456	0.416	0.337	0.421	0.432	0.399	0.330	0.446	0.463	0.426	0.334	0.387	0.385	0.353	0.317
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002
Mean	Mean	0.595	0.578	0.554	0.514	0.590	0.563	0.539	0.490	0.590	0.561	0.537	0.491	0.589	0.561	0.537	0.496
	95% CI	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002

Appendix VIII: References used in Table 4.1

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M. and Courchamp, F. 2013 Will climate change promote future invasions?, Global Change Biology, 19(12), pp. 3740–3748. doi: 10.1111/gcb.12344.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M. and Swanson, A. K. 2011 Modeling plant ranges over 75 years of climate change in California, USA: Relating transferability to species traits, Ecological Monographs, 81(2), pp. 241–257. doi: doi:10.1890/10-1325.1.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., … E. Zimmermann, N. 2006 Novel methods improve prediction of species' distributions from occurrence data, Ecography, 29(2), pp. 129–151. doi: 10.1111/j.2006.0906-7590.04596.x.

Elith, J. and Graham, C. H. 2009 Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models, Ecography, 32, pp. 66–77. doi: 10.1111/j.1600-0587.2008.05505.x.

Guisan, A., Zimmermann, N. E., Elith, J., Graham, C. H., Phillips, S. and Peterson, A. T. 2007 What matters for predicting spatial distribution of tree occurences: techniques, data or specie's characteristics?, Ecological Monographs, 77(4), pp. 615–630.

Heikkinen, R. K., Marmion, M. and Luoto, M. 2012 Does the interpolation accuracy of species distribution models come at the expense of transferability?, Ecography, 35, pp. 276–288. doi: 10.1111/j.1600-0587.2011.06999.x.

Huang, J. and Frimpong, E. A. 2016 Limited transferability of stream-fish distribution models among river catchments: reasons and implications, Freshwater Biology, 61, pp. 729–744. doi: 10.1111/fwb.12743.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K. and Thuiller, W. 2009 Evaluation of consensus methods in predictive species distribution modelling, Diversity and Distributions, 15(1), pp. 59–69. doi: 10.1111/j.1472-4642.2008.00491.x.

Meynard, C. N. and Quinn, J. F. 2007 Predicting species distributions: a critical comparison of the most common statistical models using artificial species, Journal of Biogeography, 34, pp. 1455–1469. doi: 10.1111/j.1365-2699.2007.01720.x.

Mi, C., Huettmann, F., Guo, Y., Han, X. and Wen, L. 2017 Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence, PeerJ, 2017(1). doi: 10.7717/peerj.2849.

Norberg, A., Abrego, N., Blanchet, F. G., Adler, F. R., Anderson, B. J., Anttila, J., Araújo, M. B., Dallas, T., … Ovaskainen, O. 2019 A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels, Ecological Monographs, 89(3). doi: 10.1002/ecm.1370.

Pearson, R. G., Raxworthy, C. J., Nakamura, M. and Peterson, A.T. 2007 Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar, Journal of Biogeography, 34(1), pp. 102–117. doi: 10.1111/j.1365-2699.2006.01594.x.

Peterson, A.T. and Geng-ping, Z. 2017 Do consensus models outperform individual models? Transferability evaluations of diverse modeling approaches for an invasive moth, Biological Invasions. Springer International Publishing, 19(9), pp. 2519–2532. doi: 10.1007/s10530-017-1460-y.

Peterson, A.T., Papeş, M. and Eaton, M. 2007 Transferability and model evaluation in ecological niche modeling: A comparison of GARP and Maxent, Ecography, 30(4), pp. 550–560. doi: 10.1111/j.2007.0906-7590.05102.x.

Qiao, H., Soberón, J. and Peterson, A. T. 2015 No silver bullets in correlative ecological niche modelling: Insights from testing among many potential algorithms for niche estimation, Methods in Ecology and Evolution, 6(10), pp. 1126–1136. doi: 10.1111/2041-210X.12397.

Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M. and Guisan, A. 2006 Are niche-based species distribution models transferable in space?, Journal of Biogeography, 33(10), pp. 1689–1703. doi: 10.1111/j.1365-2699.2006.01466.x.

Rapacciuolo, G., Roy, D. B., Gillings, S., Fox, R., Walker, K. and Purvis, A. 2012 Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change, PLoS ONE, 7(7). doi: 10.1371/journal.pone.0040212.

Segurado, P. and Araújo, M. B. 2004 An evaluation of methods for modelling species distributions, Journal of Biogeography, 31(10), pp. 1555–1568. doi: 10.1111/j.1365-2699.2004.01076.x.

Sor, R., Park, Y. S., Boets, P., Goethals, P. L. M. and Lek, S. 2017 Effects of species prevalence on the performance of predictive models, Ecological Modelling. Elsevier B.V., 354, pp. 11–19. doi: 10.1016/j.ecolmodel.2017.03.006.

Vayssières, M. P., Plant, R. E. and Allen-Diaz, B. H. 2000 Classification trees: An alternative non-parametric approach for predicting species distributions, Journal of Vegetation Science, 11(5), pp. 679–694. doi: 10.2307/3236575.

Wenger, S. J. and Olden, J. D. 2012 Assessing transferability of ecological models: An underappreciated aspect of statistical validation, Methods in Ecology and Evolution, 3(2), pp. 260–267. doi: 10.1111/j.2041-210X.2011.00170.x.

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., Elith, J., Dudík, M., … Zimmermann, N. E. 2008 Effects of sample size on the performance of species distribution models, Diversity and Distributions, 14(5), pp. 763–773. doi: 10.1111/j.1472-4642.2008.00482.x.

Appendix IX: Chapter 4 results tables

Table A17 Average model performance (AUC) and 95% confidence interval (+/-) for predictions of habitat suitability within the reference area. Predictions made using 8 different model algorithms and an average weighted ensemble for the 20 species.

		Bioclim	**BRT**	**Domain**	**Ensemble**	**GAM**	**GLM**	**Maxent**	**RF**	**SVM**
A.scirpaceus	Mean	0.750	0.869	0.693	0.908	0.873	0.845	0.866	0.960	0.866
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
A. scolopendrium	Mean	0.709	0.790	0.618	0.871	0.800	0.689	0.791	0.943	0.824
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000
B. jonellus	Mean	0.636	0.829	0.658	0.879	0.825	0.775	0.819	0.940	0.841
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.001	±0.001
B. ibis	Mean	0.818	0.911	0.728	0.938	0.869	0.870	0.901	0.954	0.904
	95% CI	±0.003	±0.002	±0.004	±0.001	±0.003	±0.003	±0.002	±0.001	±0.002
C. brunneus	Mean	0.718	0.820	0.630	0.890	0.829	0.794	0.819	0.953	0.846
	95% CI	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
D. rotundifolia	Mean	0.722	0.837	0.716	0.899	0.841	0.804	0.836	0.957	0.854
	95% CI	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
G. rhamni	Mean	0.785	0.854	0.690	0.910	0.863	0.820	0.859	0.958	0.870
	95% CI	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. lagopus	Mean	0.840	0.902	0.818	0.935	0.907	0.865	0.905	0.966	0.912
	95% CI	±0.001	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.001
L. megera	Mean	0.707	0.808	0.651	0.881	0.809	0.728	0.789	0.947	0.837
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
L. timidus	Mean	0.880	0.953	0.878	0.971	0.960	0.941	0.957	0.986	0.958
	95% CI	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
L. flavirostris	Mean	0.679	0.866	0.713	0.903	0.870	0.844	0.858	0.952	0.874
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
L. vulgaris	Mean	0.761	0.834	0.704	0.907	0.842	0.733	0.835	0.959	0.854
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
M. martes	Mean	0.784	0.874	0.723	0.937	0.887	0.790	0.885	0.969	0.914
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
N. ossifragum	Mean	0.711	0.830	0.721	0.895	0.823	0.803	0.813	0.958	0.844
	95% CI	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Q. petraea	Mean	0.722	0.786	0.662	0.872	0.800	0.652	0.785	0.944	0.824
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
R. hipposideros	Mean	0.839	0.901	0.799	0.939	0.913	0.878	0.910	0.968	0.928
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
T.baccata	Mean	0.780	0.842	0.661	0.906	0.855	0.750	0.846	0.960	0.867
	95% CI	±0.001	±0.000	±0.001	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000
T. jacobaeae	Mean	0.730	0.802	0.621	0.876	0.809	0.781	0.805	0.936	0.816
	95% CI	±0.001	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
T. alba	Mean	0.568	0.707	0.591	0.824	0.725	0.652	0.713	0.916	0.753
	95% CI	±0.000	±0.000	±0.001	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Z.vivipara	Mean	0.555	0.700	0.532	0.844	0.696	0.608	0.690	0.927	0.763
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001
Mean	Mean	0.735	0.836	0.690	0.899	0.840	0.781	0.834	0.953	0.857
	95% CI	±0.001	±0.001	±0.001	±0.000	±0.001	±0.001	±0.001	±0.000	±0.001

Table A18 Average model performance (AUC) and 95% confidence interval (+/-) for predictions of habitat suitability within the target area. Predictions made using 8 different model algorithms and an average weighted ensemble for the 20 species.

		Bioclim	**BRT**	**Domain**	**Ensemble**	**GAM**	**GLM**	**Maxent**	**RF**	**SVM**
A.scirpaceus	Mean	0.722	0.780	0.428	0.809	0.699	0.872	0.795	0.687	0.586
	95% CI	±0.002	±0.002	±0.004	±0.002	±0.004	±0.002	±0.002	±0.004	±0.005
A. scolopendrium	Mean	0.459	0.435	0.452	0.508	0.409	0.562	0.474	0.436	0.479
	95% CI	±0.001	±0.002	±0.001	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
B. jonellus	Mean	0.471	0.513	0.474	0.501	0.483	0.480	0.463	0.516	0.464
	95% CI	±0.001	±0.002	±0.001	±0.002	±0.002	±0.002	±0.001	±0.003	±0.002
B. ibis	Mean	0.591	0.720	0.594	0.799	0.589	0.846	0.780	0.762	0.801
	95% CI	±0.002	±0.006	±0.003	±0.004	±0.007	±0.003	±0.003	±0.005	±0.006
C. brunneus	Mean	0.532	0.658	0.452	0.722	0.698	0.668	0.686	0.643	0.570
	95% CI	±0.001	±0.002	±0.002	±0.001	±0.002	±0.001	±0.001	±0.002	±0.002
D. rotundifolia	Mean	0.465	0.601	0.508	0.635	0.580	0.637	0.577	0.597	0.587
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
G. rhamni	Mean	0.420	0.651	0.534	0.610	0.541	0.665	0.623	0.513	0.420
	95% CI	±0.001	±0.002	±0.001	±0.002	±0.003	±0.001	±0.002	±0.003	±0.004
L. lagopus	Mean	0.631	0.729	0.604	0.712	0.606	0.673	0.711	0.643	0.549
	95% CI	±0.001	±0.001	±0.001	±0.002	±0.002	±0.001	±0.001	±0.002	±0.003
L. megera	Mean	0.564	0.645	0.467	0.668	0.582	0.728	0.607	0.520	0.527
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.003
L. timidus	Mean	0.662	0.390	0.656	0.607	0.524	0.634	0.631	0.456	0.403
	95% CI	±0.000	±0.001	±0.001	±0.001	±0.002	±0.000	±0.001	±0.002	±0.002
L. flavirostris	Mean	0.481	0.740	0.660	0.813	0.614	0.865	0.746	0.743	0.695
	95% CI	±0.002	±0.002	±0.003	±0.002	±0.005	±0.001	±0.004	±0.002	±0.002
L. vulgaris	Mean	0.483	0.556	0.509	0.558	0.503	0.549	0.477	0.518	0.442
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
M. martes	Mean	0.522	0.481	0.551	0.498	0.522	0.431	0.491	0.475	0.508
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002
N. ossifragum	Mean	0.507	0.625	0.539	0.646	0.627	0.625	0.605	0.627	0.611
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
Q. petraea	Mean	0.479	0.385	0.371	0.540	0.519	0.645	0.469	0.441	0.400
	95% CI	±0.002	±0.003	±0.002	±0.002	±0.003	±0.002	±0.002	±0.003	±0.003
R. hipposideros	Mean	0.440	0.590	0.384	0.710	0.666	0.762	0.609	0.486	0.504
	95% CI	±0.001	±0.004	±0.001	±0.002	±0.003	±0.001	±0.003	±0.004	±0.003
T.baccata	Mean	0.553	0.690	0.649	0.706	0.597	0.680	0.644	0.592	0.575
	95% CI	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002	±0.002
T. jacobaeae	Mean	0.736	0.545	0.623	0.736	0.688	0.579	0.710	0.600	0.701
	95% CI	±0.002	±0.003	±0.002	±0.002	±0.003	±0.002	±0.003	±0.003	±0.003
T. alba	Mean	0.437	0.475	0.477	0.559	0.498	0.568	0.509	0.479	0.553
	95% CI	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001	±0.001
Z.vivipara	Mean	0.415	0.480	0.359	0.510	0.482	0.439	0.440	0.458	0.445
	95% CI	±0.002	±0.003	±0.002	±0.002	±0.002	±0.002	±0.002	±0.003	±0.002
Mean	Mean	0.528	0.585	0.514	0.642	0.571	0.645	0.602	0.559	0.541
	95% CI	±0.001	±0.002	±0.001	±0.002	±0.001	±0.002	±0.002	±0.001	±0.002

Appendix X: California ACP IDW

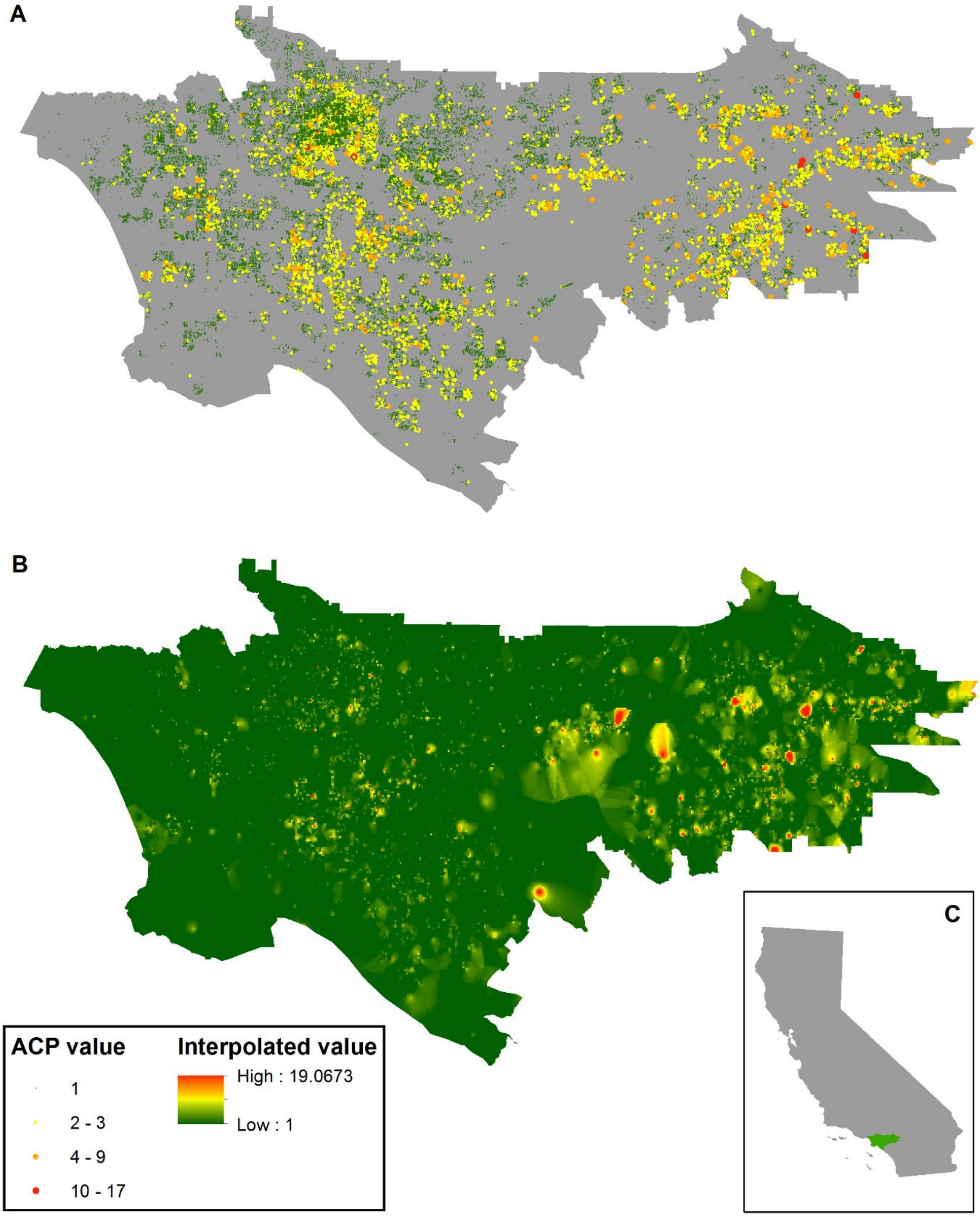


Figure A1 Maps showing ACP recordings (A), and interpolated ACP value layer (B) for the study area within California (C), for cycle 5 of the data.

Appendix XI: Florida Risk Maps

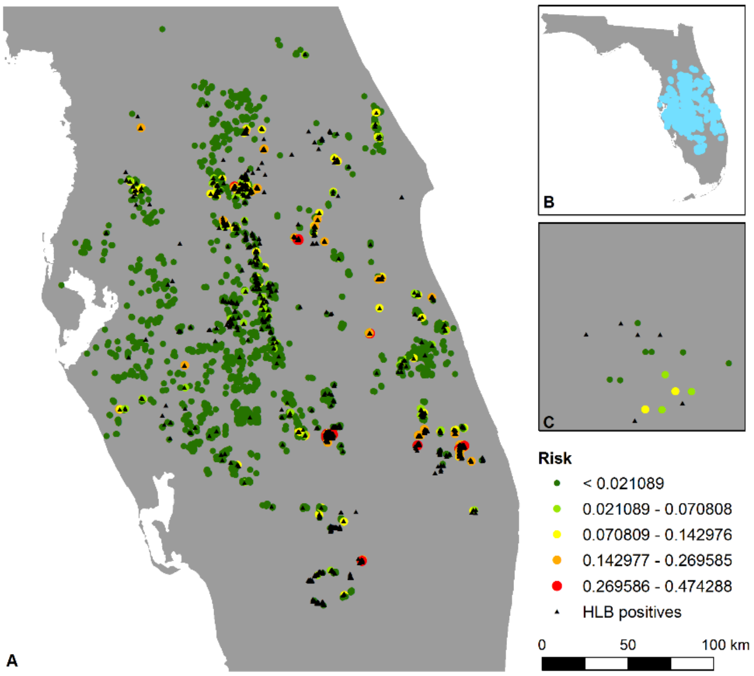


Figure A2 Map of risk of HLB spread in Florida, predicted for cycle 2. A) Whole state of Florida with all infected and uninfected trees. B) position of trees sampled within the state. C) a more detailed image of an area within Florida showing risk of infection predicted from previous cycle positive locations and actual positive trees in cycle 2.

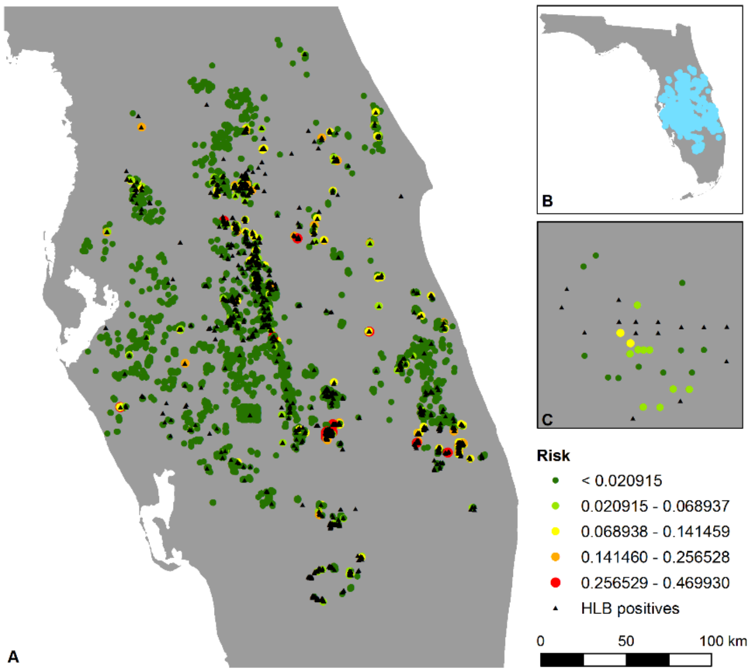


Figure A3 Map of risk of HLB spread in Florida, predicted for cycle 3. A) Whole state of Florida with all infected and uninfected trees. B) position of trees sampled within the state. C) a more detailed image of an area within Florida showing risk of infection predicted from previous cycle positive locations and actual positive trees in cycle 3.

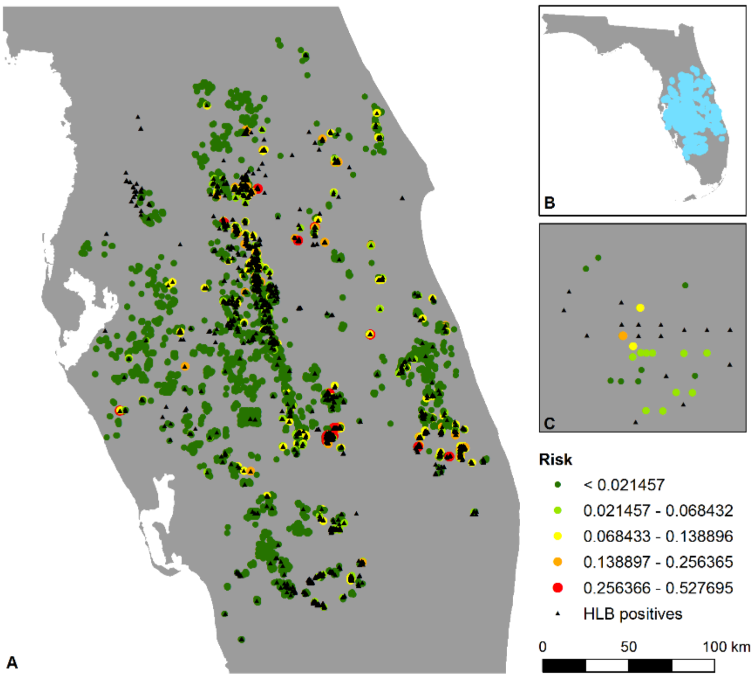


Figure A4 Map of risk of HLB spread in Florida, predicted for cycle 4. A) Whole state of Florida with all infected and uninfected trees. B) position of trees sampled within the state. C) a more detailed image of an area within Florida showing risk of infection predicted from previous cycle positive locations and actual positive trees in cycle 4.

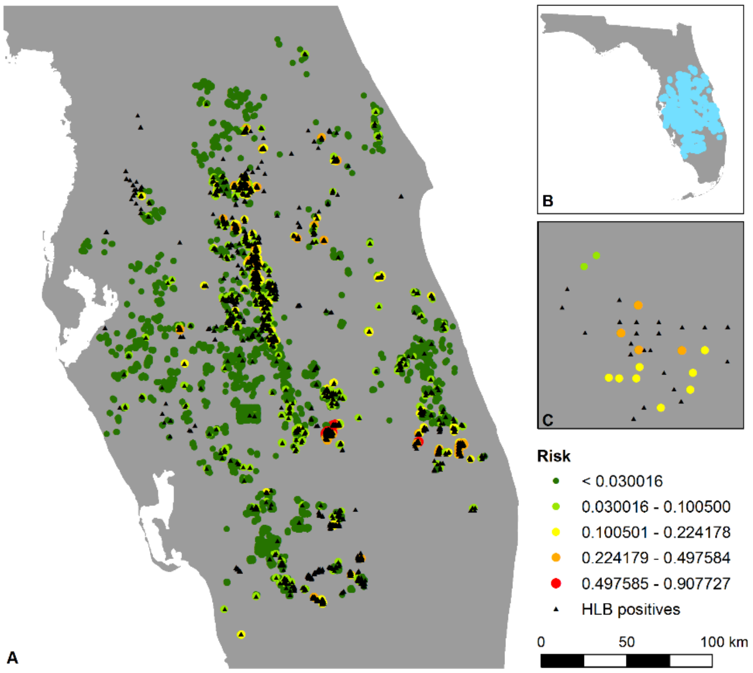


Figure A5 Map of risk of HLB spread in Florida, predicted for cycle 5. A) Whole state of Florida with all infected and uninfected trees. B) position of trees sampled within the state. C) a more detailed image of an area within Florida showing risk of infection predicted from previous cycle positive locations and actual positive trees in cycle 5.

Appendix XII: California Risk Maps

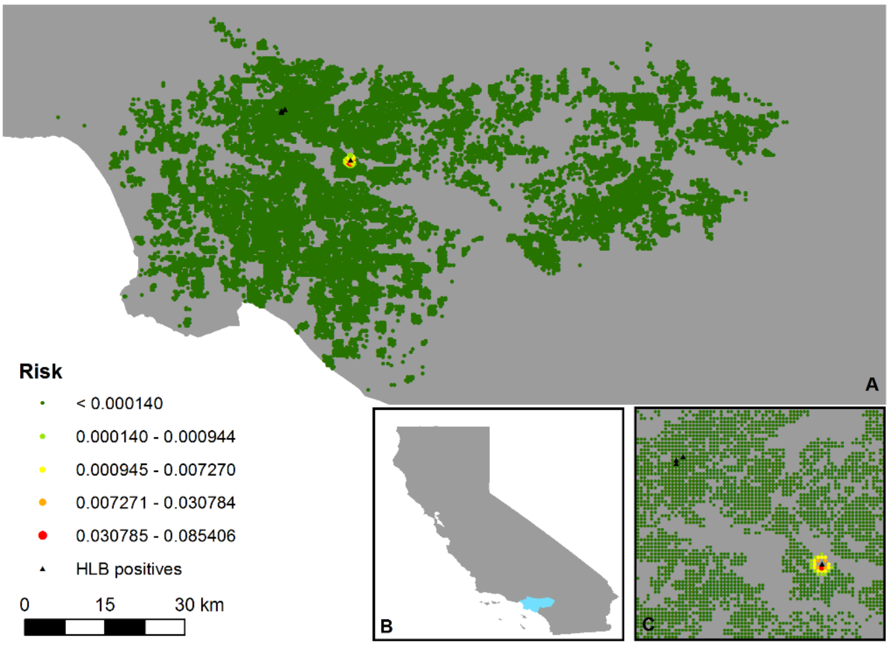


Figure A6 Map of risk of HLB spread in California, predicted for cycle 4, using the transferred model from Florida and a dispersal distance parameter of 250 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

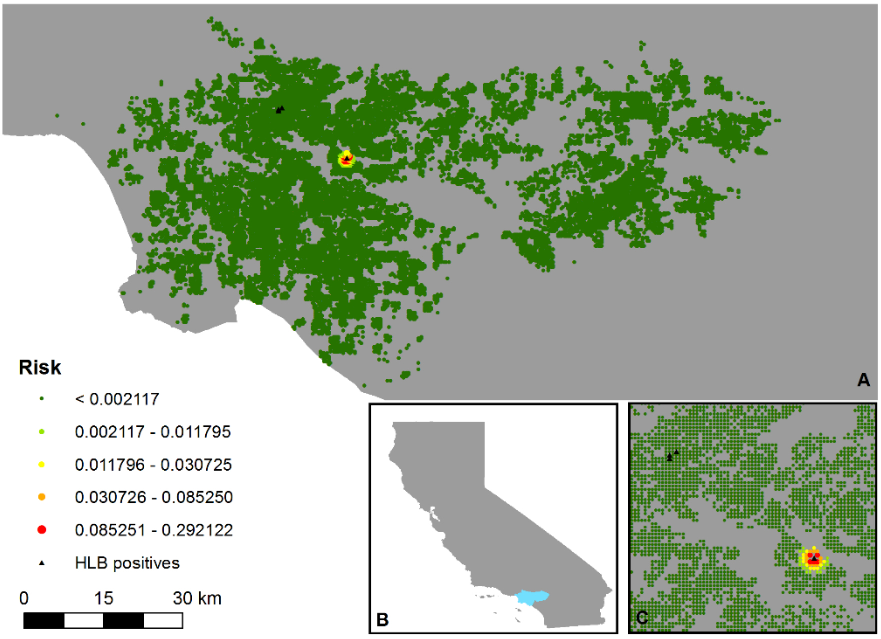


Figure A7 Map of risk of HLB spread in California, predicted for cycle 4, using the transferred model from Florida and a dispersal distance parameter of 500 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

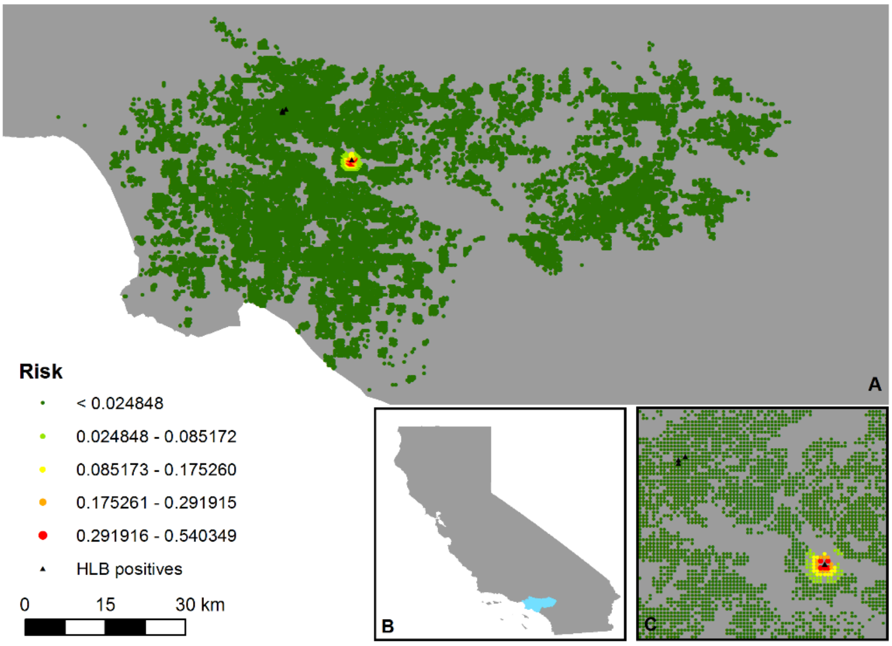


Figure A8 Map of risk of HLB spread in California, predicted for cycle 4, using the transferred model from Florida and a dispersal distance parameter of 1,000 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

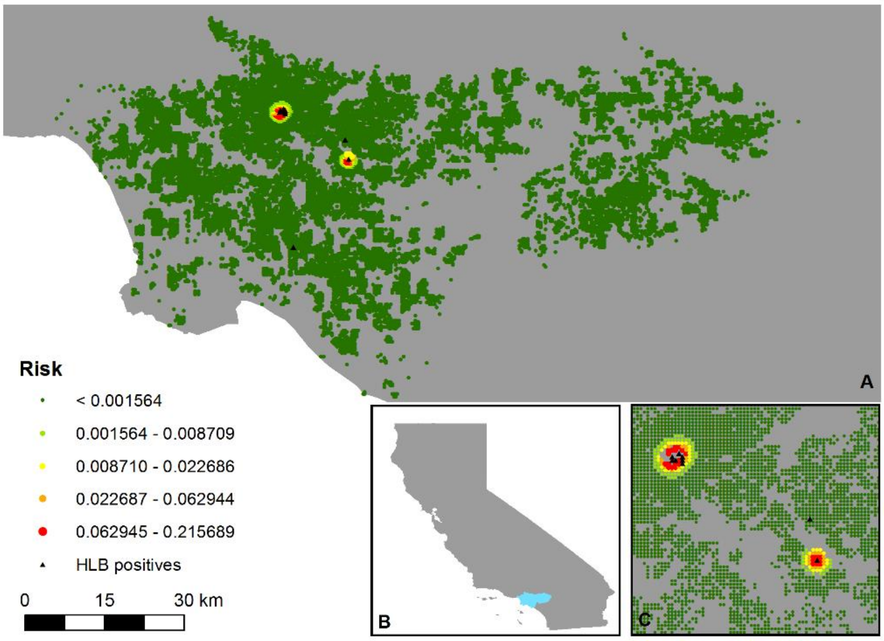


Figure A9 Map of risk of HLB spread in California, predicted for cycle 5, using the transferred model from Florida and a dispersal distance parameter of 500 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

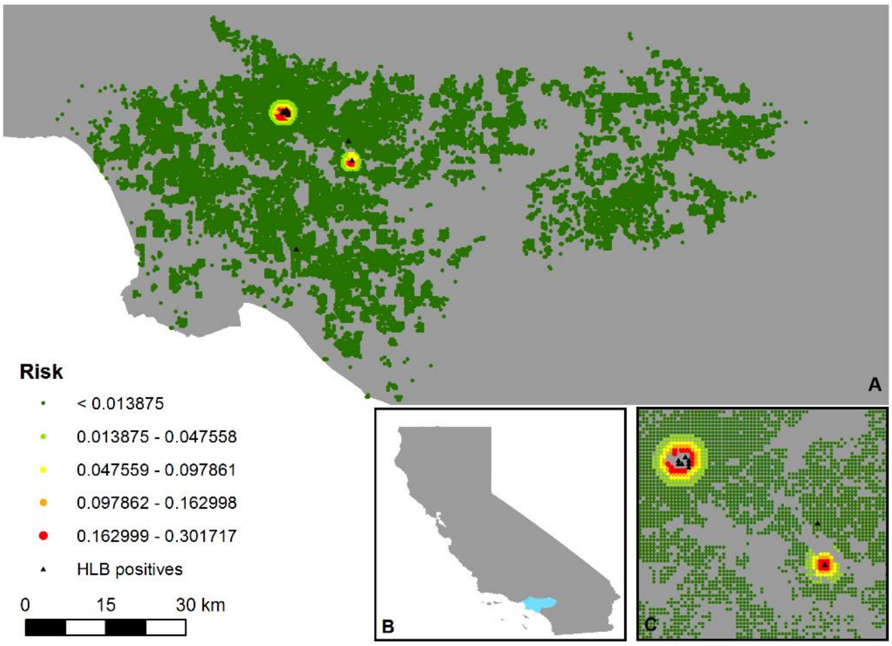


Figure A10 Map of risk of HLB spread in California, predicted for cycle 5, using the transferred model from Florida and a dispersal distance parameter of 1,000 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

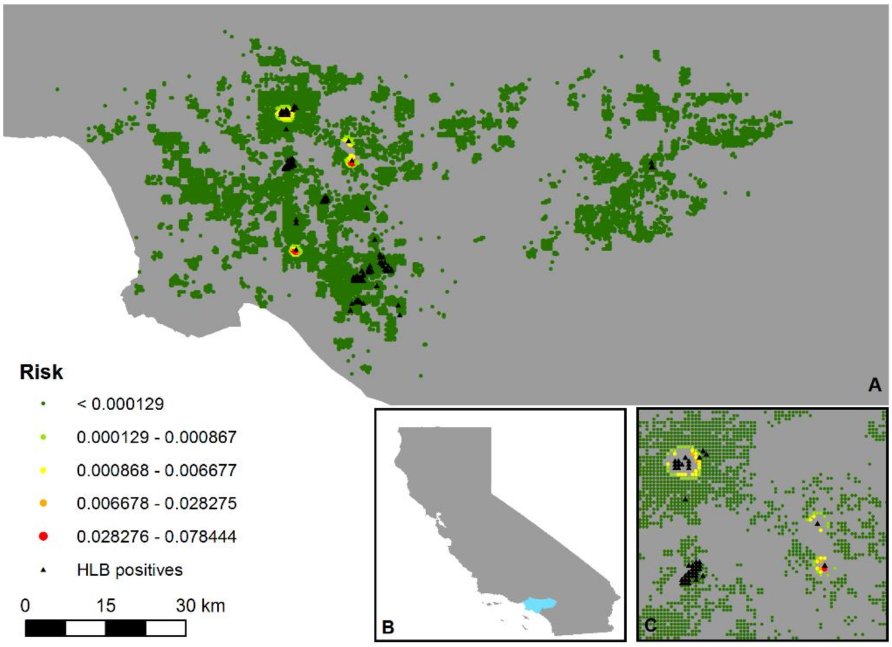


Figure A11 Map of risk of HLB spread in California, predicted for cycle 6, using the transferred model from Florida and a dispersal distance parameter of 250 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

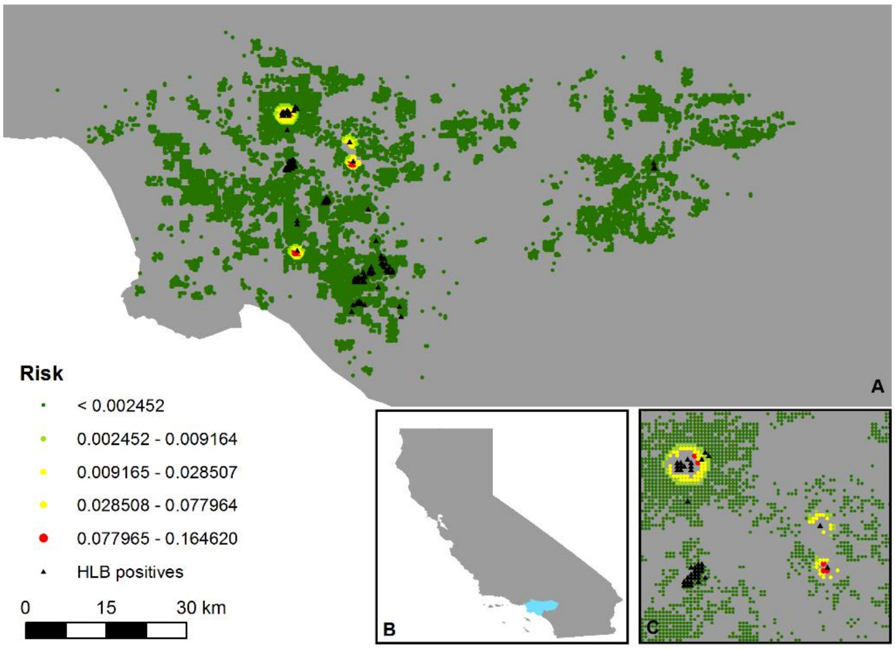


Figure A12 Map of risk of HLB spread in California, predicted for cycle 6, using the transferred model from Florida and a dispersal distance parameter of 500 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.

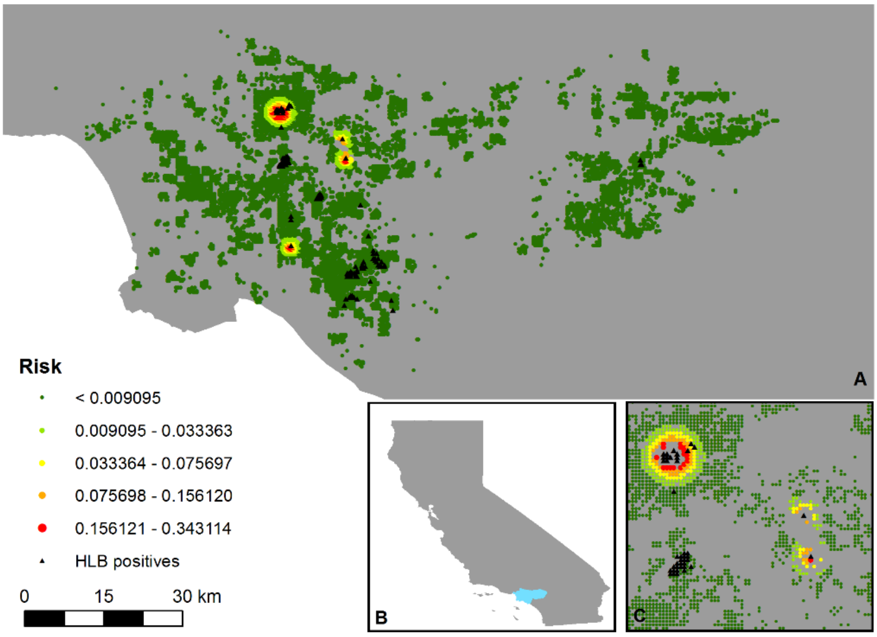


Figure A13 Map of risk of HLB spread in California, predicted for cycle 6, using the transferred model from Florida and a dispersal distance parameter of 1,000 m. A) shows the area within the LA basin, California with infected trees and predicted risk. B) position of trees sampled within the state. C) a more detailed image of an area within California, showing risk and infected trees.