DEDUCING SPACE FROM TIME

MODELLING THE DISTRIBUTION OF INVASIVE SPECIES UNDER CLIMATE AND LAND USE CHANGE SCENARIOS

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DECLARATION

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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CONTENTS

ABSTRACT

Invasive plant species represent a serious threat to biodiversity, precipitating a sustained global effort to eradicate or at least control the spread of this phenomenon. Current distribution ranges of many invasive species are likely to be modified by climate and land use change. This thesis presents a series of papers that aims at mapping the current distribution and predicting the potential future distribution of *Rhododendron ponticum* L. (family: Ericaceae). The series of papers aims to determine, a) the most important abiotic (environmental) factors affecting the distribution of *R. ponticum* in the UK, focussing on Wales as a case study, b) whether the niche of this species has shifted or remained conserved in the UK (compared to its native range), c) the selection of optimum modelling parameters for correlative species distribution model, d) future land use and land cover change maps for the study area and finally, e) assessing the combined effects of land use and climate change on potential future distribution of *R. ponticum* in the UK. The main results suggest that land cover and topography are critical in limiting the distribution of this invasive plant. Furthermore, ecological niche of *R. ponticum* has shifted in the UK compared to the Iberian Peninsula (native range), arguably due to hybridization. Model performance in the training areas improve with decreasing grain size of predictors (50 m > 300m > 1 km). However, model transferability requires optimum grain size which should be determined by testing a range of grain sizes. In most of the future land use and climate change scenarios, invasiveness of *R. ponticum* is likely to decrease by as much as 40 % of the currently invaded area. The results highlight the importance of considering a range of land use and climate change scenarios and including regional policy-based land use change projections to test the potential of invasive species to expand or retreat in future. Eastern belt and south western parts of Wales are vulnerable to future invasion of *R. ponticum* because of possible increase in temperature and forest cover under future scenarios. Invasion risk maps produced in this study could guide pre-emptive management strategies.

Chapter 1

INTRODUCTION

1. BIOLOGICAL INVASION

Over centuries, species have been transported across the globe by humans. In the recent past, the intensification of international trade has accelerated species' displacement [1]. The displaced species were often introduced to the environments where they did not exist before [2]. Many of these species had the potential to cause modifications to the landscape or ecosystem function in the area where they were introduced [3]. Such species became invasive and are now considered a major threat to the native biodiversity [4]. Invasive species are non-native species that are introduced by humans either accidentally or intentionally and are potentially able to spread to a level that causes ecological or economic damages [5]. The European Union defines invasive species as those species which are present outside of their natural range or distributional area and threaten biodiversity [6]. Although introduction of exotic species to long-established ecosystems is a natural phenomenon, the phenomenon is greatly accelerated by human migrations, earlier in the age of discovery, and more recently for international trade [7].

There are four stages in biological invasion; transportation, colonization, establishment, and spread [8]. **Transportation:** This is the first stage of a biological invasion in which a potential invader is transported to a new region, where its previous absence was usually as a result of geographical distance from its native range. **Colonization:** Species transported to a new area may not necessarily colonize their destination as survival of the introduced species depends on the abiotic environmental conditions and biotic processes in the neighbourhood. To successfully colonise new environment, the introduced species needs to achieve a positive growth rate at low densities. If the introduced species survives the new conditions and achieves a positive growth rate in the introduced territory, it is said to have colonized the area. Generally, around 10% of transported or introduced species lead to naturalized populations [8]. **Establishment:** This is the third stage of biological invasion, where an invasive species develops self-sustaining and expanding populations. **Spread:** This is the last stage of biological invasion where an invasive species is able to disperse within the new region over long periods of time [8].

There is a suite of typical traits of introduced species which help them to outcompete native species. Although there are contradicting opinions on whether invasive species can be identified using species' traits, evidence suggest that traits of invasive species can be considered as 'invasiveness markers' since they allow to identify the invasive potential of a large number of invasive species [9][10]. Such traits include fast individual and population growth, higher rates of reproductions, high seed dispersal potential, phenotype plasticity, a wide range of tolerance to environmental conditions, ability to feed on a range of sources (generalists), and prior history of invasion [11]. An introduced species may become invasive by outcompeting native species for carbohydrates, water, light, nutrients or other critical resources or it may also use the resources that were previously not available to the native species (e.g., colonizing previously uninhabited soil types or exploiting deep water table through longer roots). Also, some invasives colonize large areas by limiting growth of native species by the release of toxic chemicals (allelopathy) or harbouring pathogens which are harmful to native species [12].

In addition to the traits of introduced species that may help to identify the invasive potential of a species, some studies have highlighted characteristics of ecosystems vulnerable to invasion. For example, some earlier studies suggested that ecosystems with high species richness are less vulnerable to biological invasion due to fewer available niches [13]. Furthermore, ecosystems that are similar to those where potential invaders have evolved are more likely to experience invasion. Also, ecosystems that have experienced human-induced disturbances are vulnerable to potential invasion. For example, human activities typically favour the establishment of invasive species by simplifying existing ecosystem structure and thus reducing competitive pressure from natives and/or by enhancing resource availability by creating underutilised or empty niches [14].

In ecosystems, the amount of available resources and the extent to which those resources are used by organisms modifies the effects of additional species on the ecosystem. In uninvaded ecosystems, equilibrium exists in the use of available resources. When an invasive species is introduced in an ecosystem, it competes with the native species for the available resources. Some forms of the competition – in case of invasive plant species may include shielding a plant from sunlight, making use of most of the nutrients found in the soil, or limiting the amount of water a native plant receives, while consuming it. If the invasive species is not controlled, the ecosystem, in general, can severely suffer, especially the native organisms of the ecosystem. In some cases, an invasive species can cause native species of an ecosystem to face extinction. This would, in turn, reduce the biodiversity of that ecosystem. Therefore, these mechanisms describe a situation in which the ecosystem suffers a disturbance, which changes the fundamental nature of the ecosystem [15].

Invasive species, particularly woody plant species, have caused large-scale degradation of invaded ecosystems [16]. Invasive species complicate biodiversity conservation and challenge the integrity of ecosystems by reducing genetic variation, altering ecosystem functions, and eroding gene pools by eliminating local species [17]. In addition to ecological consequences, invasive species have economic impacts, which are often valued as financial costs based on extrapolations of some of the most widespread invasive species [16]. Economic damages from invasive species are either *direct costs,* which are the financial losses in the form of production losses in agriculture and forestry sector or *management costs,* which include the expenditures of eradiating or controlling the invasive species. It is estimated that the total cost of invasive species in the US alone exceeds $138 billion annually. Besides, there could be other costs associated with invasive species, such as loss of recreational or tourism sites. An accurate estimation of the financial value of the impacts of invasive species is difficult because of complicated invasion dynamics and the difficulty of monetizing biodiversity and ecosystem service [18].

2. SPECIES DISTRIBUTION MODELLING

With increasingly numerous and evident impacts of invasive species across the globe, forecasting future patterns of invasion by identifying susceptible areas has become a key subject in ecological research [19]. This is primarily because once established in an area, a complete eradication of invasive species is unlikely to take place due to significant financial costs, labour requirements, and logistical problems [20][17]. Thus, forecasting the introduction of invasive species could be critical to preventing the introduction or expansion of invasive species [20]. Species distribution models (SDMs) - also known as ecological niche models, habitat suitability models or climate envelope models – are used to generate invasion risk maps that forecast the potential distribution of invasive species as a function of a set of variables, most importantly climate gradients [21]. SDMs show the relative likelihood of establishment of invasive species, should the invasives be introduced to the study area being modelled [22]. These invasion risk maps can help prioritizing the potential hotpots of future invasion and thus aid surveillance and management [23] of potential spread of emerging invasive species [21]. Moreover, SDMs help understanding the mechanisms underpinning the invasions [24]. Conservation agencies around the world are now investing in predictive modelling to forecast invasion risks. For example, 'Pratique' (www.secure.fera.defra.gov.uk/pratique/) is an initiative of European Union that is aimed at pest risk analysis and focusses on mapping pest ranges. Similarly, in the United States, NAPPFAST [25] database is being used by the Animal and Plant Health Inspection Service to run risk assessment models, while in Australia, climate suitability of ecologically important species is modelled by the Department of Agriculture, Forestry and Fisheries using a climate matching system called, CLIMATE [26]. Thus, there is a global interest in combining different biodiversity databases to modelling tools to conduct risk mapping.

The philosophy of SDMs largely rest upon the idea of a 'niche', which was first presented in early 1900's by Joseph Grinnell and Charles Elton. Grinnell [27] defined niche as a subdivision of the habitat that contains the environmental resources or conditions required for a species for survival and reproduction. These environmental conditions determine the distribution and abundance of species. In 1920's - a decade after Grinnell presented this idea of ecological niche - Elton [28] presented his notion of niche and focussed on the functional role of a species in a community. Unlike Grinnell, Elton's focus was more on species interaction in a community rather than where a species could occur. Elton's idea of niche laid the foundation for the later elaborations and applications of this concept, most importantly the contribution of Hutchinson [29] who devised the distinction between the fundamental and the realized niche. Hutchinson defined fundamental niche as "the set of resources—physical and biological—that a species could use that would enable it to exist indefinitely". Therefore, the fundamental niche is determined by intrinsic properties of a species—how it responds to the environment—rather than by extrinsic properties of the environment independent of the species. On the other hand, the realized niche is defined as, "the subset of the fundamental niche to which a species is constrained by interactions with other species (competition, predation) with which its fundamental niche overlaps". The concepts of fundamental and realized are critical to contemporary ecological niche modelling.

There are generally two approaches in ecological niche modelling; roughly based on whether the fundamental or the realized niche is adopted as the frame of reference [30][31][32]. One approach is "mechanistic modelling" that involves using information on the intrinsic traits of species in order to determine species' response to the environment; for example, using information on species' characteristics such as physiology, life-history, tolerance ranges, genetic plasticity, etc. to identify current and future sites where species' desired conditions may occur [33][34]. The second approach is called "correlative modelling" that uses values of environmental variables as measured in places where the species exists and correlates its presence with the values of the environmental variables. It is also possible to extrapolate and predict future occurrences in places where the correlated environmental features are projected to be present. Since correlative SDMs are based on species' observed distribution, they model the realized niche (the environments where a species is found), as opposed to mechanistic models which model the fundamental niche (the environments where a species can be found, or where the environment is appropriate for the survival) [35]. Most of the studies on species distribution have used correlative modelling approach, primarily because of lack of mechanistic information for species.

SDMs rests upon four basic assumptions. **First**, species are at equilibrium with environmental conditions in the native range, i.e., a species is assumed to be present on all locations within the training area where environmental conditions are suitable for the species. **Second**, niche stability is assumed, i.e. environmental factors which limit the occurrence of a species in its native range also limit its occurrence in the introduced area. **Third**, the training samples are representative of the environmental conditions across the current range, and **fourth**, assumption is that the climatic conditions in the native and introduced areas are analogous. Violations of these assumptions can lead to errors of omission or commission (false negatives or false positives) [36].

SDMs predict the species' distribution across a geographic space (and time) by using a variety of environmental data sources, e.g. precipitation, temperature, soil types, topography, land cover, etc. These models establish a relationship between species current occurrence and the value of the environmental variables on the occurrence locations and then project this relationship to predict distribution across space and time. SDMs are used to understand how different environmental factors influence the distribution of species and thus find a number of applications in ecology, conservation biology and evolutionary studies. SDM-based predictions can be used to predict species' distribution under future climate change, to track past distribution of the species to investigate evolutionary processes or potential spread of invasive species in future. SDM predictions can also provide habitat suitability for species which in turn can help in several management applications such as translocation of species, reintroduction of vulnerable species or conservation of endangered species in anticipation of climate change [37].

Although application of SDMs to invasive species and risk assessment is relatively new, it is evolving very rapidly [38][39][40][41][42][43][44]. A recent study reporting a detailed review of literature on SDMs and invasive species suggested that the major applications of SDMs are investigating species invasion ecology, estimating possible range shifts of invasive species under climate change scenarios and assessments of land use and land cover change and human footprint on the spread of invasive species [45].

3. *RHODODENDRON PONTICUM*

While choosing an invasive species for the studies presented in this thesis, I considered a number of important points. I asked questions about the ecological and economic importance of the species. Are there reliable and accurate historical presence location data available for the species? Has the species not been modelled before? How could ecological modelling of species contribute to ongoing theoretical debates and on-field policy-making and management plans? After a detailed review of literature, I considered *Rhododendron ponticum* L. (family: Ericaceae) for this thesis as this species ticked 'Yes' to all the questions mentioned above. Ecological modelling for *R. ponticum* would not only help understanding the spread of this species (which is highly problematic in the UK and Europe), but the models built for this species can be replicated for similar invasive species, e.g. *Prosopis juliflora* in Asia. *R. ponticum* (Figure 1) is an evergreen shrub of up to 8 m in height, native to the Iberian Peninsula, Black Sea Coast, and Caucasus region. *R. ponticum* was brought to the British Isles in 1763 as an ornamental plant [46]. Since its introduction, it has invaded a range of habitats in Britain, including native woodlands and non-native conifer plantations, heath, bogs, and upland grasslands [47][48]. *R. ponticum*, once established, forms a dense canopy that suppresses the growth of most plant species in the understorey due to low light intensity [46]. Eventually, this inhibits the growth of most ground flora seedlings, leading to reduced native habitat regeneration [46][49]. Since mature trees are not replaced, vast areas of dense *R. ponticum* monoculture are seen with aging tree canopies [50].

A number of factors have led to the successful invasion of *R. ponticum* in Britain. Although its native habitat is the Mediterranean, it thrives in the moist temperate climate in Britain, which increases its seedling establishment [47][49][51]. Also, it is well suited to the acidic soils along with uplands of Britain and the wetter western coast [47][48]. Another important factor responsible for the successful invasion of *R. ponticum* is a very high seed production; one bush produces more than a million seeds per year, which are small and wind-dispersed, allowing them to rapidly spread over vast distances [46][51][52]. Furthermore, *R. ponticum* is unpalatable to most herbivores due to high concentrations of phenolic compounds and grayanotoxins in its foliage, which protect it from grazing. Consequently, this species has few natural enemies in Britain, lending it a competitive advantage over native flora [46][52][53][54]. Evidence suggests that *R. ponticum* decreases soil pH and can alter nutrient cycling, which makes its invasion successful in most of the native habitats [55][56][57]. Also, this species is known to release a number of bioactive compounds into soil, which have phytotoxic effects on other flora, which inhibits the growth and germination of native plants [54]. For example, root elongation of native tree species is limited in soils where Rhododendron grows or on sites where Rhododendron was present for two months [58].

In Rhododendron-invaded woodlands, the only way for a plant species to survive is to grow over the dense Rhododendron canopy. This is problematic even for tree species which normally outgrow Rhododendron. For example, a fast growing tree such as Silver Birch finds it impossible to regenerate as seedlings struggle for sunlight. In addition to substantial biodiversity losses, the control and removal of Rhododendron cost significant amounts of money. For example, in Ireland, Rhododendron costs the Irish forestry service almost £1m a year. In Northern Ireland, the control and removal of Rhododendron cost £270,000 per year [59]. Similarly, in Snowdonia National Park (Wales), the removal of Rhododendron was estimated to cost £10m over five years [60]. However, despite such massive costs, *R. ponticum* has not been completely eradicated in most of Wales and Scotland. For example, Snowdonia National Park authorities state that, *"In several places, we are making a real impact and Rhododendron is well on its way to being eliminated. Elsewhere the battle has hardly begun."* (https://www.snowdonia.gov.wales/looking-after/invasive-species/rhododendron). This suggests that the actual cost control could be much higher than the estimates brought to light so far.

Figure 1: *Rhododendron ponticum* plant.

Introduction

4. STUDY AREA

R. ponticum is an established non-native invasive species within the UK, threatening a variety of natural and semi-natural habitats and the associated flora and fauna. It has invaded almost all parts of the UK and causes significant damages to forestry, agriculture, and livestock sector. Of the various parts of U.K. invaded by *R. ponticum*, Wales is one of the worst affected regions and therefore it was considered a suitable study area for examining the effects of climate and land use change on the distribution of *R. ponticum*. Wales is a country with an area of nearly 21 000 km^2 and a population of over 3 million, most of which live in rural communities [61]. The population is unequally distributed, with most people living in coastal areas in the northeast and south Wales. The country is characterized by a wide variety of landscapes, reflecting both its rugged topography and a long history of agricultural settlement and industrialization. Significant areas of land (approx. 6000 km^2) are at an altitude above 300 m. Welsh countryside contains a range of important habitats, including woodlands, semi-natural grasslands, heathland, fens, bogs, coastal ecosystems including sand dunes and saltmarshes, and a diverse range of upland and montane habitats [62][63]. Only a small proportion—6%—of the country is occupied by arable agriculture, while the major land use types are grazing (77%) and forestry (15%) [64][65][66]. Significantly, most decisions affecting the Welsh landscape have been devolved to the Welsh Assembly and the country thus represents a uniform regulatory environment. Figure 2 shows topographic variation and land cover classes in Wales, UK.

In addition to the UK, I included the Iberian Peninsula for the study presented in Chapter 3 of this thesis. This is because the British population of Rhododendron is native to Iberia. Thus, to examine the ecological niche conservatism of Rhododendron, ecological niche occupied by Rhododendron in the UK was compared to the one occupied by this species in Iberia.

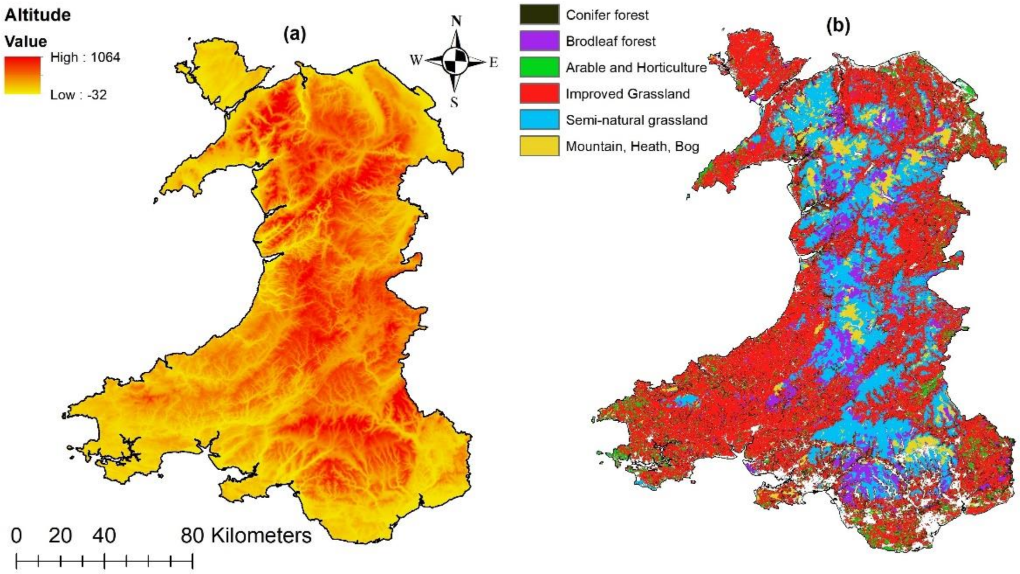

Figure 2. a) Altitude (m) and Land cover (2015) of Wales.

5. KNOWLEDGE GAPS

Ecological modelling of invasive species generally starts by asking some basic questions: What is the current distribution of the species in its invaded region? What are the key environmental determinants (environmental factors) of its distribution? What is the native range of the invasive and does it occupy the same ecological niche in its invaded range as it does in its native range? Are the current and future projections of the required data available to map the current distribution and patterns of invasion? While considering these questions, I found some knowledge gaps in literature which became the foundation of a series of studies compiled in this thesis. Following are brief notes on the identified knowledge gaps.

i. Mapping Current and Forecasting Future Distribution of *R. ponticum* In Wales

Mapping current distribution of an invasive species and generating risk maps is critical to invasive species management [67]. There is currently no study published on mapping current and future distribution of *R. ponticum* in the UK under current and future land cover and climatic conditions. Also, prior to this study, there was no literature or risk assessments maps delineating invasion hotspots for *R. ponticum* in Wales, which is the most invaded part of the UK. Although several studies had highlighted environmental factors critical to the establishment of *R. ponticum*, no ecological model was built to verify the relationship of *R. ponticum* distribution to the identified ecological factors driving the spread of *R. ponticum* in the UK.

ii. Testing Niche Conservation Hypothesis for *R. ponticum*

A critical assumption in SDMs is that the niche of a species is conserved, i.e. it occupies the same environmental conditions in the invaded range as it does in the native range [68]. *R. ponticum* was introduced to the British Isles as an ornamental plant from mainland Europe in the eighteenth century [69]. At the moment, there is no consensus on whether the niche of *R. ponticum* is conserved between its native range in the Iberian Peninsula and invaded range, Britain. The suitability of *R. ponticum* to the British environment and its invasiveness were first thought to result from a hybridization of *R. ponticum* with *R. catawbiense*, (a North American species), a process which supposedly lent frost hardiness to the British *R. ponticum* population [69]. However, this thesis was later rejected by other reports which did not find any genetic evidence of such hybridization [70]. The spread of *R. ponticum* thus represents an opportunity to test how the current niche occupied in Britain corresponds to that in its native Iberia. Knowledge gaps thus exist as to whether, (a) the native and invaded niches are equivalent (native and invasive niches are interchangeable), and (b) the native and invaded niches are similar (the native and invasive niches are more similar than expected by chance).

iii. Understanding the Role of Grain Size in SDMs Performance and Transferability

The role of grain size (the spatial resolution of GIS data layers) is critical in SDMs [71] but only a handful of studies had addressed this issue. A detailed review of literature revealed that over-reliance on bioclimatic variables may lead to an unnecessary compromise on the grain size of critical variables, with potentially negative impact on the accuracy of model predictions and transferability. An important knowledge gap is to test the accuracy of SDMs with and without bioclimatic variables and assess whether the decreasing the grain size improves model performance.

iv. Projection of Land Use Change of Wales Under Contrasting Policy Scenarios

A large majority of SDMs, when projecting into future, rely only on future climate change scenarios [72][73][74][75]. However, it is repeatedly reported that land cover is critical to predicting the distribution of invasive species [76]. Currently no study exists on the projecting likely future trends of land use and land cover (LULC) change in Wales. Thus, a knowledge gap is to map historical patterns of LULC and LULC change in Wales and develop contrasting future LULC scenarios based on (i) current trends and (ii) an alternative policy which may then be fed into SDMs to model the distribution of *R. ponticum* under different land use change scenarios.

v. Combined Effects of Climate and Land Use Changes on The Future Distribution of *R. ponticum*

Effects of land use and climate change on the distribution of species are often studied in isolation, with only a handful of studies assessing the combined effect of these two drivers on the distribution of species [76]. Particularly, no study exists that studies the effects of policy-driven land use change scenarios and future climate change scenarios on the distribution of invasive species. A knowledge gap bridged by this study relates to the combined effect of climate change and LULC projections on future distribution of *R. ponticum* in Wales to make a theoretical contribution to the debate on combining climate change and LULC changes to predict species distribution and, at the same time, generate risk assessment maps that are directly applicable to managing future invasion patterns of *R. ponticum* in Wales.

Introduction

6. AIMS & OBJECTIVES

The aim of this thesis is to understand the drivers of distribution of *R. ponticum* in the UK and predict its distribution in near future under a set of climate and land use change scenarios.

To achieve the above-mentioned aims, following objectives were set:

i. To test the effects of bioclimatic, topographic and anthropogenic (proximate) factors on the distribution of *R. ponticum* in Wales.

ii. To test if the ecological niche of *R. ponticum* is conserved in its invaded range (UK) as compared to its native range (Iberian Peninsula).

iii. To generate policy-driven land use change scenarios for Wales.

iv. To test the combined effects of future climate and land use change on the future distribution of *R. ponticum* in Wales.

7. HYPOTHESES

At the start of the research, I anticipated that land cover would be the most important predictor of *R. ponticum* distribution because it is a 'habitat specialist' (i.e. its distribution is strictly associated with woodlands - be it conifer, broadleaf or mixed species woodlands – as it inevitably requires canopy cover to spread under 'the cover') and therefore likely to be strictly associated with its preferred habitat type. Moreover, as is the case with many other invasive species reported in literature, I thought that the future land use and climate change would increase the invasive potential of this species and expected the niche of *R. ponticum* to be conserved in its invaded range. Therefore, I formulated following main hypotheses and designed the studies to test them which are presented in this thesis:

i. Ecological niche of *R. ponticum* in conserved in its invaded niche.

ii. Land cover is a more important determinant of the distribution of *R. ponticum* as compared to climate.

iii. Species distribution models improve with decreasing grain size of predictor variables.

iv. Climate and land use change will enhance *R. ponticum* invasion in the UK.

8. EVOLUTION OF RESEARCH IDEAS AND THESIS OUTLINE

The basic idea of this PhD research sprung in 2015 when I studied the severity of damage caused by *Prosopis juliflora* (L.), an invasive shrub in the irrigated forest plantations of Pakistan. I submitted a research proposal for ecological modelling of invasive plant species quoting *P. juliflora* as an example and was awarded Commonwealth PhD scholarship to study at the University of Reading, UK in 2016. While reviewing the literature in the first few weeks of my PhD, I found surprising similarities between *R. ponticum* in the UK and *P. juliflora* in Pakistan. Both are shrub-like plants, invade woodlands and cause substantial economic and ecological damage to invaded ecosystems. At that point, I decided to replace *Prosopis* with *Rhododendron* as the focal species of my PhD due to better historical data availability and easier access to local expertise. The plan is to adapt the UK models and the modelling methodology for *Prosopis* in Pakistan at a later stage. In late 2016, I conducted a **pilot study** in which I mapped the current distribution of *R. ponticum* in Wales using climatic, topographic, and land cover variables. I concluded that land cover is central to predicting the future distribution of this invasive species in Wales. Based on the initial findings, I designed the first study **(Chapter 2),** where I modelled the current and future distribution of *R. ponticum* in Snowdonia National Park, Wales, using future climate and LULC change scenarios. In a pattern typical of many research undertakings, the results of this study raised a number of further research questions:

i. A reviewer of the resulting paper (presented in Chapter 2) questioned why the species distribution model for *R. ponticum* was **not trained in its native range** (Iberian Peninsula) to predict its distribution in the UK? At that time, there were no reports on the ecological niche conservatism of *R. ponticum.* This simple question eventually led to the plan to investigate the ecological niche dynamics of *R. ponticum*. **Chapter 4** of this thesis addresses this question.

ii. The SDM presented in Chapter 2 had a spatial resolution of 1 km. Thinking about the assumption that finer scale representation of landscape processes is able to represent them better, I decided to test this notion by running the model at a different spatial resolutions and see how it would affect its performance and transferability across space. This question was addressed in **Chapter 3** of this thesis.

iii. The future LULC change scenario used in Chapter 2 was just a business-as-usual projection of past trends. But future changes are not likely to follow a linear trajectory of change (e.g. Brexit). How would the current land management policies of Welsh government affect the future LULC changes in Wales and to what extent would such a scenario differ from the B-a-U scenario? The study presented in **Chapter 5** attempts to answer this question.

iv. After the completion of the first four studies (Chapters 2-5), I thought it would be interesting to combine the individual lessons learnt each by combining them to run the SDM for *R. ponticum* at national scale in Wales using the optimum grain size, a range of climate and LULC change scenarios to test the effect of climate and land use on the future distribution of this invasive species (presented in **Chapter 6** of this thesis).

A conceptual framework of this thesis is presented in Figure 3.

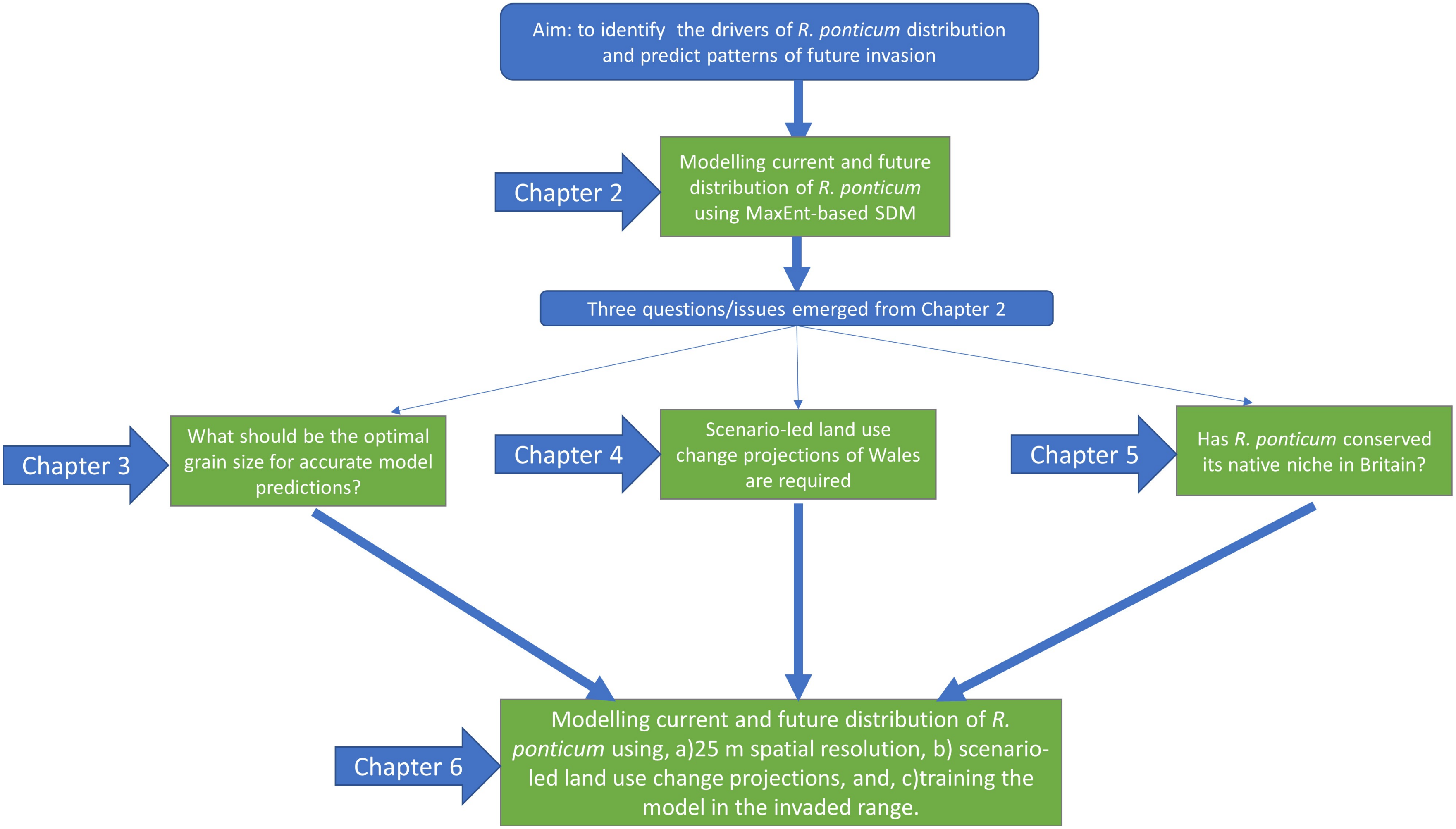

Figure 3. Conceptual framework of thesis.

REFERENCES

1. Hulme, P.E.; Brundu, G.; Carboni, M.; Dehnen-Schmutz, K.; Dullinger, S.; Early, R.; Essl, F.; González-Moreno, P.; Groom, Q.J.; Kueffer, C.; et al. Integrating invasive species policies across ornamental horticulture supply chains to prevent plant invasions. *J. Appl. Ecol.* **2018**, *55*, 92–98.
2. Buckley, Y.M.; Csergo, A.M. Predicting invasion winners and losers under climate change. *Proc. Natl. Acad. Sci. U. S. A.* **2017**, *114*, 4040–4041.
3. Caplat, P.; Hui, C.; Maxwell, B.D.; Peltzer, D.A. Cross-scale management strategies for optimal control of trees invading from source plantations. *Biol. Invasions* **2014**, *16*, 677–690.
4. Richardson, D.M.; Rejmánek, M. Trees and shrubs as invasive alien species - a global review. *Divers. Distrib.* **2011**, *17*, 788–809.
5. Ehrenfeld, J.G. Ecosystem Consequences of Biological Invasions. *Annu. Rev. Ecol. Evol. Syst.* **2010**, *41*, 59–80.
6. Tsiamis, K.; Gervasini, E.; D'Amico, F.; Deriu, I.; Katsanevakis, S.; Crocetta, F.; Zenetos, A.; Arianoutsou, M.; Backeljau, T.; Bariche, M.; et al. The EASIN Editorial Board: Quality assurance, exchange and sharing of alien species information in Europe. *Manag. Biol. Invasions* **2016**, *7*, 321–328.
7. Hulme, P.E. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* **2009**, *46*, 10–18.
8. Theoharides, K.; Dukes, J. Plant invasion across space and time: factors affecting nonindigenous …. *New Phytol.* **2007**, 256–273.
9. Kolar, C.S.; Lodge, D.M. Progress in invasion biology: predicting invaders. *Ecol. Evol.* **2001**, *16*, 199–-204.
10. Reichard, S.H.; Hamilton, C.W. Predicting Invasions of Woody Plants Introduced into North America. Prediccion de Invasiones de Plantas Lenosas Introducidas a Norteamerica. *Conserv. Biol.* **1997**, *11*, 193–203.
11. Ewel, J.J.; O'Dowd, D.J.; Bergelson, J.; Daehler, C.C.; D'Antonio, C.M.; Gómez, L.D.; Gordon, D.R.; Hobbs, R.J.; Holt, A.; Hopper, K.R.; et al. Deliberate Introductions of Species: Research Needs. *Bioscience* **1999**, *49*, 619–630.
12. Funk, J.L. The physiology of invasive plants in low-resource environments. *Conserv. Physiol.* **2013**, *1*, 1–17.
13. Downing, A.S.; van Nes, E.H.; Mooij, W.M.; Scheffer, M. The Resilience and Resistance of an Ecosystem to a Collapse of Diversity. *PLoS One* **2012**, *7*, 1–7.
14. Tilman, D. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U. S. A.* **2004**, *101*, 10854–10861.
15. Byers, J.E.; Hampshire, N.; Road, C. Impact of non-indigenous species on natiUes enhanced by anthropogenic alteration of selection regimes. *Forum Fam. Plan. West. Hemisph.* **2013**, 449–458.
16. Vilà, M.; Basnou, C.; Pyšek, P.; Josefsson, M.; Genovesi, P.; Gollasch, S.; Nentwig, W.; Olenin, S.; Roques, A.; Roy, D.; et al. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front. Ecol. Environ.* **2010**, *8*, 135–144.
17. Hulme, P.E. Weed risk assessment: A way forward or a waste of time? *J. Appl. Ecol.* **2012**, *49*, 10–19.
18. Epanchin-Niell, R.S. Economics of invasive species policy and management. *Biol. Invasions*

2017, *19*, 3333–3354.

19. Gundale, M.J.; Pauchard, A.; Langdon, B.; Peltzer, D.A.; Maxwell, B.D.; Nuñez, M.A. Can model species be used to advance the field of invasion ecology? *Biol. Invasions* **2014**, *16*, 591–607.
20. Gallien, L.; Douzet, R.; Pratte, S.; Zimmermann, N.E.; Thuiller, W. Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Glob. Ecol. Biogeogr.* **2012**, *21*, 1126–1136.
21. Jiménez-Valverde, A.; Peterson, A.T.; Soberón, J.; Overton, J.M.; Aragón, P.; Lobo, J.M. Use of niche models in invasive species risk assessments. *Biol. Invasions* **2011**, *13*, 2785–2797.
22. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudik, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).* **2006**, *29*, 129–151.
23. Gormley, A.M.; Forsyth, D.M.; Griffioen, P.; Lindeman, M.; Ramsey, D.S.L.; Scroggie, M.P.; Woodford, L. Using presence-only and presence-absence data to estimate the current and potential distributions of established invasive species. *J. Appl. Ecol.* **2011**, *48*, 25–34.
24. Broennimann, O.; Treier, U.A.; Müller-Schärer, H.; Thuiller, W.; Peterson, A.T.; Guisan, A. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* **2007**, *10*, 701–709.
25. Magarey, R.D.; Fowler, G.A.; Borchert, D.M.; Sutton, T.B.; Colunga-Garcia, M.; Simpson, J.A. NAPPFAST: An internet system for the weather-based mapping of plant pathogens. *Plant Dis.* **2007**, *91*, 336–345.
26. Bomford, M.; Barry, S.C.; Lawrence, E. Predicting establishment success for introduced freshwater fishes: A role for climate matching. *Biol. Invasions* **2010**, *12*, 2559–2571.
27. Joseph, G. The niche-relationships of the California Thrasher. *Auk* **1917**, *34*, 427–433.
28. Charles, E. *Animal Ecology*; Sedgwick and Jackson, London, 1927;
29. Hutchinson, G. Concluding remarks. In Proceedings of the Cold Spring Harb Symp Quant Biol; 1957; Vol. 22, pp. 415–427.
30. Pearson, R.G.; Dawson, T.P. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **2003**, *12*, 361–371.
31. Lee, T.M.; Markowitz, E.M.; Howe, P.D.; Ko, C.Y.; Leiserowitz, A.A. Predictors of public climate change awareness and risk perception around the world. *Nat. Clim. Chang.* **2015**, *5*, 1014–1020.
32. Jorge, S. View of Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. *Biodivers. Informatics* **2005**, *2*, 1–10.
33. Kearney, M.; Porter, W. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **2009**, *12*, 334–350.
34. Williams, S.E.; Shoo, L.P.; Isaac, J.L.; Hoffmann, A.A.; Langham, G. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **2008**, *6*.
35. Hijmans, R.J.; Graham, C.H. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Chang. Biol.* **2006**, *12*, 2272–2281.
36. Richmond, O.M.W.; McEntee, J.P.; Hijmans, R.J.; Brashares, J.S. Is the climate right for pleistocene rewilding? using species distribution models to extrapolate climatic suitability for mammals across continents. *PLoS One* **2010**, *5*, 1–11.
37. Guillera-Arroita, G.; Lahoz-Monfort, J.J.; Elith, J.; Gordon, A.; Kujala, H.; Lentini, P.E.; Mccarthy, M.A.; Tingley, R.; Wintle, B.A. Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* **2015**, *24*, 276–292.
38. Poulos, H.M.; Chernoff, B.; Fuller, P.L.; Butman, D. Ensemble forecasting of potential

habitat for three invasive fishes. *Aquat. Invasions* **2012**, *7*, 59–72.
39. Padalia, H.; Srivastava, V.; Kushwaha, S.P.S. Modelling potential invasion range of alien invasive species, Hyptis suaveolens (L.) Poit. in India: Comparison of MaxEnt and GARP. *Ecol. Inform.* **2014**, *22*, 36–43.
40. Yan, H.; Feng, L.; Zhao, Y.; Feng, L.; Zhu, C.; Qu, Y.; Wang, H. Predicting the potential distribution of an invasive species, Erigeron canadensis L., in China with a maximum entropy model. *Glob. Ecol. Conserv.* **2020**, *21*, e00822.
41. Bazzichetto, M.; Malavasi, M.; Bartak, V.; Acosta, A.T.R.; Rocchini, D.; Carranza, M.L. Plant invasion risk: A quest for invasive species distribution modelling in managing protected areas. *Ecol. Indic.* **2018**, *95*, 311–319.
42. Petrovskaya, N.; Zhang, W. When seeing is not believing: Comparative study of various spatial distributions of invasive species: Topological analysis of spatial distributions of invasive species. *J. Theor. Biol.* **2020**, *488*, 110141.
43. Fernandes, R.F.; Honrado, J.P.; Guisan, A.; Roxo, A.; Alves, P.; Martins, J.; Vicente, J.R. Species distribution models support the need of international cooperation towards successful management of plant invasions. *J. Nat. Conserv.* **2019**, *49*, 85–94.
44. Santamarina, S.; Alfaro-Saiz, E.; Llamas, F.; Acedo, C. Different approaches to assess the local invasion risk on a threatened species: Opportunities of using high-resolution species distribution models by selecting the optimal model complexity. *Glob. Ecol. Conserv.* **2019**.
45. Srivastava, V.; Lafond, V.; Griess, V.C. Species distribution models (SDM): Applications, benefits and challenges in invasive species management. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* **2019**, *14*.
46. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
47. Cross, J.R. Biological flora of the British Isles. *Rhododendron ponticum* L. *J. Ecol.* **1975**, *63*, 345–364.
48. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–758.
49. Peterken, G.F. Ecological effects of introduced tree species in Britain. *For. Ecol. Manage.* **2001**, *141*, 31–42.
50. Eşen, D.; Zedaker, S.M. Control of rhododendron (*Rhododendron ponticum* and R. flavum) in the eastern beech (Fagus orientalis) forests of Turkey. *New For.* **2004**, *27*, 69–79.
51. Erfmeier, A.; Bruelheide, H. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora - Morphol. Distrib. Funct. Ecol. Plants* **2004**, *199*, 120–133.
52. Higgins, S.I.; Richardson, D.M. A review of models of alien plant spread. *Ecol. Modell.* **1996**, *87*, 249–265.
53. Judd, S.; Rotherham, I.D. The phytophagous insect fauna of <i xmlns=.
54. Esen, D.; Nilsen, E.T.; Yildiz, O. Ecology, competitive advantges, and integrated control of Rhododendron: An old oramental yet emerging invasive weed around the globe. *Floric. Ornam. Plant Biotechnol.* **2006**, *3*, 408–421.
55. Rotherham, I.D. The ecology of *Rhododendron ponticum* L. with special reference to its competitive and invasive capabilities., 1983.
56. Wurzburger, N.; Hendrick, R.L. Rhododendron thickets alter N cycling and soil

extracellular enzyme activities in southern Appalachian hardwood forests. *Pedobiologia (Jena).* **2007**, *50*, 563–576.

57. Horton, J.L.; Clinton, B.D.; Walker, J.F.; Beier, C.M.; Nilsen, E.T. Variation in Soil and Forest Floor Characteristics Along Gradients of Ericaceous, Evergreen Shrub Cover in the Southern Appalachians. *Castanea* **2009**, *74*, 340–352.
58. Nilsen, E.T.; Walker, J.F.; Miller, O.K.; Semones, S.W.; Lei, T.T.; Clinton, B.D. Inhibition of seedling survival under Rhododendron maximum (Ericaceae): Could allelopathy be a cause? *Am. J. Bot.* **1999**, *86*, 1597–1605.
59. Catherine, S. Invasive species cost NI economy £46.5m each year. *BBC News* 2013.
60. BBC News £10m to rid Snowdonia National Park of rhododendrons - BBC News 2014, 10.
61. *Statistical Bulletin: Annual Mid year Population Estimates: 2013*; 2014;
62. Blackstock, T.; Howe, E. a.; Stevens, J.; Howe, L.; Jones, P. Habitats of Wales: A Comprehensive Field Survey, 1979-1997 2010, 240.
63. Swetnam, R.D.; Tweed, F.S. A tale of two landscapes: Transferring landscape quality metrics from Wales to Iceland. *Land use policy* **2018**, 0–1.
64. Forestry Commission Chapter 1: Woodland Areas and Planting. *For. Stat. 2017* **2017**, 37.
65. Research Service Natural Resources Wales Forestry in Wales Quick Guide. *For. Comm. For. Stat.* **2013**, 1–5.
66. Park, C.; Park, T. Review of Land Use Climate Change An assessment of the evidence base for climate change action in the agriculture , land use and wider foodchain sectors in Wales. **2014**.
67. West, A.M.; Kumar, S.; Brown, C.S.; Stohlgren, T.J.; Bromberg, J. Field validation of an invasive species Maxent model. *Ecol. Inform.* **2016**, *36*, 126–134.
68. Warren, D.L.; Glor, R.E.; Turelli, M. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution (N. Y).* **2008**, *62*, 2868–2883.
69. Milne, R.I.; Abbott, R.J. Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. *Mol. Ecol.* **2000**, *9*, 541–556.
70. Erfmeier, A.; Tsaliki, M.; Roß, C.A.; Bruelheide, H. Genetic and phenotypic differentiation between invasive and native Rhododendron (Ericaceae) taxa and the role of hybridization. *Ecol. Evol.* **2011**, *1*, 392–407.
71. Connor, T.; Hull, V.; Viña, A.; Shortridge, A.; Tang, Y.; Zhang, J.; Wang, F.; Liu, J. Effects of grain size and niche breadth on species distribution modelling. *Ecography.* **2017**, 1-12.
72. Thapa, S.; Chitale, V.; Rijal, S.J.; Bisht, N.; Shrestha, B.B. Understanding the dynamics in distribution of invasive alien plant species under predicted climate change in Western Himalaya. *PLoS One* **2018**, *13*, 1–16.
73. Schivo, F.; Bauni, V.; Krug, P.; Quintana, R.D. Distribution and richness of amphibians under different climate change scenarios in a subtropical region of South America. *Appl. Geogr.* **2019**, *103*, 70–89.
74. Jeschke, J.M.; Strayer, D.L. Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. N. Y. Acad. Sci.* **2008**, *1134*, 1–24.
75. Khanum, R.; Mumtaz, A.S.; Kumar, S. Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modelling. *Acta Oecologica* **2013**, *49*, 23–31.
76. Betts, M.G.; Gutiérrez Illán, J.; Yang, Z.; Shirley, S.M.; Thomas, C.D. Synergistic Effects of Climate and Land-Cover Change on Long-Term Bird Population Trends of the Western USA: A Test of Modeled Predictions. *Front. Ecol. Evol.* **2019**, *7*, 1–11.

Chapter 2

LAND COVER AND CLIMATE CHANGE MAY LIMIT INVASIVENESS OF *RHODODENDRON PONTICUM* IN WALES

ABSTRACT

Invasive plant species represent a serious threat to biodiversity precipitating a sustained global effort to eradicate or at least control the spread of this phenomenon. Current distribution ranges of many invasive species are likely to be modified in the future by land cover and climate change. Thus, invasion management can be made more effective by forecasting the potential spread of invasive species. *Rhododendron ponticum* (L.) is an aggressive invasive species which appears well suited to western areas of the UK. We made use of MAXENT modelling environment to develop a current distribution model and to assess the likely effects of land cover and climatic conditions (LCCs) on the future distribution of this species in the Snowdonia National park in Wales. Six general circulation models (GCMs) and two representative concentration pathways (RCPs), together with a land cover simulation for 2050 were used to investigate species' response to future environmental conditions. Having considered a range of environmental variables as predictors and carried out the AICc-based model selection, we find that under all LCCs considered in this study, the range of *R. ponticum* in Wales is likely to contract in the future. Land cover and topographic variables were found to be the most important predictors of the distribution of *R. ponticum*. This information, together with maps indicating future distribution trends will aid the development of mitigation practices to control *R. ponticum.*

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Land cover and climate change may limit invasiveness of Rhododendron

1. INTRODUCTION

Invasive alien species are considered the second biggest threat to global biodiversity, after habitat degradation [1][2]. Invasive plant species alter the dynamics of plant communities and thus threaten the stability and functioning of established ecosystems by affecting nutrient cycles and net primary productivity, affecting soil health by increasing soil acidity, posing risk for pollinators, inhibiting regeneration of native species, and competing with native flora [3][4][5][6]. Plant invasion causes significant economic losses to crop and livestock farmers around the world [7]. Various studies estimate that the global monetary value of direct damage and associated control of invasives exceeds $100 billion per annum [8]. However, since there are many invasive species with no recorded damage costs, the true figure is likely to be many times higher than these estimates [9]. Several studies have highlighted the potential impacts of global climate change on population dynamics of invasive species, with secondary effects on host plant communities and ecosystems [10][7]. During the last century, global average temperatures have increased by 0.85◦C above pre-industrial levels and are expected to further increase by 0.3–4.8◦C by 2100 (IPCC, 2013). Changes in climatic conditions may render some regions more or less suitable for invasive plants thus increasing or decreasing their range [12]. Effects of climate change on invasiveness of alien species must be considered and any prediction of future distribution should include a range of climate change scenarios.

Once an invasive species has established itself, one of the most cost-effective ways to reduce its threat is to map its current distribution and take pre-emptive measures to prevent further expansion [13]. Such targeted management of biological invasions is not possible without information about the likely future distribution of invasive species. In this context, species distribution models (SDMs) present a workable opportunity to examine future changes in species distribution [14]. As climate is a strong determinant of habitat suitability of plant species [15], SDMs are often driven by environmental variables. Also known as ecological niche models, they are successfully being used for projecting the impacts of climate change on plant distributions [16][17]. In principle, species are assumed to exist in a "niche" described by ecological requirements of the species. SDMs characterize the ecological space of a species and subsequently identify vulnerable locations based on the environmental suitability of the species [18].

In addition to climate, distribution of invasive plant species is often strongly linked to land cover type. For instance, transportation corridors, continuous grasslands, forest areas, and proximity to human settlements are often reported as strong determinants of species spread [19]. A score of SDM studies indicates that land cover is often a far better predictor of species habitat suitability than climatic variables [20][21][22][23][24]. Changes in land cover can affect both quality and quantity of suitable habitat, in some instances the landscape variables alone can accurately predict the distribution of a species [25]. It is therefore recommended to consider climate and land cover change in combination when exploring species' niche shifts in future [26]. However, despite the fact that land cover is an integral part of species' ecological niche, the majority of SDM studies investigating species' future distribution ignore it and assume that species' future distribution is only driven by shifts in climatic variables [27][28][29]. The history of climatic changes and human land use shows that land cover types will shift, any modelling of species' future distribution based merely on climatic variables may lead to a severely misleading prediction [30].

In Europe, *Rhododendron ponticum* (L.) is an invasive plant species that was introduced to the United Kingdom in the eighteenth century as an ornamental plant. It is a perennial, evergreen shrub that generally invades woodlands [6], although it has been shown to colonize other types of habitats too. The main ancestor is reported to be the population of *R. ponticum* resident at the southern tip of Spain. The successful invasion of *R. ponticum* in the UK is attributed to a range of its ecological and biological characteristics: it produces great amounts of seeds which are wind-dispersed, can tolerate shade and thus outcompetes flora under closed canopies and can easily colonize low-nutrient sites [31]. It often prevents germination of native plant species by casting a dense shade and by releasing toxins into the soil [32]. Germination of *R. ponticum* seeds may occur on a number of substrates, including tree stumps and mosses covering bare ground [33]. The UK invasion by this shrub has been more intense in Western and North Western parts, which are the comparatively cooler and wetter areas of Britain. A genetic analysis of the British population of *R. ponticum* has confirmed the presence of genes from *R. catawbiense* (Michx), suggesting past hybridization between the two species. *R. catawbiense* is a species native to North America and characterized by greater cold tolerance [34][5][35], a trait that may increase invasiveness of *R. ponticum* in the UK. However, an in-depth analysis is still required to identify the other key environmental factors responsible for colonization and spread of this species. Of the various parts of U.K. invaded by *R. ponticum*, Wales is one of the worst affected regions. In this study, we focus on the Snowdonia National Park in Wales where *R. ponticum* is identified as a major invasive species affecting large areas of the National Park [36] indicating that current environmental, topographic and land cover conditions in Snowdonia represent a range of conditions very suitable for *R. ponticum*.

We examine the current and future distribution of *R. ponticum* in Snowdonia National Park, Wales, UK under current and future land cover and climatic conditions (LCCs). Our modelling effort aims to, (a) delineate "invasion hotspots" for *R. ponticum* in Snowdonia National Park, (b) identify key ecological factors driving the spread of *R. ponticum* in the park, and (c) identify likely spatial patterns of habitat suitability under future climate conditions to establish a theoretical reference framework for management plans to combat the potential invasion of *R. ponticum*.

2. METHODOLOGY

We used MAXENT, a maximum entropy-based machine learning algorithm to model the distribution *R. ponticum* in Snowdonia National Park. MAXENT predicts the probability distribution of a species on the basis of a given set of environmental variables and presence-only species occurrence data [37]. We selected MAXENT because, (a) it does not require absence data [38], (b) it efficiently handles complex interactions between predictor and response variables [16], (c) being a generative model, it performs better than discriminative models when it comes to modelling with presence-only records and, (d) it can be run with both categorical and continuous data variables [39]. There are several known limitations of the MAXENT modelling environment; (a) sensitivity to small sample size and questionable occurrence records [39], (b) use of overly complex models due to user over-reliance on default model calibration settings [40], and (c) biased performance due to errors in sampling effort or spatial autocorrelation of occurrence records [41]. In this study, we countered these model limitations by; (a) using reasonably large sample size and applying recommended screening and verification of occurrence records, (b) tuning the model by identifying optimal model calibration settings, and (c) accounting for sampling bias and applying spatial filters to reduce clustering.

2.1. Pre-Processing of Occurrence Records and Predictor Variables

Presence-only occurrence records of *R. ponticum* were obtained from COFNOD (Local Environmental Records Centre in Wales, UK). A dataset totaling 436 occurrence records originating from a continuous field observation campaign spanning the period between 1981 and 2016. COFNOD has confirmed that the entire area of Snowdonia National Park had been thoroughly surveyed by ground surveys and remote sensing tools, thus minimizing the possibility of sampling bias in the dataset. Consequently, in our modelling effort we covered the entire area of the national park, generating 10,000 random background points to be selected from in each replicate run of the model. Spatial uncertainty of all occurrence records was verified, and all duplicate or not georeferenced occurrence points were removed. Occurrence data were spatially rarefied by eliminating all but one point present within a single grid cell of the predictor variable layers to reduce clustering. As a result, the number of occurrence points used for model calibration and verification was reduced from 452 to 92.

We considered a total of 23 predictor variables (Table 1) covering Snowdonia National Park at a cell resolution of 30– arc-seconds (~1 km, worldclim.org, version 1.4) [42]. These 23 variables were selected on the basis of published information on plant-habitat associations of *R. ponticum*. We included bioclimatic variables, together with a land cover variable as *R. ponticum* is a habitat-specialist and thus sensitive to land cover type. In addition, we included topographic factors such as slope, aspect and altitude as these factors are also known to limit the distribution of this species [43][44][32][45]. In all, our predictor dataset consisted of 19 climatic variables which were complemented by 3 topographic and 1 land cover variable. A Digital Elevation Model (Shuttle Radar Topography Mission, https://lta.cr.usgs.gov/SRTM1Arc) with spatial resolution of 30m was used to derive three topographic variables: altitude, aspect and slope. Land Cover data originates from "The European Space Agency CCI" global land cover product available at 300m of spatial resolution (www.esalandcover- cci.org). The whole set of 23 variables (19 climatic, 1 land cover, and 3 topographic) was re-sampled to 1 km spatial resolution and masked to the extent of Snowdonia National Park. A combination of expert knowledge, published studies on *R. ponticum* invasiveness in the UK and statistical methods was used to select an appropriate set of predictor variables to reduce the negative impact of multicollinearity and to conform to statistical assumptions [46].We removed highly correlated variables by applying a Pearson correlation coefficient cut-off of r ≤0.85 to select the variable layers for use in final model runs [47].

Table 1. Predictor variables used in the study; variables highlighted in bold were selected to run all models presented in this study.

Code	Predictor Variable	Unit
BIO 1	Annual Mean Temperature	°C
BIO 2	**Mean Diurnal Range (monthly (max temp - min temp))**	°C
BIO 3	**Isothermality (BIO2/BIO7)* 100**	
BIO 4	**Temperature Seasonality (standard deviation *100)**	C of V
BIO 5	Max Temperature of Warmest Month	°C
BIO 6	Min Temperature of Coldest Mont	°C
BIO 7	Temperature Annual Range (BIO5-BIO6)	°C
BIO 8	Mean Temperature of Wettest Quarter	°C
BIO 9	**Mean Temperature of Driest Quarter**	°C
BIO 10	Mean Temperature of Warmest Quarter	°C
BIO 11	Mean Temperature of Coldest Quarter	°C
BIO 12	Annual Precipitation	mm
BIO 13	Precipitation of Wettest Month	mm
BIO 14	Precipitation of Driest Month	mm
BIO 15	**Precipitation Seasonality (Coefficient of Variation)**	C of V
BIO 16	Precipitation of Wettest Quarter	mm
BIO 17	Precipitation of Driest Quarter	mm
BIO 18	Precipitation of Warmest Quarter	mm
BIO 19	Precipitation of Coldest Quarter	mm
Altitude	**Altitude**	m
Aspect	**Aspect**	°
Slope	**Slope**	°
Land Cover	**Land cover**	

2.2. Habitat Suitability Under Climate and Land Cover Change Scenarios

Projected future climatic conditions for the year 2050 based on the IPCC 5th assessment report was used to assess the potential effects of climate change on *R. ponticum* habitat suitability in Snowdonia National Park. We used the following six GCMs projections: BCC-CSM1-1, CCSM4, GISS-E2-R, MIROC5, HadGEM2-ES, and MPI-ESM-LR. These are some of the most recent GCMs, also used in the Fifth Assessment IPCC report and are currently considered the most reliable GCMs for future climate projections [48]. The assessment was made under two Representative Concentration Pathways: RCP 4.5 and RCP 8.5. RCP 4.5 describes a scenario where GHG emissions are stabilized and thus represents a stable scenario, while RCP 8.5 is a scenario depicting an extreme situation where GHG emissions increase until 2100 [49].

Land cover for 2050 was simulated in Terrset software [50] using recommended protocols [51][52][53]. Making use of the Multi-layer Perceptron-Markov Chain (MLP-MC) model, we projected the future land cover changes of Snowdonia National Park in 2050 based on historical changes in the land cover between 2005 and 2015. The land cover maps for 2005 and 2015 were acquired from "The European Space Agency CCI" global land cover product. Land cover transitions were modeled using a Multi-layer Perceptron neural network. A transition matrix was created to quantify the transition potential between the two time periods. For the sake of simplicity, we assumed that the transition probabilities (patterns of change) would remain unchanged in future and used these to predict land cover for 2050. We used a number of driver or explanatory variables to generate transition potential maps to improve the prediction accuracy of the model. These driver variables included elevation, aspect, hillshade, slope, distance to roads, distance to road nodes, distance to water channels, distance to hydro nodes, distance to green space sites, and distance to access points. A flow chart of the land cover and species distribution modelling is shown in Figure 1.

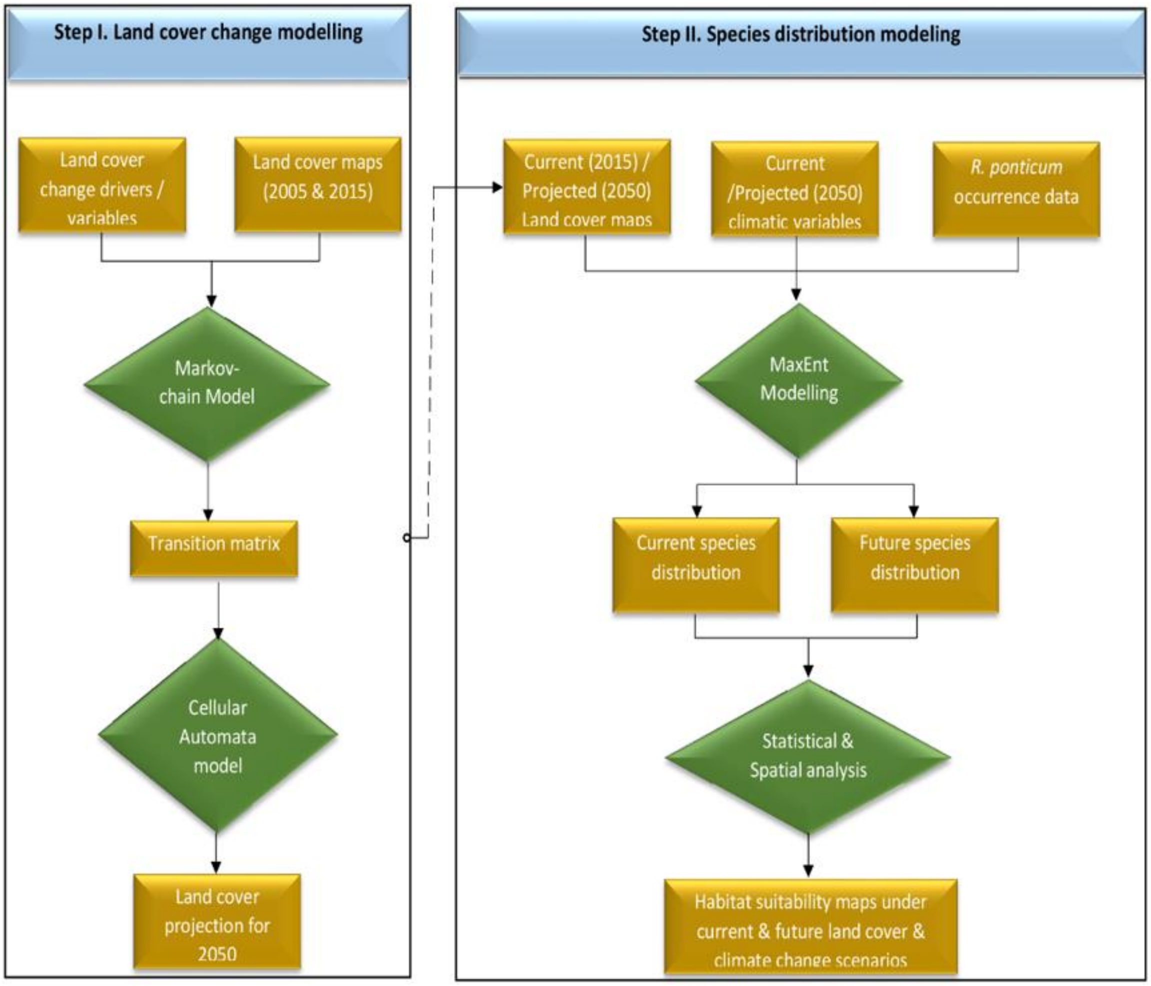


Figure 1. Flow chart detailing sequential steps carried out in land cover simulation (Step I) and Maxent based species distribution modelling (Step II) of *R. ponticum* in Snowdonia National Park, Wales.

2.3. Maxent Model Complexity and Tuning

The complexity of models resultant in MAXENT environment is primarily driven by the following two factors; feature type and regularization parameter [40]. Maxent offers a range of five function forms known as "feature types" to explain the relationship between predictor variables and the probability of species occurrence. These feature types are labelled as Linear (L), Quadratic (Q), Hinge (H), Product (P), and Threshold (T) (see [37][38][39] for details). Maxent allows users to select and combine different function forms manually or picks functions or their combinations automatically when left in the default "Auto Feature" mode. Most of the published MAXENT-based studies rely on the default options of feature type and regularization parameters, which means that model complexity and the risk of over-fitting is completely ignored by the researchers [51]. The second key factor that determines the complexity of MAXENT models is the regularization parameter. As part of the modelling process, MAXENT pushes or modifies the predictor values (such as variance and mean) of environmental variables as close as possible to the values describing actual presence points, which frequently leads to overfitting of the model. To counter over-fitting, MAXENT uses the regularization parameter to control the complexity of models (the default value is 1). The regularization parameter limits the number of "features" in the model, depending on the number of presence records (fewer records allow for fewer features to be included). A higher value of the regularization parameter penalizes the number of features and thus leads to less complex models [52]. Various studies have confirmed that calibrating MAXENT models with default settings frequently leads to highly complex models, a species-specific tuning of the model is thus recommended [40]. In this study, we generated all possible combinations of features types in combination with a range of regularization parameter values; 0.1, and then 1–10 with an increment of 1. We then used ENMeval R package to select the model with the lowest AICc (corrected Akaike Information Criterion) value which was then used as the most appropriate (least over-fitted model) out of the whole suite of models [53][51].

2.4. Model Calibration and Evaluation

We ran MAXENT (version 3.3.3a) with the default convergence threshold of 10−6 and with 5,000 iterations. This number of iterations was set to allow the model a reasonable scope for convergence, thus reducing the risk of over-predicting or under-predicting the model relationships. The selected model used the "Linear" and "Quadratic" feature types and the regularization parameter of 2, as indicated by the lowest AICc value. We processed 20 model replications with bootstrap resampling which randomly allocated 75% of the occurrence records to calibration and 25% to validation. We used the average of the 20 replicate models to produce habitat suitability maps under current and future scenarios. MAXENT produces continuous suitability index in its output, 10 percentile training presence thresholds was employed to convert this index into binary form (suitable and unsuitable habitat) [54].

AUC (Area under the receiver operating characteristic curve) was used to test the performance of the model against actual observations [16]. An AUC value of 0.5 shows that the model does not predict any better than random chance, whereas a value closer to 1 indicates better performance of the model. Based on the AUC value, a conventionally used guide for ranking the model performance is: 0.5–0.6 = Failed; 0.6– 0.7 = Poor; 0.7–0.8 = Fair; 0.8–0.9 = Good; 0.9–1 = Excellent [55]. Jackknife test and percent variable contribution were used to assess the relative significance of predictor variables. Fitted response curves were used to visually investigate the relationship between individual variables and predicted index of environmental suitability of *R. ponticum*.

AUC was suggested not being sufficiently reliable for model evaluation, as an alternative, the Continuous Boyce Index (CBI) can be utilized a complementary evaluation index [56]. The Boyce index requires presence data only and measures how much model predictions differ from random distribution of observed presence across the prediction gradient. The continuous values of Boyce index vary between −1 and +1. Positive values indicate a model where predictions are consistent with the distribution of actual presence data, values close to zero mean that the model is not different from a random model and negative values indicate counter predictions (e.g., predicting no occurrence in areas where actual presence is recorded, [57][58].

3. RESULTS

3.1. Model Performance

The calibration test of the model specification selected on the basis of the lowest AICc showed encouraging predictive capacity: AUCtrain = 80.0, AUCtest = 75.61, and CBI = 0.82. These results suggest that the predictor variables used during model calibration can predict the presence of *R. ponticum* in the Snowdonia National park with a fairly good degree of accuracy. Current distribution of *R. ponticum* on a continuous habitat suitability map for the present day LCCs is shown in Figure 2.

Comparing the predictor variables used in this model, Land Cover type contributed the most predictive power (43.3%), followed by aspect (21.5%), and altitude (15.5%, Table 2). The Jackknife test suggests that the variable which decreases the gain the most when omitted is land cover, indicating that it contains the most information absent in the other variables (Figure 3).

Table 2. Analysis of variable contribution

Variable	Description of variables	Percent contribution
Landcover	-	43.3
Aspect	-	21.5
Altitude	-	15.5
Bio15	Precipitation Seasonality	9.4
Bio3	Isothermality	4.1
Bio9	Mean Temperature of Driest Quarter	3.4
Bio2	Mean Diurnal Range	1.6
Slope	-	0.9
Bio4	Temperature Seasonality	0.3

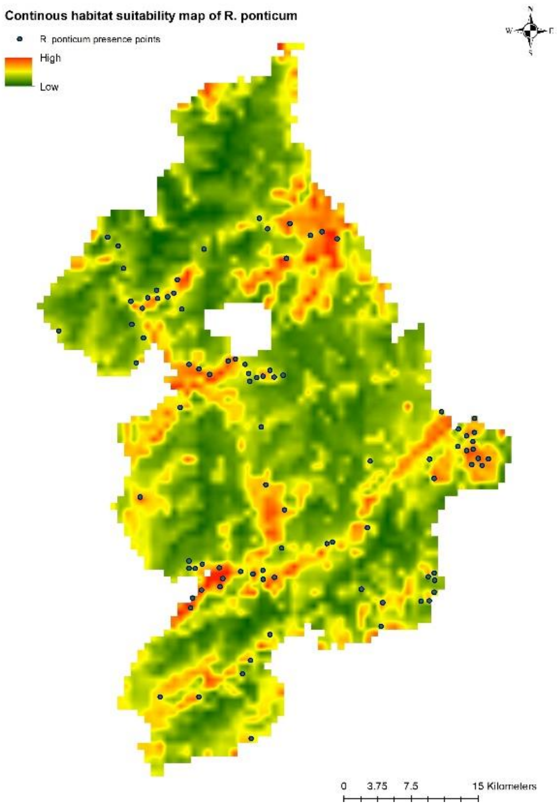


Figure 2. Continuous habitat suitability map of *R. ponticum* generated in Maxent model under current LCCs in Snowdonia National Park. Blue dots on the map show current distribution of species occurrence records.

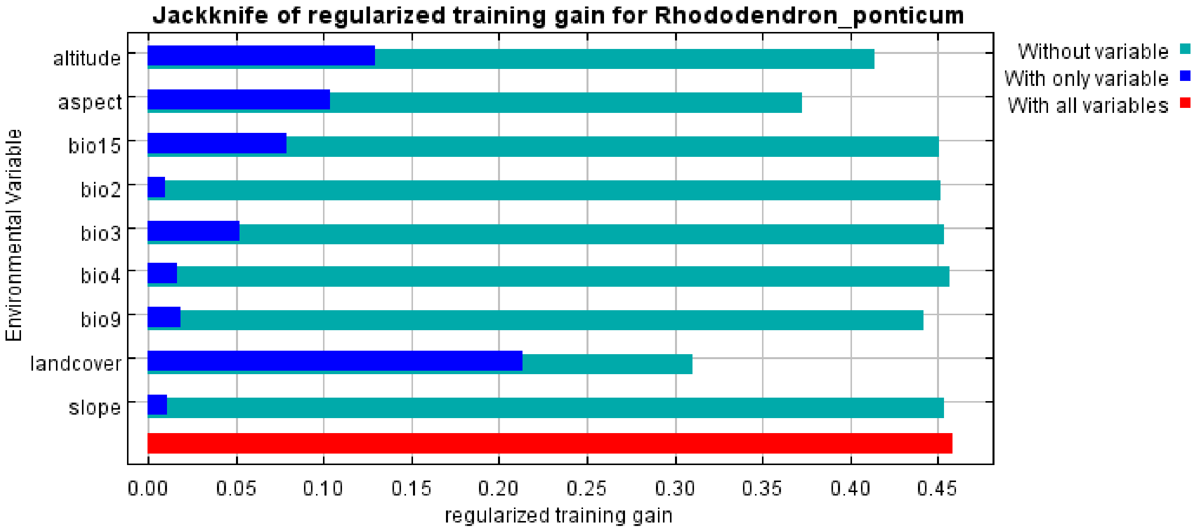


Figure 3. Jackknife of regularized training gain for presence of *Rhododendron ponticum* as predicted by the set of 9 selected predictor variables.

Land cover and climate change may limit invasiveness of Rhododendron

Close inspection of individual response curves Figure 4 shows how the logistic prediction by a variable changes when the rest of the predictor variables are artificially kept at their average values. Starting with Land Cover, the only categorical predictor used in this study, it suggests that the presence of several land use types may have a major influence on the probability of *R. ponticum* occurrence in Snowdonia National park. The likelihood of presence is the highest in Land Cover type "8" (Mosaic tree and shrub), followed by Land Cover type "6" (Needle leaved forest). Aspect was found to be an efficient predictor of *R. ponticum* distribution, indicating that the probability of occurrence is the highest in Northern Aspect (azimuth values ranging from 337.5 to 360◦). The response curve of Altitude shows that the probability of presence is negatively correlated with this variable as increasing altitude suggests a gradual decrease in the probability of species occurrence. Precipitation seasonality (BIO 15) was shown to be negatively correlated to the probability of the presence of *R. ponticum*; the species is not likely to tolerate higher seasonal variability in precipitation in Wales. It is noteworthy that the probability of species occurrence decreases from 67 to as low as 27 within a narrow band defined by 22 and 25mm of precipitation seasonality. Response curve of BIO 9 (Mean Temperature of the Driest Quarter) shows a similar trend, *R. ponticum* probability of occurrence decreases as the mean temperature of the driest quarter increases. BIO 2 (Mean Diurnal Range) and BIO 3 are only two climatic variables which appear to be positively correlated with the probability of *R. ponticum* occurrence. BIO 4 (the coefficient of variation of the mean of monthly temperatures, represents the seasonal variation in temperature) and Slope contributed the least to the model. Response curves of both these variables suggest that probability of species occurrence would decrease with increasing values of these variables.

Our land cover change simulation of Snowdonia National Park for the year 2050 revealed that broadleaved deciduous trees, needle-leaved evergreen trees and grasslands may experience a contraction in their extent, while the area under herbaceous cover, mosaic tree and shrub, mosaic herbaceous cover and shrub, or herbaceous cover may increase (Table 3).

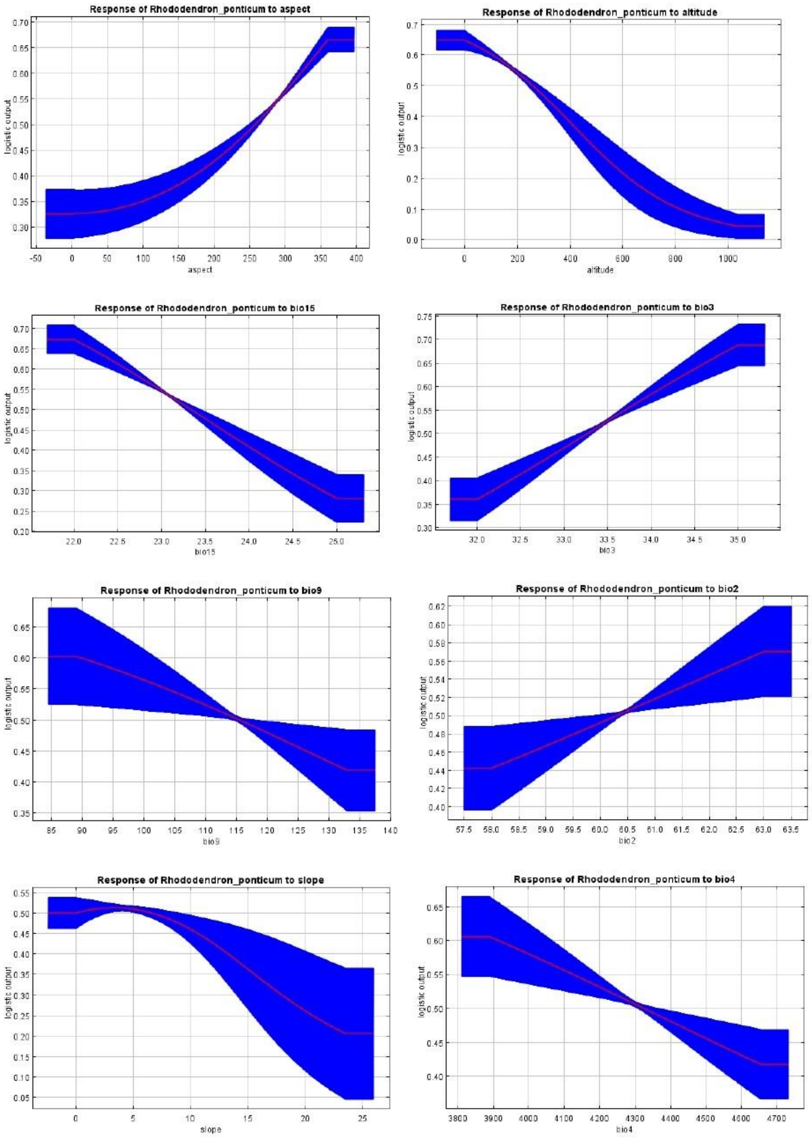


Figure 4. Probability of presence of *Rhododendron ponticum* in Snowdonia National Park, as influenced by A) aspect (° azimuth), B) altitude (m.a.s.l), C) precipitation seasonality (BIO15, mm), D) isothermality (BIO3), E) mean temperature of the driest quarter (BIO9, °C), F) mean diurnal range (BIO2, °C), F) G) slope (°) and H) E) coefficient of variation of mean of monthly temperatures (BIO4)

Table 3: Change in area (sq. km) under the 16 land cover classes of Snowdonia National Park between current (2015) and projected (2050) maps.

Class ID	Land Use Class	2015 (km²)	2050 (km²)	Change (%)
1	Cropland	0.5586	0.5586	0
2	Herbaceous cover	3.72	4.9	28.7
3	Mosaic cropland	8.19	8.19	0
4	Mosaic natural vegetation	6.08	6.08	0
5	Broadleaved Deciduous Trees	19.61	12.53	-36.1
6	Needle-leaved Evergreen Trees	229.64	223.62	-2.62
7	Needle-leaved Deciduous Trees	0.3724	0.3724	0
8	Mosaic tree and shrub	141.44	147.84	4.52
9	Mosaic herbaceous cover	627.55	637.98	1.66
10	Grassland	930.37	925.28	-0.54
11	Sparse Vegetation	85.15	85.15	0
12	Shrub or herbaceous cover	25.75	25.94	0.73
13	Urban Areas	2.85	2.85	0
14	Bare Areas	10.42	10.42	0
15	Unconsolidated Bare Areas	1.55	1.55	0
16	Water Bodies	32.27	32.27	0

3.2. Habitat Suitability Under Current & Future Land Use and Climate Change Scenarios

Binary maps of predicted distribution of *R. ponticum* in Snowdonia National park under current and future LCCs are shown in Supplementary Data S1. Based on the output of our model, nearly 50% of the total area of the park (1,050 of 2,132 km²) is currently suitable for *R. ponticum* invasion. Looking into the future, the extent of habitat suitable for *R. ponticum* in Snowdonia National park is likely to be negatively affected by land cover and climate change under all considered scenarios (Table 4).

Table 4: Variation in suitable area (in %) for *R. ponticum* in Snowdonia National Park for current time with those identified in land cover & six future climate change scenarios for 2050 at two Representative Concentration Pathways (4.5 & 8.5)

GCM's	RCP 4.5 (%)	RCP 8.5 (%)
BCC-CSM1-1	-39.23	-31.84
CCSM4	-10.73	-19.13
GISS-E2-R	-35.67	-44.07
HadGEM2-ES	-8.39	-7.97
MIROC5	-3.45	-12.91
MPI-ESM-LR	-40.13	-46.78

Under RCP 4.5, minimum contraction (−3.45%) is predicted under MIROC5 while maximum contraction (−40.13%) in suitable area may take place under MPI-ESM-LR. Under RCP 8.5, minimum (−7.97%) and maximum (−46.78%) reduction in suitability range for *R. ponticum* may be expected under GCMs HadGEM2-ES and MPI-ESM-LR, respectively. A comparison of the current habitat suitability with the minimum and maximum future range contraction (binary maps) is shown in Figure 5. Results indicate that most of the northern, northeastern and central areas of the national park are likely to become unsuitable for *R. ponticum* by 2050 (in case of maximum contraction under GCMMPI-ESM, RCP 8.5). Detailed habitat suitability maps of all future LCCs are presented in Supplementary Data S1.

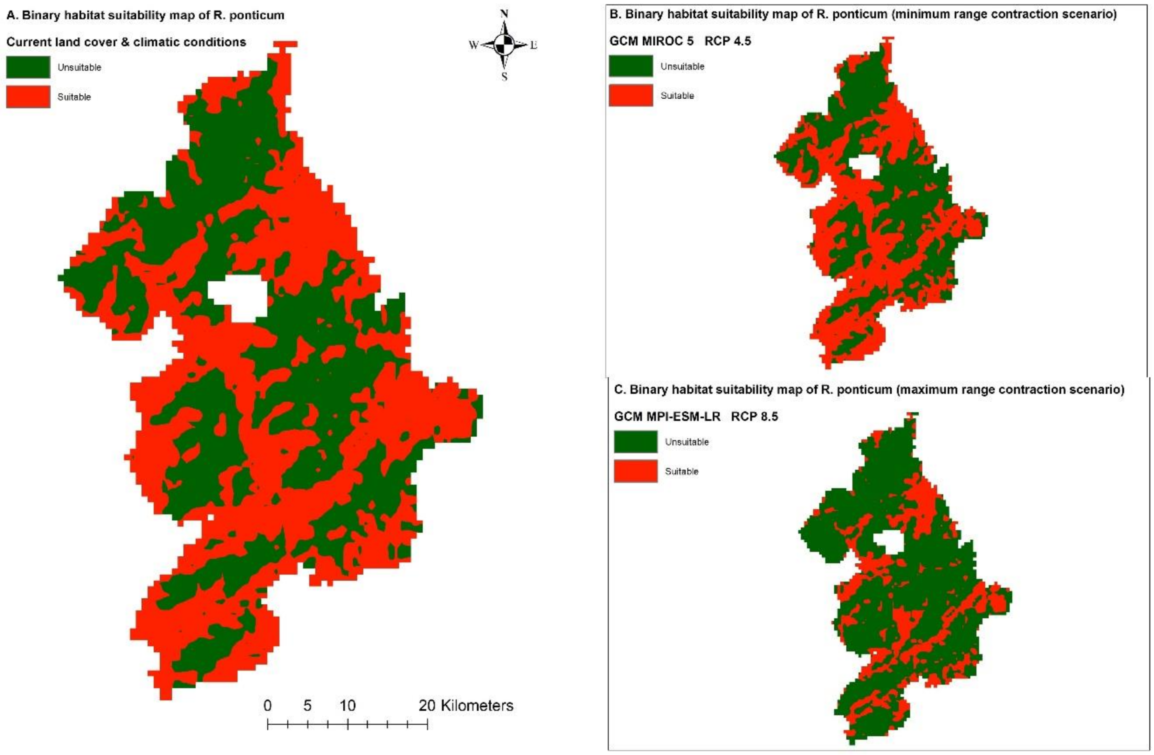


Figure 5. Comparison of suitable habitat range of *R. ponticum* in Snowdonia National Park under current LCCs with the minimum and maximum range contraction scenarios in future LCCs.

4. DISCUSSION

This study presents the first attempt to delineate current distribution and investigate the impacts of changing landscape and climate on future distribution of *R. ponticum* in Snowdonia National Park. Both current and future distributions of this invasive plant are governed by an interaction of a range of factors. In the case of *R. ponticum* in Snowdonia, land cover and topography have been shown as the most influential, complemented by a range of climatic factors.

Land use has repeatedly been shown to be the key predictor variable determining plant species distribution [20]. *R. ponticum* can invade a range of land cover categories, including natural to semi-natural, upland heaths, and occasionally grasslands. In Britain, earlier studies reporting on its occurrence suggest that woodland is the land cover type most affected by the invasion of *R. ponticum* [59]. Our findings are in agreement with these reports; *R. ponticum* has the highest probability of occurrence in land cover categories representing “6: Mosaic Tree & Shrub” and “8: Needle Leaved Forest.” There are numerous reasons why *R. ponticum* favours woodland in Wales, for example, the availability of a microenvironment suitable for seed germination [32] or growing under tree canopies to spread “under-cover” and thus avoid eradiation likely play a role. Crucially, the presence of dead plant material or moss cover may be critical to *R. ponticum* establishment [33]. In our study, Mosaic Tree & Shrub and Forests were the land cover categories which are likely to contain these substrates in the understory. Both of these land cover categories favored by *R. ponticum* are predicted to experience only a minor change (a decrease of −2.62% in category “6” while an increase of 4.52% in category “8”). Thus, the range contraction in *R. ponticum* seems to be much larger than the predicted change of suitable habitat types. This suggests that the predicted contraction in *R. ponticum* future range may not be primarily governed by land cover changes. These results are in agreement with some earlier studies suggesting that species’ range may drastically contract even if there is only a little shift in land cover types [60]. Among topographic variables, aspect makes a major contribution in our model. We show that *R. ponticum* clearly favors the northern aspect for its establishment and growth. North-facing slopes at the latitude of Wales are likely to offer greater soil moisture, in addition to lower direct insulation intensity. Many other studies on *R. ponticum*, *R. simsii*, and *R. ferrugineum* suggest that northern slopes (in the Northern hemisphere) offer more favourable conditions for Rhododendron growth [61][62][63]. Our results show that the probability of occurrence of *R. ponticum* in Snowdonia is negatively correlated with slope. Earlier studies have suggested that shallow-slope areas are typically those with high soil moisture and nutrient availability, thus offering more favourable microenvironment for plant proliferation [64]. Altitude explained a minor share of the variation in the training set of occurrence observations in this study. Even though altitude is considered an indirect variable since it has no direct effect on plant growth and physiology, it acts as a very good proxy of other un-measured or un-used variables. The reported altitudinal range of Rhododendron in Snowdonia National Park is well within the global range inhabited by this species. Therefore, it is likely that altitude per se does not represent a set of critically limiting variables in our study, but more likely acts as a proxy for auxiliary variables such as hydrology, exposure to light, wind speed, soil type and others which are not included in our model. There is strong evidence that the inclusion of indirect variables can enhance the predictive performance of SDMs, however their collinearity with direct variables must be addressed [65][66].

For climatic variables, our results indicate that both temperature- and precipitation-related variables make significant contribution to model prediction, which is in agreement with earlier studies which posit that the future distribution of *R. ponticum* in Wales may be affected by climatic predictors [64]. Under all GCMs considered here, habitat suitability range decreases from the current situation. Global mean temperatures may increase by as much as 4◦C by the end of next century [48]. Increasing temperature and changes in precipitation are likely to impact species distribution [67], however, existing investigations paint a mixed picture; plant species may experience an increase or a decrease of their current range [12][68]. A study investigating potential changes in the future distribution of a 100 of the world's worst invasive species concluded that potential range of the majority of these species would increase [69]. Contrary to this, there is evidence of a range reduction of over 80 invasive species in South Africa under varying climate change scenarios [67]. Similarly, many other ecological modelling studies have reported a possible contraction in suitable habitat of different species [70]. There are studies even predicting a complete loss of species' suitable habitat [71][72][72][73]. Detailed studies are thus required to investigate how an existing plant invasion will be modified by changing climatic conditions; it is not likely that all invasive species will benefit from new conditions.

The fact that *R. ponticum* is an alien invasive species in the area under consideration is an important aspect of this study. Invasion is a dynamic process guided by an inherited set of traits and environmental conditions [43]. One of the ways to build a species distribution model is to use climatic data and occurrence records from the native range of the invasive species under consideration and to project it to the invaded region [74]. However, we argue that this approach may yield a poorly performing model due to the mismatch between key environmental variables between native and invaded regions. This argument is borne out by the notion that invasives are a good example of species with a potential to expand their range beyond the climatic envelope defined in their native range [75]. A number of studies have confirmed this idea by concluding that invaded locations cannot necessarily be predicted from native distribution records of invasive species [76]. If the goal is to evaluate range expansion of invasive species then it could be useful to fit the model with data from native range [77], but when building models to predict changes in the invaded area under climate change scenarios, it may be much more useful to use data describing affected location [78].

4.1. Recommendations for Future Studies

Given that 14 out of 19 climatic variables originally considered for this study were excluded due to high correlation with variables chosen for the best performing model, an in-depth analysis of the sensitivity of *R. ponticum* distribution to the remaining variables may reveal interesting insights. We made use of only six GCMs and two RCPs scenarios for the sake of simplicity, but further studies including more numerous GCMs and RCPs may prove useful for improved prediction of future distribution and a better understanding of the sensitivity of *R. ponticum* to climate change. In line with the consideration of native vs. invaded climate envelope, further studies should compare model performance based on training on native and invaded climatic envelope range. Distribution models may be improved by the inclusion of high resolution variables derived from remote sensing and lidar (canopy height, cover, vertical distribution ratio etc.), variables such as vegetation density or stand height have been shown to significantly improve SDMs [20][79]. In this study, the land cover variable is considered as a proxy for the soil properties [80]. For example, *R. ponticum* is known to grow under semi-shade on moist, loamy soils. Thus, the land cover types "Forest" "Bog & Mosses" & "Herbaceous cover" can be thought to act as proxy for these soil types while land cover types such as "open fields," "bare land", "urban areas," and "rocks" can be considered the areas where soils types are the least favourable for this species. Results of this study confirm these observations. However, we recommend incorporating soil variables for future studies to further improve the accuracy of the model.

In this study, we projected land cover changes from 2015 to 2050 based on the land cover transition potential between 2005 and 2015. This is a simplistic and frequently adopted, "business-as-usual" approach of land use change modelling, which however may not be realistic. We suggest that the impact of contrasting socio-economic scenarios on likely future land use should be included to achieve a more representative prediction of future distribution.

CONCLUSIONS

This study presents the results of correlative ecological modelling exercise based on an assumption that land cover and climatic variables have a dominant role in current and future distribution of *R. ponticum* and that the ecological niche for this species remains conserved across time. We show that, contrary to expectation, future distribution range of this species in Snowdonia National Park may decrease as a result of projected climate and land use changes. An extension of this modelling approach to the entire landscape of UK might help to understand the combined effects of these predictor variables to future distribution of *R. ponticum* across the country.

SUPPLEMENTARY DATA S1

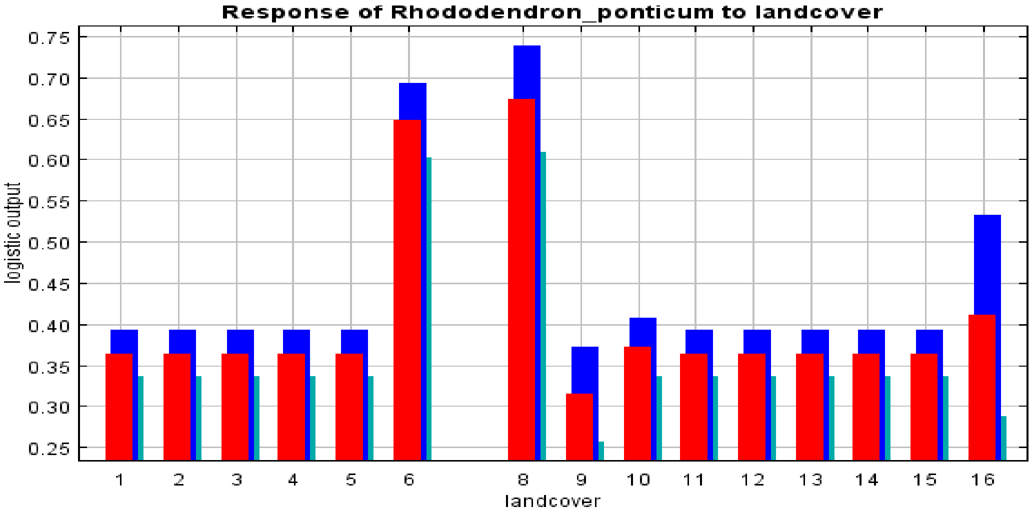
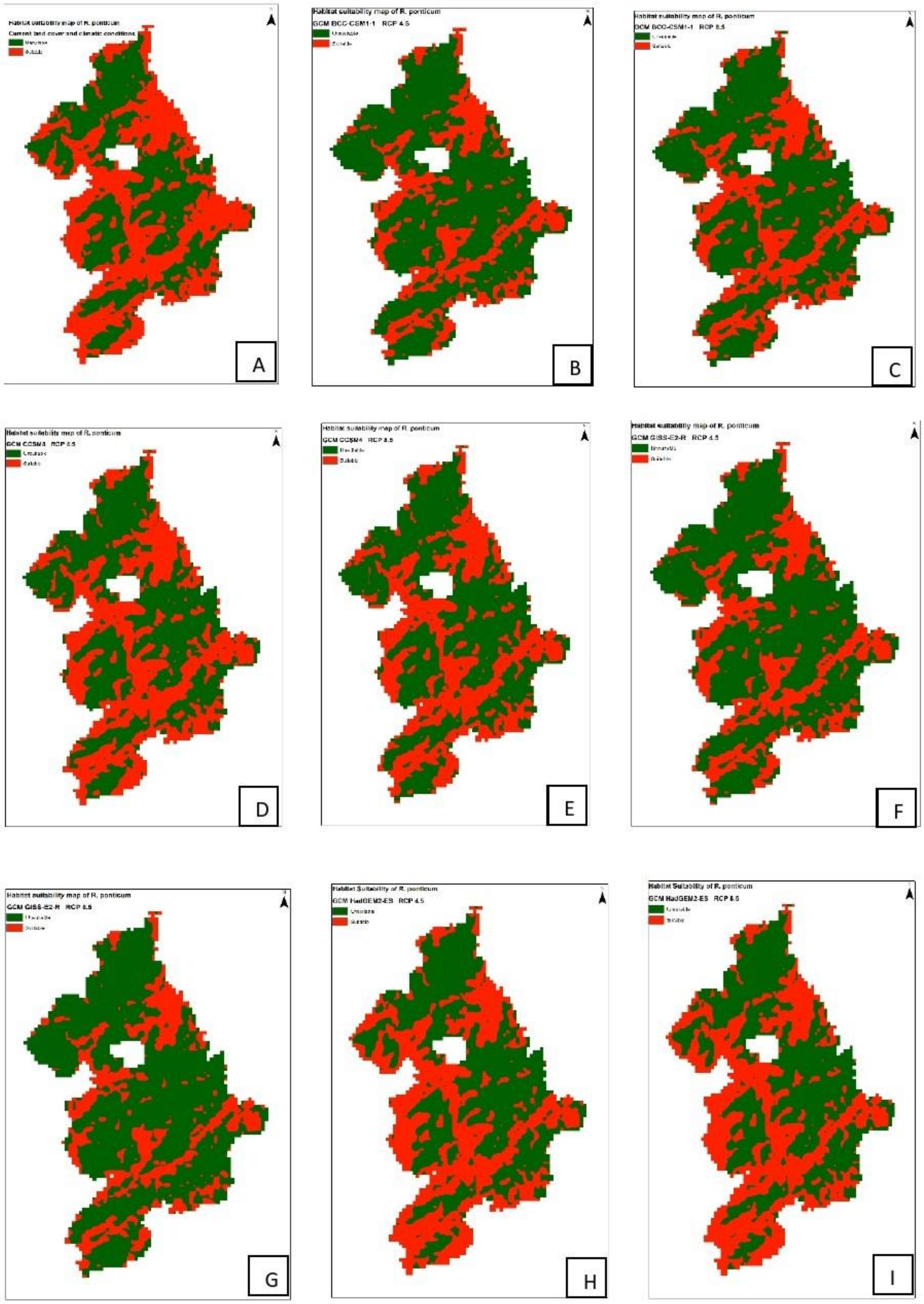


Figure 1. Probability of presence of *Rhododendron ponticum* in Snowdonia according to the land cover type. Red bars indicate mean response of 100 replicates while blue bars denote standard deviation. X-axis legend: (1) Cropland, rainfed. (2) Herbaceous cover. (3) Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%). (4) Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%). (5) Tree cover, broadleaved, deciduous, closed to open (>15%). (6) Tree cover, needleleaved, evergreen, closed to open (>15%). (7) Mosaic tree and shrub. (>50%) / herbaceous cover (<50%). (8) Mosaic herbaceous cover. (>50%) / tree and shrub. (<50%) (9) Shrubland. (10) Grassland. (11) Lichens and mosses. (12) Sparse vegetation (tree, shrub, herbaceous cover) (<15%). (13) Shrub or herbaceous cover, flooded, fresh/saline/brakish water. (14) Urban areas. (15) Bare areas. (16) Water bodies.


Habitat suitability map of R. ponticum
Current land cover and climatic conditions
Unsuitable
Suitable
A
Habitat suitability map of R. ponticum
GCM BCC-CSM1-1 RCP 4.5
Unsuitable
Suitable
B
Habitat suitability map of R. ponticum
GCM BCC-CSM1-1 RCP 8.5
Unsuitable
Suitable
C
Habitat suitability map of R. ponticum
GCM CCSM4 RCP 4.5
Unsuitable
Suitable
D
Habitat suitability map of R. ponticum
GCM CCSM4 RCP 8.5
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E
Habitat suitability map of R. ponticum
GCM GISS-E2-R RCP 4.5
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GCM HadGEM2-ES RCP 4.5
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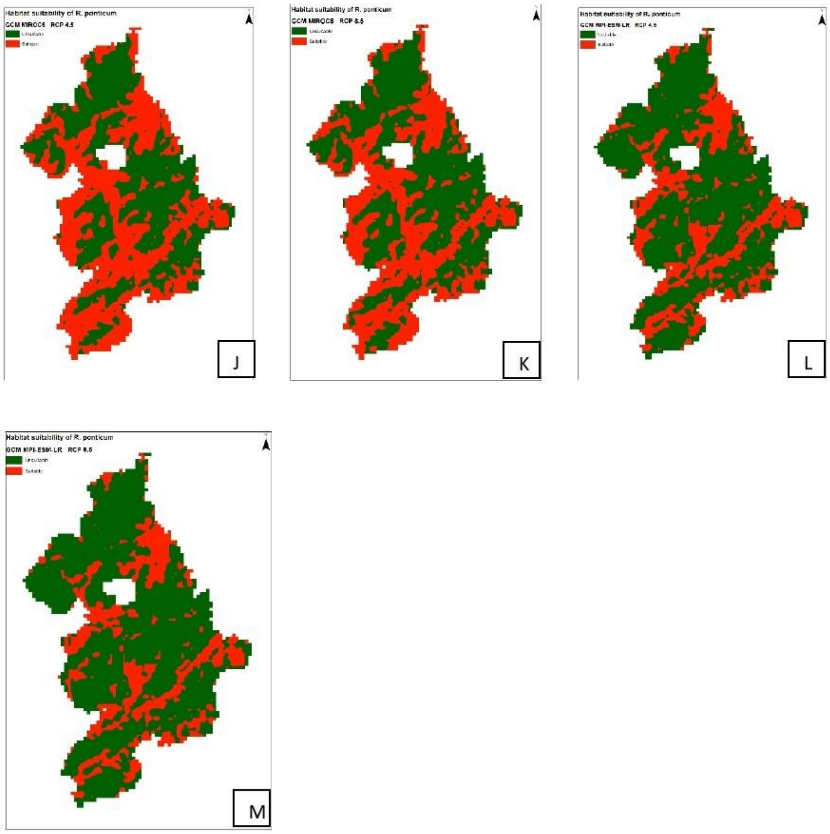

Figure 2. Binary habitat suitability maps of *R. ponticum* in Snowdonia National Park under current land cover and climatic conditions (A) and future land cover and climate change scenarios: BCC-CSM1-1 (B), BCC-CSM1-1 (C), CCSM4 (D), CCSM4 (E), GISS-E2-R (F), GISS-E2-R (G), HadGEM2-ES (H), HadGEM2-ES (I), MIROC5 (J), MIROC5 (K), MPI-ESM-LR (L), MPI-ESM-LR (M

REFERENCES

1. Gurevitch, J.; Padilla, D.K. Are invasive species a major cause of extinctions ? **2004**, *19*.
2. Powell, K.I.; Chase, J.M.; Knight, T.M. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science (80-.).* **2013**, *339*, 316–318.
3. Manchester, S.J.; Bullock, J.M. The impacts of non-native species on UK biodiversity and the effectiveness of control. *J. Appl. Ecol.* **2000**, *37*, 845–864.
4. Ehrenfeld, J.G. Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems* **2003**, *6*, 503–523.
5. Snowdonia Rhododendron Partnership The Ecosystem Benefits of managing the invasive non–native plant *Rhododendron ponticum* in Snowdonia Snowdonia Rhododendron Partnership 2015 Rhododendron in Snowdonia. **2015**.
6. Tiedeken, E.J.; Stout, J.C. Insect-flower interaction network structure is resilient to a temporary pulse of floral resources from invasive *Rhododendron ponticum*. *PLoS One* **2015**, *10*, 1–19.
7. Peterson, A.T.; Stewart, A.; Mohamed, K.I.; Araújo, M.B. Shifting global invasive potential of European plants with climate change. *PLoS One* **2008**, *3*, 1–7.
8. Pimentel, D.; Zuniga, R.; Morrison, D. Update on the environmental and economic costs associated with alien-invasive species in the United States. **2005**, *52*, 273–288.
9. Roiz, D.; Fournier, A.; Bradshaw, C.J.A.; Leroy, B.; Barbet-massin, M.; Salles, J. of invasive insects. **2016**.
10. Chapin III, F.S.; Zavaleta, E.S.; Eviner, V.T.; Naylor, R.L.; Vitousek, P.M.; Reynolds, H.L.; Hooper, D.U.; Lavorel, S.; Sala, O.E.; Hobbie, S.E.; et al. Consequences of changing biodiversity. *Nature* **2000**, *405*, 234–242.
11. Ipcc Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Intergov. Panel Clim. Chang. Work. Gr. I Contrib. to IPCC Fifth Assess. Rep. (AR5)(Cambridge Univ Press. New York)* **2013**, 1535.
12. Bradley, B.A.; Wilcove, D.S.; Oppenheimer, M. Climate change increases risk of plant invasion in the Eastern United States. *Biol. Invasions* **2010**, *12*, 1855–1872.
13. Alves, C.; Zenni, R.; Ziller, S.R.; Almeida, N. De; Passamani, M. Assessing the risk of invasion of species in the pet trade in Brazil. *Perspect. Ecol. Conserv.* **2017**.
14. Taylor, S.; Kumar, L.; Reid, N.; Kriticos, D.J. Climate change and the potential distribution of an invasive shrub, Lantana camara L. *PLoS One* **2012**, *7*, 1–14.
15. Marino, J.; Bennett, M.; Cossios, D.; Iriarte, A.; Lucherini, M.; Pliscoff, P.; Sillero-Zubiri, C.; Villalba, L.; Walker, S. Bioclimatic constraints to Andean cat distribution: A modelling application for rare species. *Divers. Distrib.* **2011**, *17*, 311–322.
16. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudik, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).* **2006**, *29*, 129–151.
17. Ramírez-Albores, J.E.; Bustamante, R.O.; Badano, E.I. Improved predictions of the geographic distribution of invasive plants using climatic niche models. *PLoS One* **2016**, *11*, 1–14.
18. Trivedi, M.R.; Berry, P.M.; Morecroft, M.D.; Dawson, T.P. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Glob. Chang. Biol.* **2008**, *14*, 1089–1103.
19. Decker, K.L.; Allen, C.R.; Acosta, L.; Hellman, M.L.; Jorgensen, C.F.; Stutzman, R.J.; Unstad, K.M.; Williams, A.; Yans, M. Land Use, Landscapes, and Biological Invasions. *Invasive Plant Sci. Manag.* **2012**, *5*, 108–116.
20. Yang, X.Q.; Kushwaha, S.P.S.; Saran, S.; Xu, J.; Roy, P.S. Maxent modelling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in Lesser Himalayan foothills. *Ecol. Eng.* **2013**, *51*, 83–87.
21. Alkhamis, M.A.; Arruda, A.G.; Morrison, R.B.; Perez, A.M. Novel approaches for Spatial and

Molecular Surveillance of Porcine Reproductive and Respiratory Syndrome Virus (PRRSv) in the United States. *Sci. Rep.* **2017**, *7*, 4343.

22. Padalia, H.; Bahuguna, U. Spatial modelling of congruence of native biodiversity and potential hotspots of forest invasive species (FIS) in central Indian landscape. *J. Nat. Conserv.* **2017**, *36*, 29–37.
23. Bosso, L.; De Conno, C.; Russo, D. Modelling the Risk Posed by the Zebra Mussel Dreissena polymorpha: Italy as a Case Study. *Environ. Manage.* **2017**, *60*, 304–313.
24. Guo, Y.; Li, X.; Zhao, Z.; Wei, H.; Gao, B.; Gu, W. Prediction of the potential geographic distribution of the ectomycorrhizal mushroom Tricholoma matsutake under multiple climate change scenarios. *Sci. Rep.* **2017**, *7*, 46221.
25. Hailu, B.T.; Silijander, M.; Maeda, E.E.; Pellikka, P. Assessing spatial distribution of Coffea arabica L. in Ethiopia's highlands using species distribution models and geospatial analysis methods. *Ecol. Inform.* **2017**.
26. Dale, V.H. The Relationship Between Land-Use Change and Climate Change Author (s): Virginia H . Dale Published by : Wiley on behalf of the Ecological Society of America Stable URL : http://www.jstor.org/stable/2269433 Wiley , Ecological Society of America are coll. **2017**, *7*, 753–769.
27. Khanum, R.; Mumtaz, A.S.; Kumar, S. Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modelling. *Acta Oecologica* **2013**, *49*, 23–31.
28. Khadka, K.K.; James, D.A. Modelling and mapping the current and future climatic-niche of endangered Himalayan musk deer. *Ecol. Inform.* **2017**, *40*, 1–7.
29. Qin, A.; Liu, B.; Guo, Q.; Bussmann, R.W.; Ma, F.; Jian, Z.; Xu, G.; Pei, S. Maxent modelling for predicting impacts of climate change on the potential distribution of Thuja sutchuenensis Franch., an extremely endangered conifer from southwestern China. *Glob. Ecol. Conserv.* **2017**, *10*, 139–146.
30. de Chazal, J.; Rounsevell, M.D.A. Land-use and climate change within assessments of biodiversity change: A review. *Glob. Environ. Chang.* **2009**, *19*, 306–315.
31. Dehnen-Schmutz, K.; Williamson, M. *Rhododendron ponticum* in Britain and Ireland: Social, economic and ecological factors in its successful invasion. *Environ. Hist. Camb.* **2006**, *12*, 325–350.
32. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–758.
33. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
34. Erfmeier, A.; Tsaliki, M.; Roß, C.A.; Bruelheide, H. Genetic and phenotypic differentiation between invasive and native Rhododendron (Ericaceae) taxa and the role of hybridization. *Ecol. Evol.* **2011**, *1*, 392–407.
35. Die, J. V.; Arora, R.; Rowland, L.J. Proteome dynamics of cold-acclimating Rhododendron species contrasting in their freezing tolerance and thermonasty behavior. *PLoS One* **2017**, *12*, 1–17.
36. Jackson, P. Rhododendron in Snowdonia and a strategy for its control. *Snowdownia Natl. Park Auth.* **2008**.
37. Phillips SJ Dudik M, S.R.E. A maximum entropy approach to species distribution modelling. **2004**, 655–662.
38. Phillips, S.B.; Aneja, V.P.; Kang, D.; Arya, S.P. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *Int. J. Glob. Environ. Issues* **2006**, *6*, 231–252.
39. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A statistical explanation of

MaxEnt for ecologists. *Divers. Distrib.* **2011**, *17*, 43–57.

40. Moreno-Amat, E.; Mateo, R.G.; Nieto-Lugilde, D.; Morueta-Holme, N.; Svenning, J.C.; Garc??a-Amorena, I. Impact of model complexity on cross-temporal transferability in Maxent species distribution models: An assessment using paleobotanical data. *Ecol. Modell.* **2015**, *312*, 308–317.
41. Veloz, S.D. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *J. Biogeogr.* **2009**, *36*, 2290–2299.
42. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978.
43. Erfmeier, A.; Bruelheide, H. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora - Morphol. Distrib. Funct. Ecol. Plants* **2004**, *199*, 120–133.
44. Eşen, D.; Zedaker, S.M.; Kirwan, J.L.; Mou, P. Soil and site factors influencing purple-flowered rhododendron (*Rhododendron ponticum* L.) and eastern beech forests (Fagus orientalis Lipsky) in Turkey. *For. Ecol. Manage.* **2004**, *203*, 229–240.
45. Harris, C.M.; Stanford, H.L.; Edwards, C.; Travis, J.M.J.; Park, K.J. Integrating demographic data and a mechanistic dispersal model to predict invasion spread of *Rhododendron ponticum* in different habitats. *Ecol. Inform.* **2011**, *6*, 187–195.
46. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. *PLoS One* **2013**, *8*.
47. Graham, M.H. Confronting Multicollinearity in Ecological Multiple Regression. **2003**, *84*, 2809–2815.
48. IPCC *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Summaries, Frequently Asked Questions, and Cross-Chapter Boxes*; 2014; ISBN 9789291691418.
49. Akhter, S.; McDonald, M.A.; van Breugel, P.; Sohel, S.; Kj??r, E.D.; Mariott, R. Habitat distribution modelling to identify areas of high conservation value under climate change for Mangifera sylvatica Roxb. of Bangladesh. *Land use policy* **2017**, *60*, 223–232.
50. Eastman, J.R. Guide to GIS and Image Processing. *Clark Univ. Worcester, MA, USA* **2006**, *1*, 87–131.
51. Muscarella, R.; Galante, P.J.; Soley-Guardia, M.; Boria, R.A.; Kass, J.M.; Uriarte, M.; Anderson, R.P. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for <scp>Maxent</scp> ecological niche models. *Methods Ecol. Evol.* **2014**, *5*, 1198–1205.
52. Merow, C.; Smith, M.J.; Silander, J.A. A practical guide to MaxEnt for modelling species' distributions: What it does, and why inputs and settings matter. *Ecography (Cop.).* **2013**, *36*, 1058–1069.
53. Warren, D.L.; Seifert, S.N. Ecological niche modelling in Maxent : the importance of model complexity and the performance of model selection criteria C ommunications C ommunications. *Ecol. Appl.* **2011**, *21*, 335–342.
54. Rebelo, H.; Jones, G. Ground validation of presence-only modelling with rare species: A case study on barbastelles Barbastella barbastellus (Chiroptera: Vespertilionidae). *J. Appl. Ecol.* **2010**, *47*, 410–420.
55. Swets, J.A. Measuring the accuracy of diagnostic systems. *Science* **1988**, *240*, 1285–1293.
56. Breiner, F.T.; Guisan, A.; Bergamini, A.; Nobis, M.P. Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol. Evol.* **2015**, *6*, 1210–1218.
57. Boyce, M.S.; Vernier, P.R.; Nielsen, S.E.; Schmiegelow, F.K.A. Evaluating resource selection functions. *Ecol. Modell.* **2002**, *157*, 281–300.
58. Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* **2006**, *199*, 142–152.
59. Dehnen-Schmutz, K.; Perrings, C.; Williamson, M. Controlling *Rhododendron ponticum* in British Isles: An economic analysis. *J. Environ. Manage.* **2004**, *70*, 323–332.

60. Charbonnel, A.; Laffaille, P.; Biffi, M.; Blanc, F.; Maire, A.; Némoz, M.; Sanchez-Perez, J.M.; Sauvage, S.; Buisson, L. Can recent global changes explain the dramatic range contraction of an endangered semi-aquatic mammal species in the French pyrenees? *PLoS One* **2016**, *11*, 1–21.
61. Taylor, S.L.; Hill, R.A.; Edwards, C. Characterising invasive non-native *Rhododendron ponticum* spectra signatures with spectroradiometry in the laboratory and field: Potential for remote mapping. *ISPRS J. Photogramm. Remote Sens.* **2013**, *81*, 70–81.
62. Christiaens, A.; Lootens, P.; Roldán-Ruiz, I.; Pauwels, E.; Gobin, B.; Van Labeke, M.C. Determining the minimum daily light integral for forcing of azalea (Rhododendron simsii). *Sci. Hortic. (Amsterdam).* **2014**, *177*, 1–9.
63. Francon, L.; Corona, C.; Roussel, E.; Lopez Saez, J.; Stoffel, M. Warm summers and moderate winter precipitation boost Rhododendron ferrugineum L. growth in the Taillefer massif (French Alps). *Sci. Total Environ.* **2017**, *586*, 1020–1031.
64. Kang, W.; Minor, E.S.; Lee, D.; Park, C.R. Predicting impacts of climate change on habitat connectivity of Kalopanax septemlobus in South Korea. *Acta Oecologica* **2016**, *71*, 31–38.
65. Austin, M.P. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecol. Modell.* **2002**, *157*, 101–118.
66. West, A.M.; Kumar, S.; Brown, C.S.; Stohlgren, T.J.; Bromberg, J. Field validation of an invasive species Maxent model. *Ecol. Inform.* **2016**, *36*, 126–134.
67. Bezeng, B.S.; Morales-Castilla, I.; Van Der Bank, M.; Yessoufou, K.; Daru, B.H.; Davies, T.J. Climate change may reduce the spread of non-native species. *Ecosphere* **2017**, *8*.
68. Midgley, G.; Hannah, L. Extinction risk from climate change. *Biodivers. Clim. Chang. Transform. Biosph.* **2019**, 294–296.
69. Bellard, C.; Thuiller, W.; Leroy, B.; Genovesi, P.; Bakkenes, M.; Courchamp, F. Will climate change promote future invasions? *Glob. Chang. Biol.* **2013**, *19*, 3740–3748.
70. Smale, D.A.; Wernberg, T. Extreme climatic event drives range contraction of a habitat-forming species. *Proc. R. Soc. B Biol. Sci.* **2013**, *280*, 20122829–20122829.
71. Midgley, G.F.; Hannah, L.; Millar, D.; Rutherford, M.C.; Powrie, L.W. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Glob. Ecol. Biogeogr.* **2002**, *11*, 445–451.
72. Bomhard, B.; Richardson, D.M.; Donaldson, J.S.; Hughes, G.O.; Midgley, G.F.; Raimondo, D.C.; Rebelo, A.G.; Rouget, M.; Thuiller, W. Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Glob. Chang. Biol.* **2005**, *11*, 1452–1468.
73. Sarmento Cabral, J.; Jeltsch, F.; Thuiller, W.; Higgins, S.; Midgley, G.F.; Rebelo, A.G.; Rouget, M.; Schurr, F.M. Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. *Divers. Distrib.* **2013**, *19*, 363–376.
74. Kaplan, H.; Van Zyl, H.W.F.; Le Roux, J.J.; Richardson, D.M.; Wilson, J.R.U. Distribution and management of Acacia implexa (Benth.) in South Africa: A suitable target for eradication? *South African J. Bot.* **2012**, *83*, 23–35.
75. Rödder, D.; Lötters, S. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (Hemidactylus turcicus). *Glob. Ecol. Biogeogr.* **2009**, *18*, 674–687.
76. Fernandez, M.; Hamilton, H. Ecological niche transferability using invasive species as a case study. *PLoS One* **2015**, *10*, 1–17.
77. Araújo, M.B.; Guisan, A. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **2006**, *33*, 1677–1688.
78. Jeschke, J.M.; Strayer, D.L. Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. N. Y. Acad. Sci.* **2008**, *1134*, 1–24.
79. Ackers, S.H.; Davis, R.J.; Olsen, K.A.; Dugger, K.M. The evolution of mapping habitat for northern spotted owls (Strix occidentalis caurina): A comparison of photo-interpreted, Landsat-based, and lidar-based habitat maps. *Remote Sens. Environ.* **2015**, *156*, 361–373.

80. Davis, H.T.; Aelion, C.M.; Lawson, A.B.; Cai, B.; McDermott, S. Associations between land cover categories, soil concentrations of arsenic, lead and barium, and population race/ethnicity and socioeconomic status. *Sci. Total Environ.* **2014**, *490*, 1051–1056.

Chapter 3

SPECIES DISTRIBUTION MODEL TRANSFERABILITY AND MODEL GRAIN SIZE – FINER MAY NOT ALWAYS BE BETTER.

ABSTRACT

Species distribution models have been used to predict the distribution of invasive species for conservation planning. Understanding spatial transferability of niche predictions is critical to promote species-habitat conservation and forecasting areas vulnerable to invasion. Grain size of predictor variables is an important factor affecting the accuracy and transferability of species distribution models. Choice of grain size is often dependent on the type of predictor variables used and the selection of predictors sometimes rely on data availability. This study employed the MAXENT species distribution model to investigate the effect of the grain size on model transferability for an invasive plant species. We modelled the distribution of *Rhododendron ponticum* in Wales, U.K. and tested model performance and transferability by varying grain size (50 m, 300 m, and 1 km). MAXENT-based models are sensitive to grain size and selection of variables. We found that over-reliance on the commonly used bioclimatic variables may lead to less accurate models as it often compromises the finer grain size of biophysical variables which may be more important determinants of species distribution at small spatial scales. Model accuracy is likely to increase with decreasing grain size. However, successful model transferability may require optimization of model grain size.

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Species distribution model transferability and model grain size

1. INTRODUCTION

Species distribution models (SDMs) are becoming increasingly important in predicting spatial patterns of biological invasions, identification of hotspots for early detection and informing management of invasive species [1]. SDMs relate the presence/absence records of species to relevant environmental variables and subsequently project modelled relationships across geographical space using gridded layers of environmental data, producing a map indicating areas of potential species distribution [2]. One of the key features of gridded data is the 'grain size' – a term describing the geographical representation (spatial resolution) of the map layers. Grain size of predictor variables strongly affects the interpretation of biogeographic characteristics of modelled species [3]. Use of smaller or finer grain size allows for a more accurate representation of the effect of local environmental conditions and biotic interactions in model prediction [4].

The challenge in using smaller grain size in SDMs is finding the optimum balance between data quality, data availability, and model performance [5]. Grain size represents the geographical space unit which contains all the information on characteristic attributes of the study area [6]. A decrease in grain size enhances the details of the landscape by sharpening the features it contains and by making the rare land use types in the landscape more prominent and distinguishable [7]. Conversely, coarse grain size of predictor variables in SDMs negatively affects the delineation of habitat features in a landscape, a feature of critical importance to modelling species presence. Selection of grain size and its relationship with habitat features is a crucial factor in SDM based studies [3][7][8][9]. Most literature to date reports on species distribution models built at a grain size of 1 km, a fact recently subjected to some scrutiny and critique [7][10]. Earlier observations indicate that the use of 1 km grain size may be too coarse to generate reliable SDM outputs [7], especially for studies at small spatial scales. The challenge, therefore, is to establish the threshold grain size at which predictor variables correctly describe local conditions and biotic interactions which play an important role in defining species' range [11].

The choice of grain size in SDM studies is sometimes based on data availability [12] rather than relevant factors like species' ecology and spatial scale of study. A review of more than 200 SDM-based research papers concluded that the choice of variables is 'frequently opportunistic' and that the majority of the studies, instead of making a tailored choice of variables, rely on a standard set of 19 bioclimatic variables [13] which are available at a minimum of 1 km grain size. In a complementary analysis designed to provide an overview of current practice, we reviewed 59 recent SDM based studies published in peer-reviewed journals in 2016–2017 (Supplementary Data S1). We confirmed that the most frequently used variables in MAXENT based ecological modelling studies are indeed, the 19 bioclimatic variables available from the 'Global Climate Data' (www.worldclim.org). We found that 55 out of the 59 studies selected the above-mentioned bioclimatic variables as input. Of these 55 studies 34 had used additional biophysical variables such as topography and land cover. These biophysical variables are available at a grain size as 100 meters or less. Since the grain size of all input variables in SDMs need to be harmonized, these biophysical variables are resampled to 1 km in when used in combination with the bioclimatic variables. Intriguingly, the results of 22 out of these 34 studies (which had both bioclimatic and biophysical variables) suggest that the variables critical to accurate species distribution prediction were the biophysical variables. Given the earlier argument that a finer grain size is more likely to improve model accuracy, the following speculation can be made: had these 22 studies not coarsened the biophysical variables – by avoiding the 'customary' choice of bioclimatic variables - this would have resulted in a more accurate prediction of species distribution. This speculation might appear to question the significance of bioclimatic variables in ecological models. It is a fact that bioclimatic variables are among the most frequently used variables in SDM based studies and rightly so as climate is a strong determinant of species' distribution. However, an injudicious use of these variables without considering factors like species' ecology, scale of study and optimal grain size is questionable [13][14]. Thus, we speculate that in many SDM based studies – especially at small spatial scale of study area - biophysical variables may be the more important ones and inclusion of bioclimatic variables in such cases may reduce the model accuracy.

One of the motivations for creating SDMs is to use them to predict the behaviour of a species colonizing new territory. Successful transferability of SDMs across space or time is extremely valuable in context of conservation planning. A basic assumption underlying SDMs is that the model is spatially and temporally transferable, i.e. the niche attributes are conserved across space and time [2]. Although the effect of grain size in SDMs is well documented [15][16][17], its role in model transferability has not been put to sufficient scrutiny. There is evidence that although SDMs can accurately predict species distribution in the training area, their transferability to new areas is challenging due to numerous complex phenomena [18][19]. Among many factors, grain size has been reported as critical to satisfactory model performance and transferability [20][21].

In this study we aim to test the role of grain size in SDMs both in the training and the transfer areas. Based on our review of literature, we speculate that over-reliance on easily available bioclimatic variables may lead to an unnecessary compromise on the grain size of critical variables, with potentially negative impact on the accuracy of model predictions and transferability. Specifically, we use a MAXENT modelling environment [22] to model the distribution of *Rhododendron ponticum* (L.) in the Snowdonia National Park, Wales and then transfer the model to the Brecon Beacons National Park, Wales. The objectives of this study were to assess whether the decreasing the grain size improves model performance both in the training and the transfer area.

2. Methodology

2.1. Species Description

Rhododendron ponticum (L.) is an invasive plant species in the United Kingdom, having been introduced in the 18th century as an ornamental plant. The main ancestor is reported to be the population of *R. ponticum* resident in the southern tip of Spain [23]. It is a perennial, evergreen shrub that generally invades woodlands [24], although it has been shown to colonize other types of habitat too. The UK invasion by this shrub has been more intense in Western and North-Western areas of Britain, which are comparatively cooler and wetter. We chose Wales as the study region because it is one of the most affected regions of the UK to be impacted by invasions of *R. ponticum*. In this study, we trained the model on the dataset for the Snowdonia National Park in Wales [25] and then transferred the model to the Brecon Beacons National Park. Given the scale of the invasion, it is clear that the current environmental, topographic and land cover conditions both in Snowdonia and the Brecon Beacons represent a range of conditions very suitable for *R. ponticum*.

2.2. Species Distribution Modelling Algorithm

We used MAXENT, a maximum-entropy based machine learning (presence/pseudo-absence) algorithm to model the distribution *R. ponticum* (L.) in Snowdonia National Park (the training area) and projected the model to the Brecon Beacons National Park (the transfer area). MAXENT predicts the probability distribution of a species on the basis of a given set of predictor variables and presence-only species occurrence data [22]. We selected MAXENT because, a) it does not require absence data [26], b) it efficiently handles complex interactions between predictor and response variables [27], c) being a generative model, it performs better than discriminative models when it comes to modelling with presence-only records, d) it can be run with both categorical and continuous data variables [28] and, e) it efficiently transfers the model projections to another geographical area [2]. We used a reasonably large sample size [29] and applied the recommended screening and verification of occurrence records.

2.3. Presence Records for Model Training and Validation

For the training area (Snowdonia National Park), presence-only occurrence records of *R. ponticum* (L.) were obtained from COFNOD (Local Environmental Records Centre in Wales, UK). A dataset of 152 occurrence records was created by a continuous field observation campaign between 1981 and 2000. COFNOD has confirmed that the entire area of Snowdonia National Park was thoroughly surveyed by ground surveys and remote sensing tools, thus minimizing the possibility of sampling bias in the dataset. Consequently, we targeted the entire area of the National Park, generating 10,000 random background points to be selected during each replicate run of the model. We used independent occurrence records of *R. ponticum* (L.) in the Brecon Beacons National Park downloaded from the National Biodiversity Network (NBN) online database (www.nbnatlas.org), yielding 100 observations. Spatial uncertainty of all occurrence records was addressed by removing all duplicate or non-geo-referenced occurrence points. Occurrence data were spatially rarefied using SDM toolbox 2.0 [30] in

ArcGIS 10.5 by eliminating all but one point present within a single grid cell of the predictor variable layers to avoid double counting of presence points.

2.4. Selection of Predictor Variables

Predictor variables were selected in the following three steps. In the first step, two categories of variables were compiled. The first category of variables comprised the most frequently used variables in SDM studies: 'Bioclimatic Variables' (BCV). The second category of variables was based on our expert knowledge and a review of literature on the ecology of *R. ponticum* (L.): 'Biophysical Variables' (BPV). A set of 19 bioclimatic variables from 'Global Climate Data' (www.worldclim.org, version 2, 1970–2000) [31], identified as the most commonly used suite of variables in SDM research13, formed the BCV category. An extensive review of literature and background knowledge of the *R. ponticum* ecology yielded the most important biophysical variables, namely; topography (altitude, aspect and slope), land cover and 'distance from water channels' which formed the BPV category [32][33][34][35]. Although Rhododendron is sensitive to many other ecological factors, we kept the BPV category to the above mentioned variables as these variables were the most pertinent ones at the current spatial scale of study.

In the second step of variable selection, a sub-set of variables from the BCV and BPV categories was created on the basis of grain size. The first variable set (VS-1) included both BCV and BPV categories, with the latter resampled to a 1 km grain size which is the smallest cell size of BCV. The second variable set (VS-2) comprised the BPV at 300 m grain size. The third variable set (VS-3) consisted of the same BPV but at 50 m grain size (Tables 1 and 2). The VS-1 represents the commonly reported approach used in SDM studies and thus can be considered the 'control' scenario. The VS-2 & VS-3 represent scenarios where bioclimatic variables are excluded to conserve the finer grain size of BPV. All input data layers were re-sampled using nearest neighbour (for discrete variables) and bilinear interpolation (for continuous variables) resampling techniques [36][37][38]. Collinearity among predictor variables negatively impacts the model due to the substantial amount of information shared between collinear variables. Therefore, collinearity in variables makes it difficult to correctly interpret the relative contribution or importance of variables in the model predictions [39]. A Pearson correlation coefficient cut-off of r ≤ 0.70 was applied to select the variables for use in the final model runs [38] for all three sets of variables (VS-1, VS-2 and VS-3). The aim of this step was to reduce the negative impact of multicollinearity and to conform to statistical assumptions [40].

Table 1. Predictor variables used in the study. Acronyms VS-1, VS-2 & VS-3 refer to variable set 1, variable set 2 & variable set 3 respectively.

VS-1		**VS-2**		**VS-3**	
Grain Size 1 km		**Grain Size 300 m**		**Grain Size 50 m**	
Predictor Variable	**Unit**	**Predictor Variable**	**Unit**	**Predictor Variable**	**Unit**
Altitude	m	Altitude	m	Altitude	m
Aspect	°	Aspect	°	Aspect	°
Slope	°	Slope	°	Slope	°
Land Cover		Land Cover		Land Cover	
Distance from water channels	m	Distance from water channels	m	Distance from water channels	m
Mean Diurnal Range (monthly (max temp - min temp))	°C				
Isothermality (BIO2/BIO7)* 100					
Mean Temperature of Driest Quarter	°C				
Precipitation Seasonality (Coefficient of Variation)	C of V				

Table 2. Allocation of predictor variables to 'variable categories' and 'variable sets'. Acronyms BCV, BPV, VS-1, VS-2 & VS-3 refer to Bioclimatic Variables, Biophysical Variables, Variable Set 1, Variable Set 2 & Variable Set 3 respectively.

Predictor variable/s	Grain Size	Source	Variables Category	Variable Set
19 bioclimatic variables	1 km	WorldClim - Global Climate Data	BCV	VS-1
Distance from water channels	1 km	Edina Digimap Ordnance Survey	BCV	VS-1
Land Cover	300 m	Edina Digimap Ordnance Survey	BPV	VS-2
Topography (Altitude, Aspect, Slope)	300 m	Shuttle Radar Topography Mission USGS	BPV	VS-2
Distance from water channels	300 m	Edina Digimap Ordnance Survey	BPV	VS-2
Land Cover	50 m	Edina Digimap Ordnance Survey	BPV	VS-3
Topography (Altitude, Aspect, Slope)	50 m	Edina Digimap Ordnance Survey	BPV	VS-3
Distance from water channels	50 m	Edina Digimap Ordnance Survey	BPV	VS-3

2.5. Model Calibration

All three modelling scenarios were run in MAXENT (version 3.3.3a) with a default convergence threshold of 10^{-6} and with 5000 iterations to allow the model scope for convergence while reducing the risk of over- or under-predicting modelled relationships. We processed 25 model replications with a bootstrap resampling method randomly allocating 75% of the occurrence records in the training area for calibration and 25% for validation. To avoid dubious projections by the model, we used the 'fade-by-clamping' feature which removes heavily clamped (clustered) pixels from the final predictions [26]. Rest of the MAXENT calibration was set to default settings.

2.6. Model Evaluation

Training area. Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) was used to test the performance of the model against actual observations in the training area [27]. An AUC value of 0.5 shows that the model does not predict any better than random chance, whereas a value closer to 1 indicates a better performance of the model [41]. Permutation importance contribution was used to assess the relative significance of predictor variables. Fitted response curves were used to visually investigate the relationship between individual variables and predicted index of environmental suitability of *R. ponticum*. In addition to AUC, we used Continuous Boyce Index (CBI) as an additional assessment tool. The Boyce index requires presence data only and measures by how much model predictions differ from random distribution of observed presence across the prediction gradient. The continuous habitat suitability map is reclassified into i number of classes/bins. For each bin, Predicted and Expected frequencies are calculated. The Predicted Frequency is calculated by dividing the number of species' occurrence points in the bin i, as forecasted by the model, by the total number of species' occurrence points. The Expected Frequency is calculated by dividing the number of grid cells in bin i by the total number of grid cells. A P/E ratio is then calculated for each bin and a Spearman rank correlation coefficient rho (1-tailed test) evaluates if the ratio significantly increases as suitability increases ($p < 0.05$). The continuous values of the Boyce index vary between −1 and +1. Positive values indicate a model where predictions are consistent with the distribution of actual presence data, values close to zero mean that the model is no different from a random model and negative values indicate counter predictions (e.g. predicting no occurrence in areas where actual presence is recorded) [42][43].

2.7. Transfer Area (Model Transferability)

MAXENT produces continuous probability maps of habitat suitability in the selected geographical area. We used *R. ponticum* (L.) presence records in the Brecon Beacons National Park to evaluate model projection in the transfer area. Continuous Boyce Index (CBI) was used to assess how well MAXENT has transferred the model to a different geographical area [42][43]. CBI is considered one of the most appropriate metrics for assessing model predictions applied to presence-only datasets. There is some indication that CBI is a more reliable metric than AUC when it comes to validating model transferability to a different geographical area [44].

3. RESULTS

The AUC & CBI based evaluation of the three models in the training area, where each model used a different subset of predictor variables at different grain size, indicated variation in the degree of prediction accuracy. As shown in Figure 1. AUC_{train}, AUC_{test} and CBI values of VS-1, the variable set with the coarsest grain size are the lowest, indicating the least accurate predictions in the training area (Snowdonia). Variable sets VS-2 and VS-3, comprised of the same set of biophysical variables but at different grain size, indicate that the finer grain size is likely to yield better model predictions.

We used Continuous Boyce Index (CBI) to assess the transferability of the MAXENT models to an area not covered by the training dataset, in our case the Brecon Beacons National Park. The model comprising the VS-1 variables showed the poorest model transferability with a CBI value of 0.65. In comparison, the model based on the VS-2 dataset showed a high CBI of 0.90, while the third model based on VS-3 achieved a moderate CBI of 0.77. Analysis of the predictor variable contribution to model prediction (Supplementary Data S2) suggests that land cover and altitude were major contributors in all three models. Our results also suggest that the use of finer grain size improved model transferability (CBI value of Models VS-2 & VS-3 > VS-1). However, model transferability decreased at the finest grain size (50 m) of the predictor variables. Response curves for individual variables for all three modelling scenarios are provided in Supplementary Data S3.

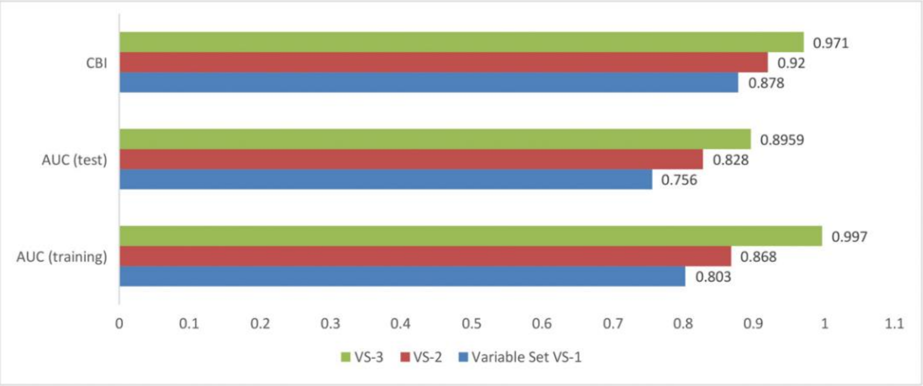


Figure 1. Area Under Curve (AUC) and Continuous Boyce Index (CBI) comparing prediction accuracy of Maxent-based models in Snowdonia National Park using three predictor variable sets at 1 km (VS-1), 300 m (VS-2) and 50 m (VS-3) resolution.

4. DISCUSSION

A number of studies have highlighted the fact that coarse grain size of predictor variables in SDMs may obscure effects of biotic interactions, small-scale heterogeneity of abiotic factors and micro habitat of species [45][46]. A review of 149-peer reviewed publications concluded that the choice of grain size is a highly neglected aspect in species distribution modelling and is a factor that significantly impacts modelling outcomes [12].

4.1. Model Performance in the Training Area

The results from this study show that MAXENT model predictions in the training area are likely to improve with smaller grain size of predictor variables (AUC in the order of 50 m > 300 m > 1000 m grain size). The Snowdonia National Park is characterized by diverse topography, with altitude ranging from sea-level to above 1000 m over a relatively short distance. Altitude is one of the key factors affecting the invasive potential of alien species and the effect of altitude was shown to be most pronounced at fine grain size [47]. It has been claimed that too coarse a grain size in SDMs leads to spatial smoothing and thus obscures the connection between, for example, land cover types and species occurrence [48]. This occurs by homogenizing the dominant land types within a grid cell resulting in the loss of useful information for accurate modelling [49]. In accordance with this assertion, the accuracy of model predictions in our study improved with decreasing grain size of the predictor variables, possibly as the result of capturing small-scale ecological interactions critical for species distribution being maximized at a finer grain size (Fernandez and Hamilton, 2015)[46][50]. In our case, the rugged topography of the area also affects factors such as soil physical and chemical properties, atmospheric humidity and wind speed/exposure over very short distances. With decreasing grain size, representation of these factors was more pronounced and improved model predictions. As grain size becomes finer, the number of mixed pixels decreases, leading to an increase in 'distinct' pixels which clearly separate different land cover, topographical or environmental units (or classes) and thus enables the algorithm to build more accurate species-habitat relationships [7]. This improvement becomes more relevant when the species being modelled is a habitat specialist. Since *R. ponticum* is considered one such species – in Wales it has a high preference for woodlands – better performance of models using small grain size data can be explained by improving representation of this community type.

As a habitat specialist, *R. ponticum* has repeatedly been shown to be strongly correlated with land cover type. In Britain woodland is the most important land cover type in the context of *R. ponticum* invasion [23], largely because of the availability of suitable micro-environments for seed germination [34]. For example, dead plant material and moss cover is critical to *R. ponticum* establishment [51]. Response curves in our study show that Forests are the most important land cover classes for *R. ponticum* distribution. Furthermore, *R. ponticum* is sensitive to topographic controls [52][53][54]. Response curves show that *R. ponticum* favours a northerly aspect for its establishment and growth as north-facing slopes at this latitude (Wales) are generally cooler, offering higher soil moisture and lower direct insulation intensity. Moreover, response curves suggest that *R. ponticum* distribution in Snowdonia is negatively correlated with slope. Shallow-slope areas are typically those with high soil moisture and nutrient availability, thus offering more favourable microenvironment for invasive species [55]. Distance from water channel was an important variable determining the habitat suitability of *R. ponticum*. This finding is compliments earlier studies suggesting that *R. ponticum* favors areas near water bodies [56] primarily because soil in vicinity of water body is moist and often has dense vegetation. Many other invasive species have been reported to be negatively correlated with distance from water sources [57].

4.2. Model Performance in the Transfer Area

After assessing model performance in the training area, the second goal of the study was to test the effects of grain size on the spatial transferability of the model. The results suggest that a coarse grain size (1000 m) produced the poorest model transferability while a medium grain size (300 m) resulted in the most accurate transfer of the model. The poor model transferability at 1 km grain size (CBI = 0.65) may be explained by the fact that key environmental factors, which in our case were land cover and topography, are 'averaged out' at coarser grain size both in the training and the transfer areas [45]. We expected the best model transferability when using data with the finest grain size. This was not the case; our transferred model had the best predictive power at medium grain size. A possible explanation is that Snowdonia National Park (training area) and Brecon Beacons National Park (transfer area) differ in the range and the character of topographical features. Since topography and land cover are best represented at small grain size, a discrepancy in the typography of landscape features between the two areas will negatively affect model transferability. Similarly, it has been shown that species occurrence data needs to be highly accurate when modelled at very fine grain size as any location [10][58] errors in the survey data may impact model performance.

In this study the CBI value of the SDM transferred at 300 m grain size was 0.90, a reasonably accurate prediction but which leaves room for improvement. We tested SDM transferability under the assumption that abiotic factors are the principal controls on species distribution. However, the distribution of any species is also likely to be constrained by biotic interactions [59]. These biotic interactions vary between geographical regions, just as topography, land cover and climatic factors differ. Even though the training and transfer areas used in the study are similar, any difference in the nature of the biotic interactions limiting *R. ponticum* may have constrained the degree of model transferability (Fernandez and Hamilton, 2015). In this context, this invasive species may have occupied only a subset of its potential niche in the invaded area so far, known as the realized niche. A species may fail to occupy the entire potential niche due to factors such as intra-species competition, dispersal limitation, scarcity of resources and other spatial limitations [60]. The distribution of species is linked to a framework known as 'Biotic Abiotic Mobility' (BAM) [61] which describes the potential niche yet to be inhabited by a species in the 'unfilled niche' [62]. Thus, correct identification of this unfilled niche may help to identify areas vulnerable for future invasion and may prove helpful in understanding the invasive behaviour of species under study [63]. Our results suggest therefore, that for habitat specialists, model transferability across geographical space becomes highly sensitive to the grain size when the model training and transfer areas differ in environmental and ecological features.

Although our study suggests that our model was transferred more accurately at 300 m grain size, it is important to mention that even at 50 m grain size, the model was also transferred with considerable success (CBI = 0.77). From an invasive species management point of view, a habitat suitability map at

50 m grain size with a lower prediction accuracy could still be more acceptable than a map with a better predictive ‘hit rate’ but at a six times coarser grain size. As an example, we include habitat suitability maps generated by model transfer to the Brecon Beacons National Park at three contrasting grain sizes (Figure 2). The land cover map legend is provided in Supplementary Data S3.

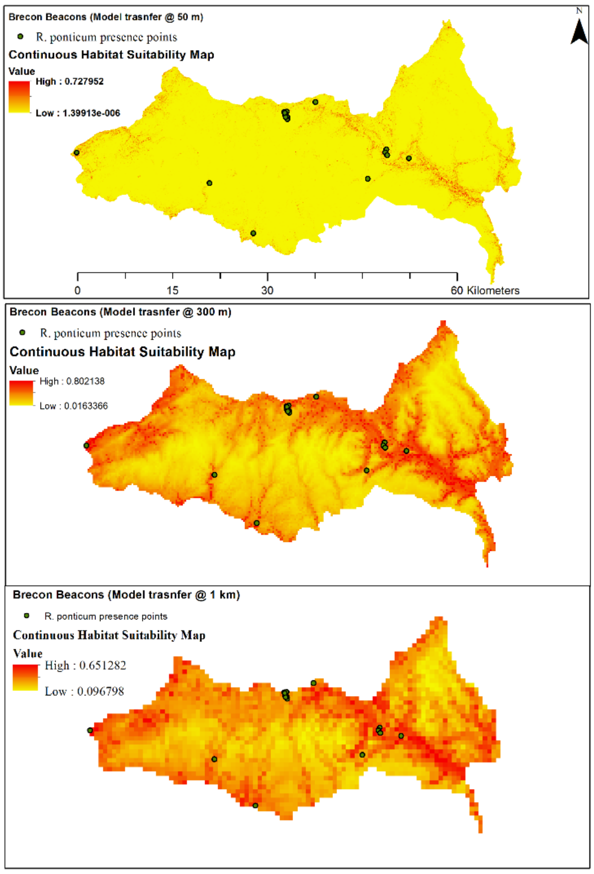


Figure 2. *Rhododendron ponticum* habitat suitability maps at 1 km, 300 m and 50 m resolutions generated in ArcGIS 10.5 (ESRI, Redlands, CA, USA, www.esri.com). A spatial distribution model was trained in Snowdonia National Park and transferred to the Brecon Beacons National Park. Blue dots indicate verified occurrence records of the species.

4.3. Bioclimatic Variables in SDMs – An Inevitable Choice?

In the context of our results it appears that unnecessary or ‘customary’ use of bioclimatic variables without considering the species’ ecology negatively affects the predictive potential of a SDM. Including these bioclimatic variables almost always comes at a cost of reducing the grain size of other variables, such as topography and land cover. However, as climate is likely to be one of the determinants of a species' fundamental niche, we suggest that expert knowledge of species' ecology and an extensive review of the literature should be carried out before deciding whether or not to include climatic variables in a SDM. Naturally, when modelling large-scale distributions (continental or global) or if the objective is a temporal prediction, perhaps to account for climate change, there currently may not be many alternatives to a 1 km grain size bioclimatic variables at a global scale. Choice of predictor variables is also a matter of the research question. If researchers are strictly interested in estimating climatic suitability or sensitivity, then the climatic variables become an appropriate choice. Our results strictly refer to cases where researchers might be interested in mapping species' distribution with high accuracy using the best possible combination of all the available predictor variables.

4.4. Limitations of The Study and Future Recommendations

Our study suggests that a grain size smaller than 1 km should be preferred in SDM studies conducted at this scale; however, models using finer grain size data should be trained and validated with carefully validated occurrence records. Training a model with predictor variables at very small grain size leads to a very specific species-habitat relationship and thus needs to be verified with accurate presence records. Our study modelled the distribution of *R. ponticum*, a habitat specialist species that showed a clear response to the changes in grain size. By contrast, generalist species may not be as sensitive to a change in grain size. Our study also suggests that there may not be a 'gold standard' for the grain size of predictor variables when it comes to model transferability across space. Ideally, transferring the model to another area requires the identification of optimum grain size by considering a range of grain sizes, perhaps on a sub-set of available occurrence data. Also, we considered only a small area for model training and transferability possibly explaining why climatic variables contributed the least in our models. For SDMs over large spatial scale, climatic variables may have greater effect in determining the distribution of species. In this study, we have only used two evaluation tools (AUC & CBI) which hint that the model with higher values might be better than the rest. For future studies we recommend applying more robust statistics to evaluate the significance of difference between modelling scenarios.

Species distribution model transferability and model grain size

SUPPLEMENTARY DATA S1

Review of Literature

Research papers published on MAXENT based Species Distribution Modelling in the years 2016-2017.

*Third column: 'Climate data at 1 km resolution (or higher)' – Studies which included bioclimatic variables

*Fourth column: 'Finer resolution Non-Climatic variables' – Studies which included Non-climatic variables which are available at a resolution finer than variables in third column.

*Fifth Column – NA: Studies which either had Climatic or Non-climatic variables. This classification is therefore *Not Applicable* to such studies.

No	Title of the research paper	Climate data at 1 km resolution (or higher)	Finer Resolution Non-climatic variables	Most important predictor variables (Climatic/Non-climatic/NA)
1	The influence of climate change on an endangered riparian plant species: The root of riparian Homonoia	Yes	Yes	Non-climatic
2	The importance of herbivore density and management as determinants of the distribution of rare plant specie	Yes	Yes	Non-climatic
3	Revealing areas of high nature conservation importance in a seasonally dry tropical forest in Brazil: Combination of modelled plant diversity hot spots and threat patterns	Yes	Yes	Climatic
4	Modelling and mapping the current and future climatic-niche of endangered Himalayan musk deer	Yes	No	NA
5	Spatial modelling of congruence of native biodiversity and potential hotspots of forest invasive species (FIS) in central Indian landscape	Yes	Yes	Non-climatic
6	Predicting current and future disease outbreaks of *Diplodia sapinea* shoot blight in Italy: species distribution models as a tool for forest management planning	Yes	Yes	Non-climatic
7	Species distribution modelling for wildlife management: Ornamental butterflies in México	Yes	No	NA
8	Environmental stress effects on reproduction and sexual dimorphism in the gynodioecious species *Silene acauli*	Yes	No	NA
9	Endemic grasshopper species distribution in an agro-natural landscape of the Cape Floristic Region, South Africa	Yes	Yes	Non-climatic

10	Factors affecting seasonal habitat use, and predicted range of two tropical deer in Indonesian rainforest	Yes	Yes	Non-climatic
11	Biodiversity hotspots and conservation gaps in Iran	Yes	Yes	Non-climatic
12	Identifying biodiversity hotspots for threatened mammal species in Iran	Yes	Yes	Non-climatic
13	Potential distributional changes of invasive crop pest species associated with global climate change	Yes	Yes	Climatic
14	Habitat distribution modelling to identify areas of high conservation value under climate change for *Mangifera sylvatica*Roxb. of Bangladesh	Yes	No	NA
15	Dynamic response of East Asian Greater White-fronted Geese to changes of environment during migration: Use of multi-temporal species distribution model	Yes	Yes	Non-climatic
16	A bird's view of new conservation hotspots in China	Yes	Yes	Non-climatic
17	Probabilistic assessment of high concentrations of particulate matter (PM_{10}) in Beijing, China	Yes	Yes	Non-climatic
18	Mapping priorities for conservation in Southeast Asia	Yes	Yes	Climatic
19	Influence of environmental factors on the distribution of *Calymperes* and *Syrrhopodon* (Calymperaceae, Bryophyta) in the Atlantic Forest of Northeastern Brazil	Yes	Yes	Climatic
20	Field validation of an invasive species Maxent model	No	Yes	NA
21	Maxent modelling for predicting the potential distribution of endangered medicinal plant (*H. riparia* Lour) in Yunnan, China	Yes	Yes	Non-climatic
22	Using species distribution models to assess the importance of Egypt's protected areas for the conservation of medicinal plants	Yes	Yes	Climatic
23	Landscape to site variations in species distribution models for endangered plants	Yes	Yes	Non-climatic
24	Detecting the richness and dissimilarity patterns of Theaceae species in southern China	Yes	Yes	Climatic
25	Predicting distribution of major forest tree species to potential impacts of climate change in the central Himalayan region	Yes	Yes	Non-climatic
26	Predicting the probable distribution and threat of invasive *Mimosa diplotricha* Suavalle and *Mikania micrantha* Kunth in a protected tropical grassland	Yes	Yes	Climatic
27	Impacts of the spatial scale of climate data on the modeled distribution probabilities of invasive tree species throughout the world	Yes	No	NA

28	Efficacy of conservation strategies for endangered oriental white storks (*Ciconia boyciana*) under climate change in Northeast China	Yes	Yes	Climatic
29	Modelling impacts of future climate on the distribution of Myristicaceae species in the Western Ghats, India	Yes	No	NA
30	Surrogate species protection in Bolivia under climate and land cover change scenarios	Yes	No	NA
31	Modelling the distributions of useful woody species in eastern Burkina Faso	Yes	Yes	Non-climatic
32	Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa	Yes	No	NA
33	Spatial distribution of dry forest orchids in the Cauca River Valley and Dagua Canyon: Towards a conservation strategy to climate change	Yes	Yes	Non-climatic
34	Geographical boundary and climatic analysis of *Pinus tabulaeformis* in China: Insights on its afforestation	Yes	Yes	Climatic
35	Niche breadth and the implications of climate change in the conservation of the genus *Astrophytum* (Cactaceae)	Yes	No	NA
36	Niche constraints to the northwards expansion of the common genet (*Genetta genetta,* Linnaeus 1758) in Europe	Yes	Yes	Climatic
37	Climate change and the distribution and conservation of the world's highest elevation woodlands in the South American Altiplano	Yes	No	NA
38	Preventing extinction and improving conservation status of Vanilla borneensis Rolfe—A rare, endemic and threatened orchid of Assam, India	No	Yes	NA
39	Influence of land use and meteorological factors on the spatial distribution of *Toxocara canis* and *Toxocara cati* eggs in soil in urban areas	Yes	Yes	Non-climatic
40	Species distribution modelling for wildlife management: Ornamental butterflies in México	Yes	No	NA
41	Impact of climate and host availability on future distribution of Colorado potato beetle	Yes	No	NA
42	Mapping the climatic suitable habitat of oriental arborvitae (Platycladus orientalis) for introduction and cultivation at a global scale	Yes	No	NA
43	Prediction of the potential geographic distribution of the ectomycorrhizal mushroom Tricholoma matsutake under multiple climate change scenarios	Yes	Yes	Non-climatic
44	Climate change and the ash dieback crisis	Yes	No	NA

45	Habitat mapping as a tool for water birds conservation planning in an arid zone wetland: The case study Hamun wetland	No	Yes	NA
46	Potential distribution of *Ursus americanus* in Mexico and its persistence: Implications for conservation	No	Yes	NA
47	The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management	No	Yes	NA
48	Current and future suitability of wintering grounds for a long-distance migratory raptor	Yes	Yes	Non-climatic
49	Distribution Modelling of three screwworm species in the ecologically diverse landscape of North West Pakistan	Yes	Yes	Non-climatic
50	Predicting impacts of climate change on habitat connectivity of *Kalopanax septemlobus* in South Korea	Yes	Yes	Climatic
51	Vulnerability to climate change of cocoa in West Africa: Patterns, opportunities and limits to adaptation	Yes	No	NA
52	Priority areas for conservation of beach and dune vegetation of the Mexican Atlantic coast	Yes	No	NA
53	Seasonal habitat suitability modelling and factors affecting the distribution of Asian Houbara in East Iran	Yes	Yes	Non-climatic
54	Kamala tree as an indicator of the presence of Asian elephants during the dry season in the Shivalik landscape of northwestern India	Yes	Yes	Climatic
55	The worrying future of the endemic flora of a tropical mountain range under climate change	Yes	No	NA
56	Taxonomy and ecological niche modelling: Implications for the conservation of wood partridges (genus *Dendrortyx*)	Yes	No	NA
57	Climate change fosters the decline of epiphytic *Lobaria* species in Italy	Yes	No	NA
58	Landscape to site variations in species distribution models for endangered plants	Yes	Yes	Non-climatic
59	Performance of one-class classifiers for invasive species mapping using airborne imaging spectroscopy	No	Yes	NA

SUPPLEMENTARY DATA S2

Analysis of Variables Contribution to Maxent-based Models

Permutation Importance of variables - Model VS-3

Variable	Permutation importance
Altitude	87.8
Land cover	5.9
Distance from water channels	5.4
Aspect	0.5
Slope	0.4

Permutation Importance of variables - Model VS-2

Variable	Permutation importance
Altitude	88.7
Land cover	4.7
Distance from water channels	2.5
Aspect	3.8
Slope	0.3

Permutation Importance of variables - Model VS-1

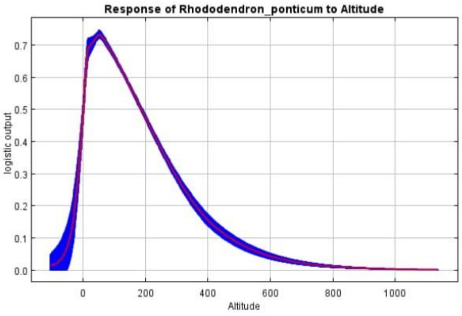
Variable	Permutation importance
Altitude	60
Land cover	14.4
Distance from water channels	14.1
bio_3	0.3
bio_2	1.7
Aspect	1
bio_9	1.4
Slope	2.3
bio_15	4.9

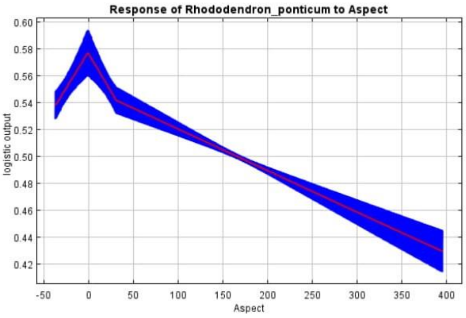
SUPPLEMENTARY DATA S3

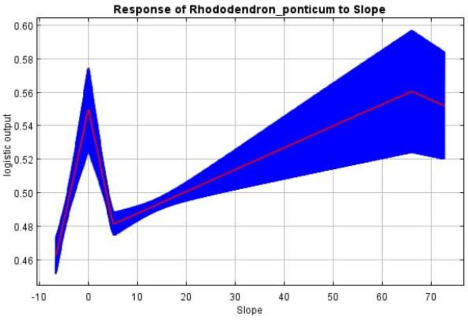
Response curves

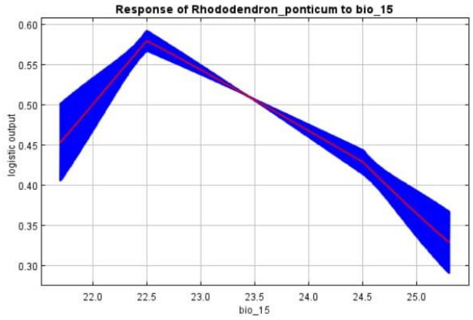
These curves show how each environmental variable affects the Maxent prediction. The curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. The curves show the mean response of the 25 replicate Maxent runs (red) and the mean +/- one standard deviation (blue, two shades for categorical variables).

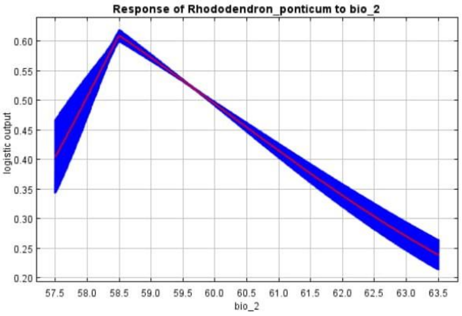
1. **Model at 1km**

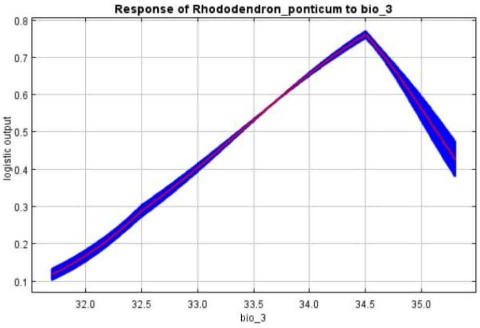


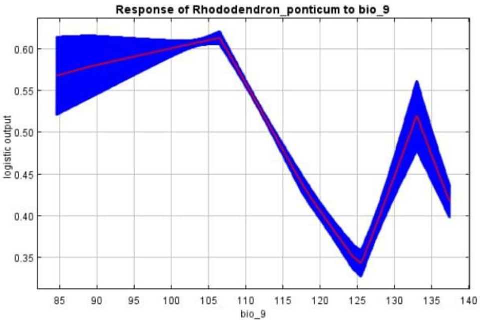


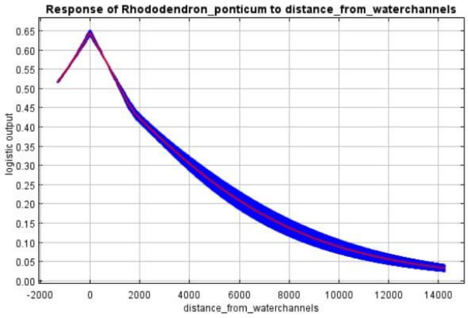


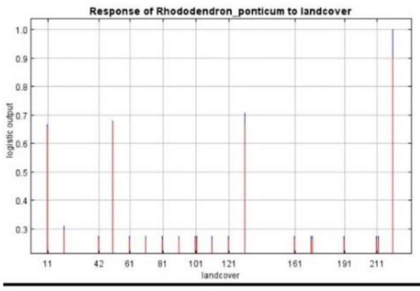




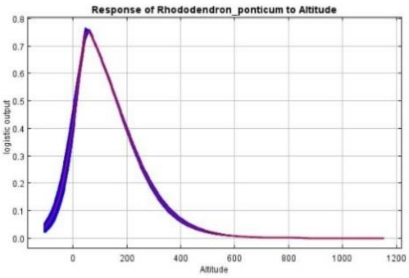


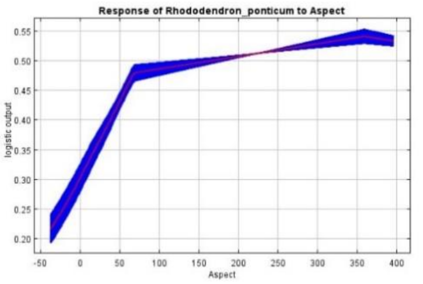


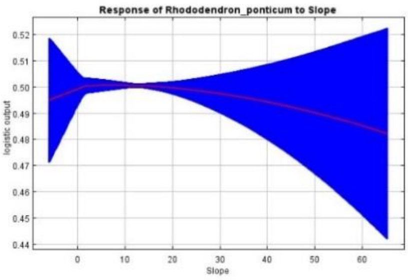


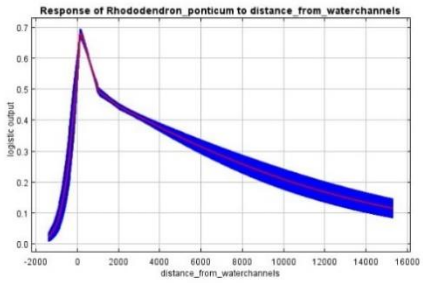


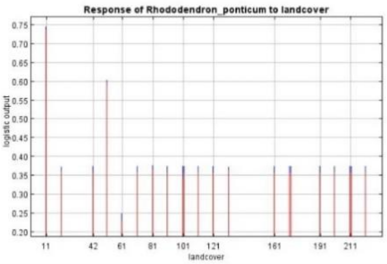
2. Model at 300 m



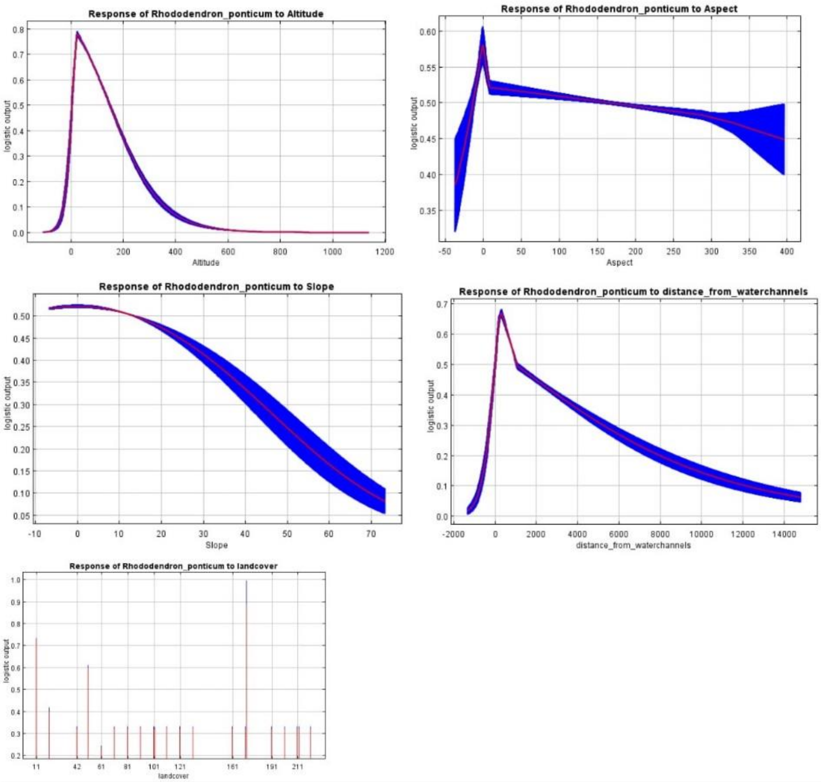








2. **Model at 50 m**



Legend for Land cover categories

11	Broad leaved woodland
21	Coniferous woodland
41	Arable cereals
42	Arable horticulture
43	Non Rotational Horticulture
51	Improved Grassland
52	Setaside Grassland
61	Neutral Grassland
71	Calcareous grassland
81	Acid grassland
91	Bracken
101	Dense dwarf shrub heath
102	Open dwarf shrub heath
111	Fen, marsh, swamp
121	Bog

131	Inland water
151	Montane habitat
161	Inland rock
171	Sub urban/rural developed
172	Continuous urban
181	Supra-littoral rock
191	Supra-littoral sediment
201	Littoral rock
211	Littoral sediment
212	Saltmarsh
221	Sea/Estuary

REFERENCES

1. Václavík, T.; Meentemeyer, R.K. Invasive species distribution modelling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecol. Modell.* **2009**, *220*, 3248–3258.
2. Verbruggen, H.; Tyberghein, L.; Belton, G.S.; Mineur, F.; Jueterbock, A.; Hoarau, G.; Gurgel, C.F.D.; De Clerck, O. Improving Transferability of Introduced Species' Distribution Models: New Tools to Forecast the Spread of a Highly Invasive Seaweed. *PLoS One* **2013**, *8*, 1–13.
3. Pearson, R.G.; Dawson, T.P. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **2003**, *12*, 361–371.
4. Soberón, J. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **2007**, *10*, 1115–1123.
5. Menke, S.B.; Holway, D.A.; Fisher, R.N.; Jetz, W. Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. *Glob. Ecol. Biogeogr.* **2009**, *18*, 50–63.
6. Wiens, J.A. Spatial Scaling in Ecology Spatial scaling in ecology1. *Source Funct. Ecol.* **1989**, *3*, 385–397.
7. Gottschalk, T.K.; Aue, B.; Hotes, S.; Ekschmitt, K. Influence of grain size on species-habitat models. *Ecol. Modell.* **2011**, *222*, 3403–3412.
8. Connor, T.; Hull, V.; Viña, A.; Shortridge, A.; Tang, Y.; Zhang, J.; Wang, F.; Liu, J. Effects of grain size and niche breadth on species distribution modelling. *Ecography (Cop.).* **2017**, 1–12.
9. Song, W.; Kim, E.; Lee, D.; Lee, M.; Jeon, S.W. The sensitivity of species distribution modelling to scale differences. *Ecol. Modell.* **2013**, *248*, 113–118.
10. Hanberry, B.B. Finer grain size increases effects of error and changes influence of environmental predictors on species distribution models. *Ecol. Inform.* **2013**, *15*, 8–13.
11. Fernandez, M.; Hamilton, H. Ecological niche transferability using invasive species as a case study. *PLoS One* **2015**, *10*, 1–17.
12. Mayer, A.L.; Cameron, G.N. Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landsc. Urban Plan.* **2003**, *65*, 201–217.
13. Porfirio, L.L.; Harris, R.M.B.; Lefroy, E.C.; Hugh, S.; Gould, S.F.; Lee, G.; Bindoff, N.L.; Mackey, B. Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One* **2014**, *9*, 1–21.
14. Wang, H.; Liu, D.; Munroe, D.; Cao, K.; Biermann, C. Study on selecting sensitive environmental variables in modelling species spatial distribution. *Ann. GIS* **2016**, *22*, 57–69.
15. Guisan, A.; Zimmermann, N.E.; Elith, J.; Graham, C.H.; Phillips, S.; Peterson, A.T. What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? *Ecol. Monogr.* **2007**, *77*, 615–630.
16. Venier, L. a; Pearce, J.; McKee, J.E.; McKenney, D.W.; Niemi, G.J. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes basin. *J. Biogeogr.* **2004**, *31*, 315–331.
17. Guisan, A.; Graham, C.H.; Elith, J.; Huettmann, F.; Dudik, M.; Ferrier, S.; Hijmans, R.; Lehmann, A.; Li, J.; Lohmann, L.G.; et al. Sensitivity of predictive species distribution models to change in grain size. *Divers. Distrib.* **2007**, *13*, 332–340.
18. Fitzpatrick, M.C.; Weltzin, J.F.; Sanders, N.J.; Dunn, R.R. The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? *Glob. Ecol. Biogeogr.* **2007**, *16*, 24–33.
19. Roach, N.S.; Hunter, E.A.; Nibbelink, N.P.; Barrett, K. Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States. *Ecosphere* **2017**, *8*.
20. Khosravi, R.; Hemami, M.R.; Malekian, M.; Flint, A.L.; Flint, L.E. Maxent modelling for predicting potential distribution of goitered gazelle in central Iran: The effect of extent and grain size on performance of the model. *Turkish J. Zool.* **2016**, *40*, 574–585.

21. Luoto, M.; Virkkala, R.; Heikkinen, R.K. The role of land cover in bioclimatic models depends on spatial resolution. *Glob. Ecol. Biogeogr.* **2007**, *16*, 34–42.
22. Phillips SJ Dudik M, S.R.E. A maximum entropy approach to species distribution modelling. **2004**, 655–662.
23. Dehnen-Schmutz, K.; Williamson, M. *Rhododendron ponticum* in Britain and Ireland: Social, economic and ecological factors in its successful invasion. *Environ. Hist. Camb.* **2006**, *12*, 325–350.
24. Tiedeken, E.J.; Stout, J.C. Insect-flower interaction network structure is resilient to a temporary pulse of floral resources from invasive *Rhododendron ponticum*. *PLoS One* **2015**, *10*, 1–19.
25. Jackson, P. Rhododendron in Snowdonia and a strategy for its control. *Snowdownia Natl. Park Auth.* **2008**.
26. Phillips, S.B.; Aneja, V.P.; Kang, D.; Arya, S.P. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *Int. J. Glob. Environ. Issues* **2006**, *6*, 231–252.
27. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudik, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).* **2006**, *29*, 129–151.
28. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **2011**, *17*, 43–57.
29. Wisz, M.S.; Hijmans, R.J.; Li, J.; Peterson, A.T.; Graham, C.H.; Guisan, A.; Elith, J.; Dudík, M.; Ferrier, S.; Huettmann, F.; et al. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **2008**, *14*, 763–773.
30. Brown, J.L. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* **2014**, *5*, 694–700.
31. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978.
32. Harris, C.M.; Stanford, H.L.; Edwards, C.; Travis, J.M.J.; Park, K.J. Integrating demographic data and a mechanistic dispersal model to predict invasion spread of *Rhododendron ponticum* in different habitats. *Ecol. Inform.* **2011**, *6*, 187–195.
33. Erfmeier, A.; Bruelheide, H. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora - Morphol. Distrib. Funct. Ecol. Plants* **2004**, *199*, 120–133.
34. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–758.
35. Eşen, D.; Zedaker, S.M.; Kirwan, J.L.; Mou, P. Soil and site factors influencing purple-flowered rhododendron (*Rhododendron ponticum* L.) and eastern beech forests (Fagus orientalis Lipsky) in Turkey. *For. Ecol. Manage.* **2004**, *203*, 229–240.
36. Choudhury, M.R.; Deb, P.; Singha, H.; Chakdar, B.; Medhi, M. Predicting the probable distribution and threat of invasive Mimosa diplotricha Suavalle and Mikania micrantha Kunth in a protected tropical grassland. *Ecol. Eng.* **2016**, *97*, 23–31.
37. Gibson, L.; McNeill, A.; Tores, P. de; Wayne, A.; Yates, C. Will future climate change threaten a range restricted endemic species, the quokka (Setonix brachyurus), in south west Australia? *Biol. Conserv.* **2010**, *143*, 2453–2461.
38. Hu, R.; Wen, C.; Gu, Y.; Wang, H.; Gu, L.; Shi, X.; Zhong, J.; Wei, M.; He, F.; Lu, Z. A bird's view of new conservation hotspots in China. *Biol. Conserv.* **2017**, *211*, 47–55.
39. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop.).* **2013**, *36*, 027–046.
40. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. *PLoS One* **2013**, *8*.

41. Swets, J.A. Measuring the accuracy of diagnostic systems. *Science* **1988**, *240*, 1285–1293.
42. Boyce, M.S.; Vernier, P.R.; Nielsen, S.E.; Schmiegelow, F.K.A. Evaluating resource selection functions. *Ecol. Modell.* **2002**, *157*, 281–300.
43. Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* **2006**, *199*, 142–152.
44. Cianfrani, C.; Le Lay, G.; Hirzel, A.H.; Loy, A. Do habitat suitability models reliably predict the recovery areas of threatened species? *J. Appl. Ecol.* **2010**, *47*, 421–430.
45. Baniya, C.B.; Solhøy, T.; Gauslaa, Y.; Palmer, M.W. Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. *Folia Geobot.* **2012**, *47*, 135–151.
46. Özesmi, U.; Mitsch, W.J. A spatial habitat model for the marsh-breeding red-winged blackbird (Agelaius phoeniceus L.) in coastal Lake Erie wetlands. *Ecol. Modell.* **1997**, *101*, 139–152.
47. Palmer, M.W. Scale dependence of native and alien species richness in North American floras. *Preslia* **2006**, *78*, 427–436.
48. Lawes, M.J.; Piper, S.E. There is less to binary maps than meets the eye: The use of species distribution data in the southern African sub-region. *S. Afr. J. Sci.* **1998**, *94*, 207–210.
49. Saura, S. Effects of minimum mapping unit on land cover data spatial configuration and composition. *Int. J. Remote Sens.* **2002**, *23*, 4853–4880.
50. Ödland, A.; Birks, H.J.B. The altitudinal gradient of vascular plant richness in Anrland, western Norway. *Ecography (Cop.).* **1999**, *22*, 548–566.
51. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
52. Taylor, S.L.; Hill, R.A.; Edwards, C. Characterising invasive non-native *Rhododendron ponticum* spectra signatures with spectroradiometry in the laboratory and field: Potential for remote mapping. *ISPRS J. Photogramm. Remote Sens.* **2013**, *81*, 70–81.
53. Francon, L.; Corona, C.; Roussel, E.; Lopez Saez, J.; Stoffel, M. Warm summers and moderate winter precipitation boost Rhododendron ferrugineum L. growth in the Taillefer massif (French Alps). *Sci. Total Environ.* **2017**, *586*, 1020–1031.
54. Christiaens, A.; Lootens, P.; Roldán-Ruiz, I.; Pauwels, E.; Gobin, B.; Van Labeke, M.C. Determining the minimum daily light integral for forcing of azalea (Rhododendron simsii). *Sci. Hortic. (Amsterdam).* **2014**, *177*, 1–9.
55. Kang, W.; Minor, E.S.; Lee, D.; Park, C.R. Predicting impacts of climate change on habitat connectivity of Kalopanax septemlobus in South Korea. *Acta Oecologica* **2016**, *71*, 31–38.
56. Evangelista, P.; Young, N.; Carter, L.; Jarnevich, C.; Birtwistle, A.; Groy, K. Mapping Habitat and Potential Distributions of Invasive Plant Species on USFWS National Wildlife Refuges. **2012**, 34.
57. Crall, A.W.; Jarnevich, C.S.; Panke, B.; Young, N.; Renz, M.; Morisette, J. Using habitat suitability models to target invasive plant species surveys. *Ecol. Appl.* **2013**, *23*, 60–72.
58. Guisan, A.; Thuiller, W. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* **2005**, *8*, 993–1009.
59. Lenoir, J.; Gégout, J.C.; Guisan, A.; Vittoz, P.; Wohlgemuth, T.; Zimmermann, N.E.; Dullinger, S.; Pauli, H.; Willner, W.; Svenning, J.C. Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography (Cop.).* **2010**, *33*, 295–303.
60. Mott, C.L. Environmental Constraints to the Geographic Expansion of Plant and Animal Species. *Nat. Educ. Knowl.* **2010**, *3*, 72.
61. Soberon, J.; Nakamura, M. Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci.* **2009**, *106*, 19644–19650.
62. Broennimann, O.; Guisan, A. Predicting current and future biological invasions: both native and invaded ranges matter. *Biol. Lett.* **2008**, *4*, 585–589.

63. Seoane, J.; Carrascal, L.M.; Alonso, C.L.; Palomino, D. Species-specific traits associated to prediction errors in bird habitat suitability modelling. *Ecol. Modell.* **2005**, *185*, 299–308.

SCENARIO-LED MODELLING OF BROADLEAF FOREST EXPANSION IN WALES

ABSTRACT

Significant changes in the composition and extent of the UK forest cover are likely to take place in the coming decades. Current policy targets an increase in forest area, for example, the Welsh Government aims for forest expansion by 2030, and a purposeful shift from non-native conifers to broadleaved tree species, as identified by the UK Forestry Standard Guidelines on Biodiversity. Using the example of Wales, we aim to generate an evidence-based projection of the impact of contrasting policy scenarios on the state of forests in the near future, with the view of stimulating debate and aiding decisions concerning plausible outcomes of different policies. We quantified changes in different land use and land cover (LULC) classes in Wales between 2007 and 2015 and used a multi-layer perceptron–Markov chain ensemble modelling approach to project the state of Welsh forests in 2030 under the current and an alternative policy scenario. The current level of expansion and restoration of broadleaf forest in Wales is sufficient to deliver on existing policy goals. We also show effects of a more ambitious afforestation policy on the Welsh landscape. In a key finding, the highest intensity of broadleaf expansion is likely to shift from south-eastern to more central areas of Wales. The study identifies the key predictors of LULC change in Wales. High-resolution future land cover simulation maps using these predictors offer an evidence-based tool for forest managers and government officials to test the effects of existing and alternative policy scenarios.

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Scenario-led modelling of broadleaf forest expansion in Wales

1. INTRODUCTION

Global forest cover has receded rapidly in the recent past, largely due to the conversion of forests into pasture and croplands [1]. In contrast to many other parts of the world where forest cover is still declining, Europe has reversed this deforestation trend and forest cover here is increasing as a consequence of land abandonment and subsequent secondary succession [2] and as a result of deliberate planting [3]. Afforestation of Great Britain is a good example of such reversal: forest cover stood at 5% in the 1920s but increased to 13% by 2013 [4]. Early twentieth-century forestry policy in Britain focused on planting fast-growing non-native conifer tree species to boost domestic timber supply [5], nearly tripling forest cover in the process. However, extensive plantations of single-species non-native conifers resulted in the loss of important habitats [6][7], with a direct negative effect on species diversity [8]. In the latter part of the twentieth century, British forestry policy gradually changed to address a wider set of objectives to complement timber production, resulting in a broad focus on the expansion of native tree species cover [5].

At present, non-native conifers constitute 36% of the total forest area in Britain. Typically represented by Sitka spruce (*Picea sitchensis* Bong.), the conversion of these woodlands to native species, where appropriate, is an aspiration stated in the UK Forestry Standard Guidelines on Biodiversity (UKFS) [9]. Non-native plantations often consist of even-aged and often single-species conifers mostly present in the uplands. UKFS guidelines on biodiversity encourage the large-scale expansion of native woodlands, primarily by replacing non-native species by native broadleaves or Scots pine (*Pinus sylvestris* L.). 'Forest conversion' in this context thus refers to the silvicultural process of changing forest stands dominated by non-native conifers into forests composed of native tree species [9].

There are several reasons why this type of forest conversion should become an important tool of forestry policy in Britain. When compared to a conifer plantation, broadleaf tree species tend to increase soil pH [10], improve growth condition for ground vegetation and soil fauna [11][12][13], enhance nesting opportunities and seasonal availability of food to bird communities [14] and decrease the prevalence of insect pests [15] and plant pathogens [16]. Further, and no less important in densely populated landscapes, forest conversion to native broadleaves impacts on landscape aesthetics—an attribute keenly perceived and appreciated by the public [17]. The conversion of conifer stands to broadleaf woodland is also supported by forestry policy in Wales, specifically the rules governing the restoration of planted ancient woodland sites (PAWS) that have historically been afforested with conifers [18]. This strategy is also supported by the objectives of the UK Biodiversity Action Plan.

There is strong political interest to enhance forest cover of the UK (e.g. [19], with the Welsh Government committed to increasing the overall forest area in Wales as its contribution to sustainable development. In 2010, the Welsh Assembly Government's Climate Change Strategy [20] recommended that woodland establishment rates be increased to 5000 ha per year for 20 years as an option for meeting Wales' carbon emission reduction targets. This figure was subsequently adopted by Welsh Government as a policy target in the form of planting 100 000 ha of new, primarily broadleaved, woodland by 2030. However, actual planting levels over the following years were insufficient to meet this. The Welsh Government then regressively reduced the target, first to 50 000 ha, and eventually to the current commitment to plant at least 2000 ha of woodland a year between 2020 and 2030 [19]. Despite these reductions in aspiration, the broad commitment to increasing woodland cover has been bolstered by recent legislation and policy development. The Environment (Wales) Act (2016) requires the Welsh Government's principal advisor on the environment and natural resources, Natural Resources Wales, to periodically produce a State of Natural Resources Report that makes an assessment of the state of natural resources in Wales and the extent to which they are sustainably managed. The first such report highlighted the need for the increased woodland cover to deliver multiple benefits [21]. In this context, maintaining a balance between conservation and sustainable development is seen as a challenge in policy making and landscape management in Wales.

Where possible, forest management policies should be evidence-based [22][23]. One tool that can be used to generate evidence and test policy scenarios is landscape modelling which can project the spatial and temporal implications of policies under consideration [24]. Spatially explicit land use and land cover (LULC) models can project land use change patterns according to given policy objectives and generate alternative scenarios [25][26], thus establishing a link between policy and implications on the ground [27]. The LULC change models offer an evidence-based approach to visualize, analyse and quantify LULC changes in what-if future scenarios, thus providing useful insights to policy makers and relevant stakeholders to set priorities and reasonable goals for sustainable forest management [28].

To date, several spatially explicit modelling environments have been developed by incorporating remote sensing and geographical information system tools to project future LULC change scenarios. Some of the most widely used models are based on Markov chain, logistic regression, artificial neural network and cellular automata models [29]. Integrated use of these models is often advised to overcome limitations of individual models and generate robust LULC change simulations [30]. In this study, we employed an integrated multi-layer perceptron–Markov chain analysis (MLP–MCA) method to quantify historic LULC change and to model future scenarios of LULC change in Wales. The MLP–MCA is a robust and well documented approach for modelling spatial and temporal LULC changes [31][32][33]. To develop realistic future scenarios of LULC change, it is critical to understand the spatial patterns of current LULC and to develop an understanding of the potential impacts of current and future policies affecting LULC change and, specifically, native woodland expansion. A key assumption underlying most LULC modelling is that socio-economic drivers of change remain stable over time; this is, however, unlikely in reality [34]. To meet this challenge, we considered the following key questions prior to embarking on the modelling exercise:

1. Under recent policies, what would the state (type and area) of forests in Wales be in 2030?
2. What are the implications of an alternative policy scenario designed to stimulate new woodland creation while considering other objectives, such as the conservation value of non-woodland habitats?

Thus, this paper presents an analysis of the current situation and likely future trends, together with an indication of policy requirements necessary to achieve the stated afforestation goal for Wales. We mapped historical patterns of LULC and LULC change in Wales and developed two contrasting future LULC scenarios based on (i) current trends and (ii) an alternative policy. We also discuss the usefulness of the resulting future LULC maps of Wales for habitat, biodiversity and ecosystem services analysis.

2. METHODOLOGY

2.1. Study Area

Wales is a country with an area of nearly 21 000 km^2 and a population of over 3 million, most of which live in rural communities [35]. The population is unequally distributed, with most people living in coastal areas in the northeast and south Wales. The country is characterized by a wide variety of landscapes, reflecting both its rugged topography and a long history of agricultural settlement and industrialization. Significant areas of land (approx. 6000 km^2) are at an altitude above 300 m. Welsh countryside contains a range of important habitats, including woodlands, semi-natural grasslands, heathland, fens, bogs, coastal ecosystems including sand dunes and saltmarshes, and a diverse range of upland and montane habitats [6][36]. Only a small proportion—6%—of the country is occupied by arable agriculture, while the major land use types are grazing (77%) and forestry (15%) [37][38][39].

2.2. Modelling Methodology

We made use of TerrSet Geospatial Monitoring and Modelling System (version 18.31, Clark Labs, Clark University, USA) [40]. Specifically, we used the 'Land Change Modeler' (LCM) tool in TerrSet to generate two future LULC change scenarios: business-as-usual and an alternative scenario.

2.3. Analysis of Past Change

The first step of this type of analysis generates the spatial pattern of changes that are discernible from the comparison of historical LULC maps. A minimum of two maps is required (describing two different points in time), the comparison seeking to understand the nature of LULC change and to generate samples of transitions to be projected [40]. We used high-resolution (25 m) LULC maps of the country from 2007 and 2015, generated from satellite imagery by the Centre for Ecology & Hydrology, UK (https://digimap.edina.ac.uk) [41]. Both LULC maps had the same legend and spatial resolution. By comparing the two maps, LCM evaluates LULC change and generates a visual representation of net change, persistence, losses and gains and transitions between different LULC categories covered by the two raster maps. In this study, we excluded LULC categories that showed a negligible transition between 2007 and 2015 and thus are not expected to change over the time horizon under consideration (e.g. urban areas) and those not relevant to our objectives (e.g. water bodies or coastal areas). The final list of LULC categories selected for our modelling exercise is presented in the electronic Supplementary Data S1, table 1. We then generated change analysis maps indicating which LULC classes changed and the spatial pattern of changes across the Welsh landscape. This analysis of LULC change in Wales between 2007 and 2015 resulted in a total of 28 transition types between different LULC classes (electronic Supplementary Data, table 1).

2.4. Explanatory Variables

2.4.1. Rationale for the Choice of Explanatory Variables

Land use change modelling is complex, and a wide range of factors is likely to affect future decisions of landowners [42]. Therefore, the kind and number of explanatory factors for future land use change can vary considerably. Spatial and temporal scale of the study also affects the choice of explanatory variables [42]. Given that the spatial focus of this study is regional (i.e. Wales) and temporal scale is only 15 years (2015–2030), we applied the following rationale to the choice of explanatory variables:

— Biophysical variables. Biophysical factors such as topography or soil type influence land use and allocation decisions. For example, expansion of arable land may be limited by slope incline and/or altitude, planting new woodlands could be driven by soil quality or land parcel accessibility. Biophysical variables, especially at a fine spatial resolution of 25 m, are very strong proxies of climatic variables which are otherwise only available at a spatial resolution of 1 km or higher and thus cannot be used in fine-scale land use change modelling (e.g. altitude is a strong proxy for temperature, wind speed, etc.) [42][43].

— Proximate variables. At a regional scale, variables such as distance to markets or roads are strong determinants of landowners' decision-making [42][44]. For example, areas closer to roads or green spaces often have a higher market price. Areas in close proximities to major road junctions are more likely to experience change [45]. Furthermore, we used variables such as distance to exiting the broadleaf forest and arable land because the expansion of a habitat is very likely to be in the near vicinity of the already existing patches of that habitat [24][46].

— Evidence likelihood of land use transition. We mapped transitions from all land cover classes to the broadleaf forest and vice versa during 2007–2015 and used the evidence likelihood function to convert the patterns of these transitions into usable continuous variables. Evidence likelihood is an empirical probability of change for a qualitative map [47] and describes the relative frequency with which different LULC categories occurred within areas that transitioned between 2007 and 2015. These variables thus represent the likelihood of finding a specific LULC at the pixel in question, if the pixel covers an area suitable for the transition. Since the decision of change on a land parcel is strongly influenced by the decisions of the neighbouring land parcel [48][49][50], these variables can have important information.

2.4.2. Explanatory Variables Used in the Study

As shown in table 1, we considered 20 variables in total as having the potential to explain LULC transitions occurring in Wales between 2007 and 2015. We collected a range of explanatory variables such as topography, soil factors or distance from key biophysical features such as water bodies and existing forests [34][51][52]. Six variables—distances between each of the six LULC classes—were dynamic, while the rest were static. Values of a dynamic variable change at each time step of the model run and thus need to be recalculated (e.g. the distance from the broadleaf forest as these forests expand). By contrast, static variables remain constant over time (e.g. altitude, slope, soil type).

Furthermore, we used the 'Evidence Likelihood Transformation' tool in the LCM to convert categorical variables to continuous [40]. The following transformations were made:

(1) We generated two Boolean images: first, change from all LULC types to Broadleaf Forest (All to Broadleaf) and change from Broadleaf Forest to all other LULC types (Broadleaf to All). In these images, 0 represents no change while 1 represents the indicated change. The Boolean images were then used in the Evidence Likelihood Transformation process to generate two continuous variables: 'Evidence Likelihood of change from Broadleaf Forest to All Other Classes' and 'Evidence Likelihood of change from All Other Classes to Broadleaf Forest'.

(2) Welsh soil type data used in this research consisted of 27 soil classes. We used the 'Evidence Likelihood Transformation' option to generate the following two continuous variables from this categorical variable: 'Evidence Likelihood of change from Broadleaf Forest to All Other Classes based on Soil type' and 'Evidence Likelihood of change from All Other Classes to Broadleaf Forest based on Soil type'.

The potential of each of the 20 variables to explain observed LULC change was tested by calculating Cramer's V [40]. Six variables were dropped from the final list on the basis of low Cramer's V value (V, 0.15) [52].

Table 1. List of explanatory variables considered in the study. Variables in italics were chosen in the final model based on Cramer's V values (V . 0.15).

	Explanatory Variables	**Cramer's V**	**Type of Variable**
1	*Altitude*	0.345	Static
2	Aspect	0.077	Static
3	*Slope*	0.168	Static
4	Hillshade	0.135	Static
5	*Distance from Access Points*	0.224	Static
6	*Distance from Green Spaces*	0.223	Static
7	Distance from Water Channels	0.011	Static
8	*Distance from Roads*	0.254	Static
9	Distance from Hydronodes	0.065	Static
10	*Distance from Motorway Junctions*	0.161	Static
11	*Distance from Broadleaf Forest*	0.155	Dynamic
12	Distance from Conifer Forest	0.081	Dynamic
13	*Distance from Arable Land*	0.21	Dynamic
14	*Distance from Improved Grassland*	0.155	Dynamic
15	*Distance from Semi Natural Grassland*	0.161	Dynamic
16	Distance from Mountain, Heath & Bog	0.013	Dynamic
17	*Evidence Likelihood of change from Broadleaf Forest to All Other Classes based on earlier land use transition*	0.249	Static
18	*Evidence Likelihood of change from All Other Classes to Broadleaf Forest based on earlier land use transition*	0.533	Static
19	*Evidence Likelihood of change from Broadleaf Forest to All Other Classes based on Soil type*	0.251	Static
20	*Evidence Likelihood of change from All Other Classes to Broadleaf Forest based on Soil type*	0.256	Static

2.4.3. Transition Sub-Models (Training and Validation)

LCM enlists all shortlisted transitions between the two LULC maps, each represented by a transition sub-model. Explanatory variables which have Cramer's V. 0.15 were used to explain the observed transitions; the accuracy rates of the transition sub-models are given in electronic Supplementary Data S1, table 2. MLP procedure in LCM was then used to run the transition sub-models to empirically model future LULC. MLP used a backwards stepwise variable selection in which all variables are tested individually and in pairs for their impact on model accuracy and finally the likelihood of model overfitting is reduced by selecting an optimum number of variables to be included in the final model. When training and validating a transition sub-model, MLP makes use of sample pixels that have undergone a transition between the two time periods. By default, MLP takes 10 000 randomly selected pixels for running each transition sub-model. One half of these pixels is used to train the model, while the other half is used for model validation. At the end of each model training run, MLP generates accuracy results for each transition sub-model. The details of transition sub-models considered in this study and their respective accuracy are given in the electronic Supplementary Data, table 2. To project future changes, we generated a projected potential map—a map of the study area showing the potential of each pixel across the landscape to undergo each of the LULC transitions. The potential map was subsequently used to project LULC change to desired future date (2030).

2.4.4. Change Demand Modelling

In this step, we used the 'Change Demand Modelling' procedure in LCM to determine the amount of change that is likely to occur in selected LULC categories at some point in the future. By default, LCM uses a Markov chain prediction process which calculates the amount of change based on historical observations and determines the area of land expected to undergo such transition in the future. At this stage, LCM generates a transition potential file in the form of a matrix which shows the probability of each LULC category to change to every other category. This potential file matrix generated by Markov chain showing probabilities of all transitions for the year 2030 is shown in table 2. LCM allows the user to manipulate these transition probabilities to create different modelling scenarios in the future. In this study, the following two scenarios for LULC transitions by 2030 were considered.

2.4.4.1. The Business-as-Usual Scenario

This is the default scenario created in the Markov chain probability matrix. The business-as-usual (B-a-U) scenario represents a linear projection of current trends to 2030; the trends were identified and modelled based on changes observed between 2007 and 2015.

2.4.4.2. Ecosystem Conservation Scenario

By manipulating the transition probability matrix generated by the Change Demand Modelling panel, we created an ecosystem conservation (EC) scenario reflecting forestry and environmental policies currently in place:

(a) Conversion of conifer to broadleaf woodland in Wales would deliver a range of environmental benefits and is specifically required to deliver policies aimed at restoring PAWS. To accommodate these considerations in the EC scenario, we assumed that the probability of Conifer-to-Broadleaf Forest conversion would increase by 50% as compared to the current trend (B-a-U scenario).

(b) Conservation of ecologically important non-forest LULC categories such as Mountain, Heath and Bog is an integral part of Welsh forestry policy, for reasons of climate change in addition to biodiversity [53]. For this reason, we assumed that in 2015–2030, the probability of the LULC class 'Mountain, Heath and Bog' persisting itself will increase by 50% as compared to the current trend (B-a-U scenario).

(c) The Climate Change Strategy for Wales [20] inspired the Welsh Government to set a target of expanding existing Welsh woodland by 100 000 ha by 2030, although subsequently reduced to a minimum of 20 000 ha for this period [54]. Such expansion reflects wider aspirations for woodland expansion in the UK, e.g. in the 'UK 25 years environmental plan' [19]. We assumed, therefore, that the current trend of LULC classes such as Semi-Natural Grassland and Improved Grassland converting to Broadleaf Forest would continue, but Broadleaf Forest will not be converted to any other LULC category during 2015–2030.

Table 2. Markov chain transition probability matrix (business-as-usual scenario, ecosystem conservation scenario) showing probability of change to 2030 in Wales, UK.

Business-as-Usual Scenario

Given	*Probability of Changing to*					
	Broadleaf Forest	Conifer Forest	Arable Land	Improved Grassland	Semi-natural Grassland	Mountain, Heath, Bog
Broadleaf Forest	0.57	0.142	0.019	0.191	0.062	0.013
Conifer Forest	0.188	0.754	0.003	0.029	0.02	0.004
Arable Land	0.052	0.009	0.098	0.752	0.079	0.007
Improved Grassland	0.04	0.008	0.057	0.784	0.103	0.006
Semi Natural Grassland	0.073	0.049	0.034	0.411	0.381	0.051
Mountain, Heath & Bog	0.061	0.088	0.019	0.167	0.452	0.211

Ecosystem Conservation Scenario

Given	*Probability of Changing to*					
	Broadleaf Forest	Conifer Forest	Arable Land	Improved Grassland	Semi-natural Grassland	Mountain, Heath, Bog
Broadleaf Forest	1	0	0	0	0	0
Conifer Forest	0.282	0.659	0.003	0.029	0.02	0.004
Arable Land	0.052	0.009	0.098	0.752	0.079	0.007
Improved Grassland	0.04	0.008	0.057	0.784	0.103	0.006
Semi Natural Grassland	0.073	0.049	0.034	0.411	0.381	0.051
Mountain, Heath & Bog	0.061	0.088	0.019	0.167	0.347	0.316

2.5. Step 5: Change Projection

In the final step, we generated future LULC maps based on the transition probability matrices of the two scenarios considered in this study.

3. RESULTS

3.1. LULC Changes (2007–2015)

We computed LULC transitions between different LULC classes that have occurred in Wales, UK between 2007 and 2015 by applying the cross-tabulation module in LCM (Figure 1a). The predictor variables considered in this study explained the LULC transitions between 2007 and 2015 well; the average accuracy of all transition sub-models considered in this study was 79% (electronic Supplementary Data S1, table 2). An accuracy rate of 75% or above is considered indicative of good model performance (Clark Labs, 2015). Gains and losses between different LULC types and net change calculation (Figure 1a) show that 'Improved Grassland' and 'Broadleaf Forest' experienced the biggest expansion (148 521 and 39875 ha, respectively). Moreover, an analysis of contributions to the net change of individual LULC types (electronic Supplementary Data S1, Figure 1) suggests that the biggest contributor to 'Broadleaf Forest' during 2007–2015 is the 'Semi-Natural Grassland' category (19 589 ha). On the other hand, around 6458 ha of 'Broadleaf Forest' was lost to 'Coniferous Forest' during this time. Of the other major LULC changes in this period, around 80 778 ha of 'Semi-Natural Grassland' and 69 688 ha of 'Arable Land' were converted to 'Improved Grassland'. A visual overview of historical and projected spatial distribution of LULC transitions in Wales is presented in electronic Supplementary Data S1, Figure 2.

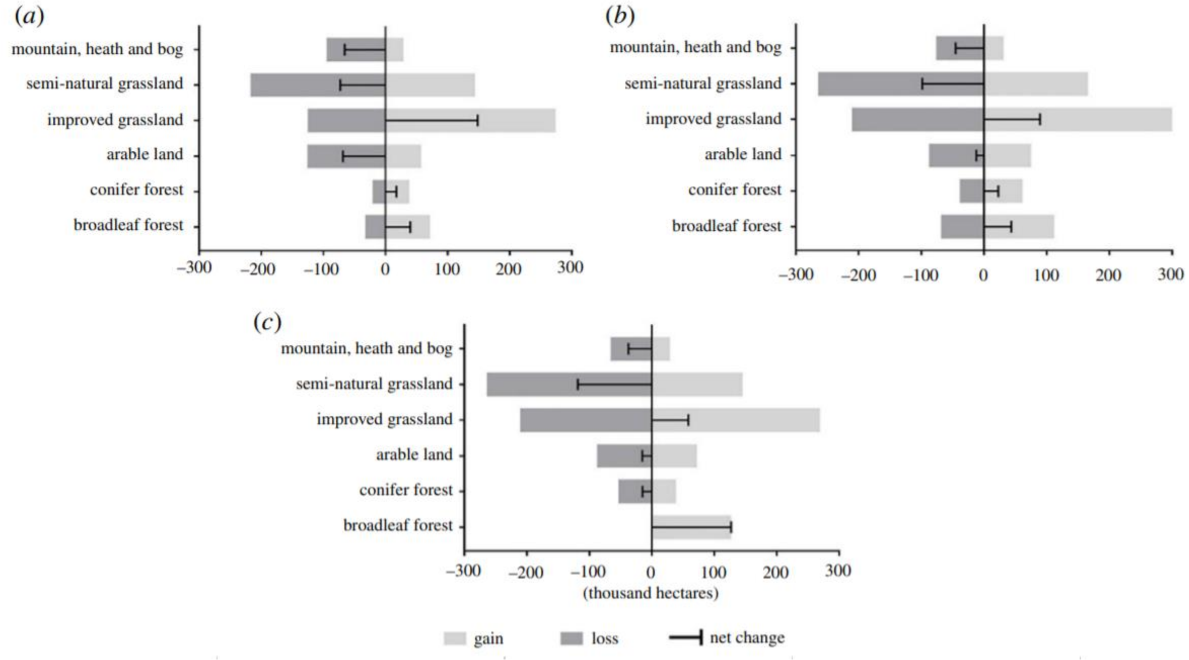

Figure 1. In Wales, UK, gains, losses and net changes between different LULC classes (hectares) during (a) 2007– 2015, (b) 2015 – 2030 (B-a-U scenario) and (c) 2015– 2030 (EC scenario).

3.2. Land Use Change Projections For 2030

3.2.1. The business-as-usual scenario

Based on LULC change observed over the period between 2007 and 2015, we generated a map showing projected LULC map of Wales for the year 2030 under the B-a-U scenario (Figure 2) which is based on the projected potential for transition in Wales (electronic Supplementary Data, table 2 and Figure 3). An analysis of the B-a-U scenario shows that the 'Broadleaf Forest' is likely to experience a net increase of 43 366 ha of area (Figure 1b), most of which is likely to come at the expense of 'Semi-Natural Grassland' (21 321 ha), 'Improved Grassland' (8815 ha) and 'Coniferous Forest' (7480 ha).

3.2.2. The Ecosystem Conservation Scenario

Projected transition potential map for the second scenario considered in this study is shown in Figure 5. An analysis of the LULC transition under this modelling scenario reveals that 'Broadleaf Forest' LULC category is expected to gain 127 129 ha of the area between 2015 and 2030 (Figure 1c). Most of the expansion in the area of 'Broadleaf Forest' under this modelling scenario is expected to come at the cost of 'Coniferous Forest' (45 322 ha), 'Improved Grassland' (39 494 ha) and 'Semi-Natural Grassland' (31 318 ha).

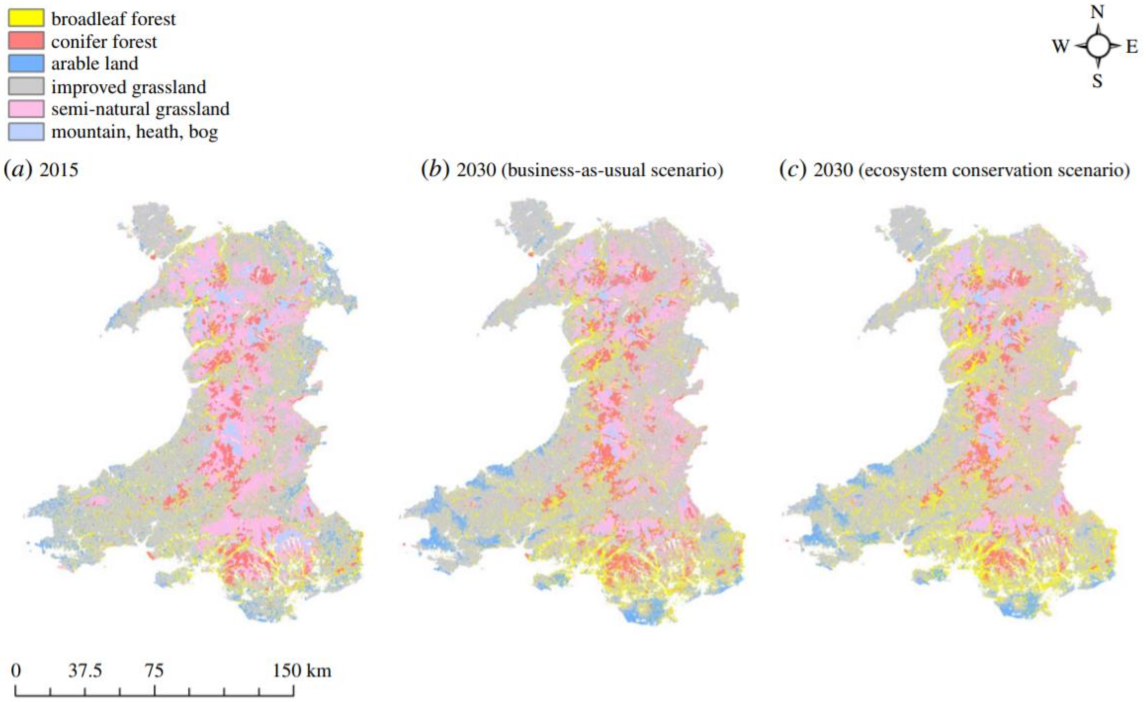

Figure 2. Current (a) and projected land use map of Wales, UK for the year 2030 under B-a-U (b) and EC (c) modelling scenarios.

3.3. State of Forests in Wales In 2030

Compared to the baseline of 159 951 ha in 2015, the 'Broadleaf Forest' category is likely to expand to 203 317 and 287 080 ha under the B-a-U and EC modelling scenarios, respectively. Existing conifer woodlands are expected to experience a conversion to broadleaf of 19% and 28% under the B-a-U and EC scenarios, respectively. The total forest area in Wales (combining broadleaf and conifer forests) is expected to increase by 66 358 and 112 280 ha under the B-a-U and EC scenarios, as compared to the total area under forests in 2015. Historically (2007–2015), most of the conversion took place in the south-eastern part of Wales. A slight modification of the geographical distribution of conversion is expected in both future scenarios modelled in this study: the contour map of conversion intensity indicates a westward and northward shift (Figure 3). As an example, showing projected change of the area of the broadleaf forest against topographic detail, we show the detail of an area of Snowdonia National Park in Wales in Figure 4.

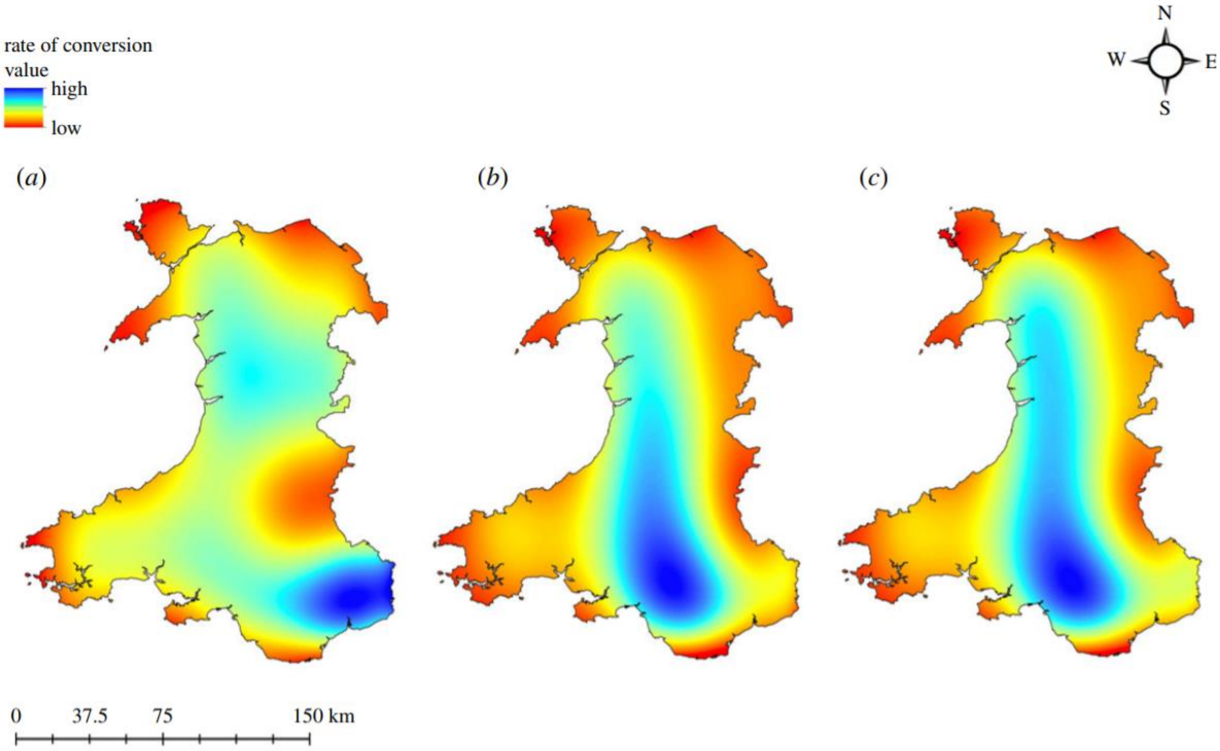

Figure 3. Spatial trend of conifer to broadleaf forest conversion in Wales, UK during 2007– 2015 (a), 2015– 2030 B-a-U scenario (b) and 2015– 2030 EC scenario (c).

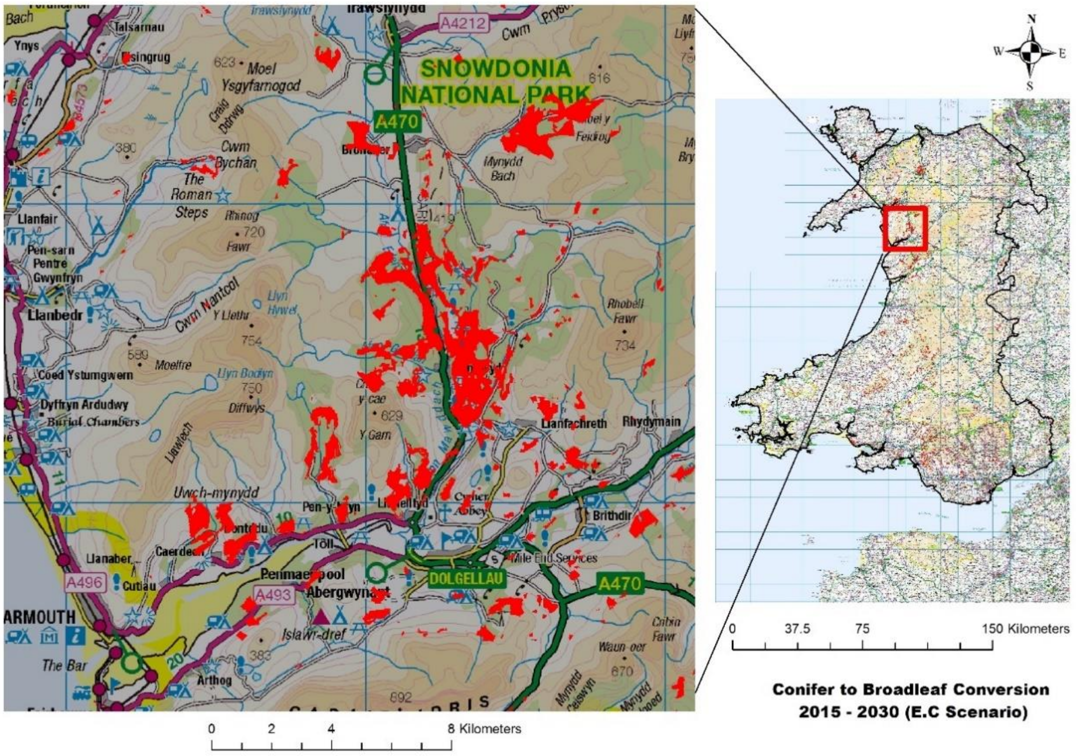

Figure 4. Projected conifer to broadleaf forest conversion in Wales during 2015 and 2030 under the EC modelling scenario. Broadleaf forest expansion in Snowdonia National Park is enlarged for detailed view (OS Crown copyright Edina Digimap).

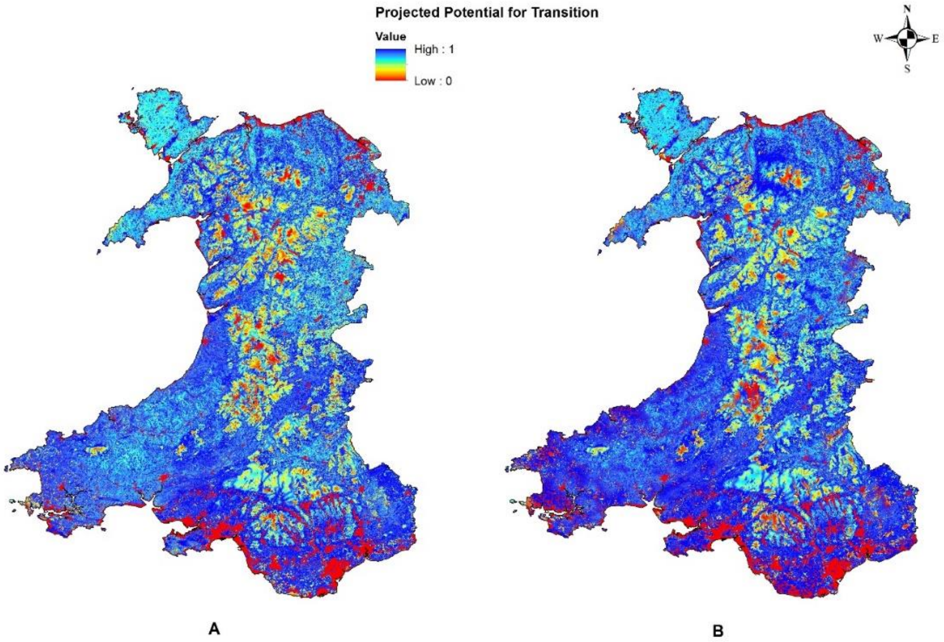

Figure 5. Projected potential for transition in Wales, UK for A. Business-As-Usual Scenario & B. Ecosystem Conservation Scenario, based on the land cover transition during 2007-2015. Areas coded with numbers 0 to 1 indicate minimum to maximum potential of transition in future.

4. DISCUSSION

Forests covered nearly 15% of the total area of Wales in 2015. Most Welsh forests were privately owned (59%), the remainder was owned by the Welsh Government Woodland Estate [55]. The forestry sector makes a significant contribution to the Welsh economy. Recent data (2015–2016) indicate that this sector contributes a gross value added of £528.6 million, supports around 700 businesses and provides over 10 000 jobs. Overall, the value of publicly owned forest in Wales in 2015 was estimated to be £642 million [55]. Besides their economic value, Welsh woodlands provide a range of ecosystem services by sequestering 1 419 000 tonnes of carbon dioxide equivalent per year and by playing a crucial role in soil and water management by reducing nutrient runoff, diffusing pollution, reducing flood risk and improving water quality [18]. Recent forest planting in Wales, however, has changed its focus from the twentieth century, the planting of broadleaf tree species increasing in comparison to conifers. Since 2001, the estimated area under conifer forests has decreased by 18 000 ha, while the estimated area under broadleaf species has increased by 35 000 ha [56]. The forested land area in Wales is very low for a European country, the average forest cover in Europe being 37% [18]. In order to increase the amount of land under forests, with the main motivation being ecosystem service provision, the Climate Change Strategy for Wales prompted the Welsh Government to set a target of increasing forest from 15% up to 19%; because of perceived the low levels of planting this target has been progressively reduced, and currently is the equivalent 20 000 ha by 2030 [54]. At the same time, the conversion of non-native conifers to native broadleaf species, primarily in the PAWS, is an aim of the UKFS [53]. In our B-a-U scenario, we found that if the current rate of change continues, the total forest area in Wales by 2030 is likely to increase from current 15 to 17%. However, in the EC scenario where the rates of afforestation and conversion to broadleaf are prioritized, future forest cover could reach the original target: 19% of the total Welsh area. This is considerably in excess of Welsh Government's revised target. This disparity is interesting and highlights the need for more informed projections of forest cover to help set policy targets. Historical conifer-to-broadleaf conversion rate projected to 2030 indicates that about 19% of existing conifers will undergo conversion, the EC scenario increases the rate by half to 28%. In standard forestry practice in Wales, where the average rotation of non-native conifers in Wales is about 60 years, the expectation is to harvest one-sixth of these woodlands every decade. The modelled B-a-U conversion rate of 19% is thus very close to the natural rotation harvest and replanting. Aiming for a higher conversion rate by 2030 implies shortening the rotation in some forests.

Although the major policy driver of conifer-to-broadleaf woodland conversion in Wales is PAWS, there are other factors that may motivate this type of conversion. For instance, the UKFS encourages diversifying forested areas in a way that a forest management unit should have at least 5% of native broadleaf trees species and should not contain more than 75% of a single species. The UKFS guidelines also advocate large-scale conversion in areas with the potential to enhance existing ancient semi-natural woodlands and on sites which are sufficiently large to overcome edge effects [53]. In a survey of private woodland managers in England, Scotland and Wales tasked with managing planted non-native conifer woodlands (but excluding PAWS), the managers were interviewed about their intentions regarding conversion to broadleaves and the reasons behind their plans. The results suggested that woodland managers are considering a conversion of anywhere between 5 and 95% of their woodlands from conifers to native broadleaf forest, even if not required to do so by environmental policy. Those willing to convert indicated biodiversity conservation, improved resilience and recreation as the chief factors behind their intention, while those unwilling to make large-scale conversions mentioned timber production, cost of conversion and—crucially—lack of guidance and advice [9].

In the recent past, considerable research has been carried out to improve understanding of costs and benefit of converting PAWS to the native broadleaf forest; however, no dedicated effort has been made on the conversion of non-PAWS, leaving a potential research gap [9]. Since the conversion needs to be gradual and well planned [9][57], our study presents a useful spatially explicit decision-making aid that pinpoints sites most suitable for conifer-to-broadleaf conversion across Wales. Projected maps of conifer-to-broadleaf conversion may also prove useful for forest managers who are hesitant of conversion by indicating site suitability on the basis of past experience. Concerns such as suitability of site and distance to already existing broadleaf seed source have been indicated by forest managers [9];

our projected LULC models address these concerns as we incorporate past LULC changes, soil factors, slope, water availability, road access and distance to the broadleaf forest as predictor variables in the models.

Analysis of the conifer-to-broadleaf forest conversion between 2007 and 2015 indicated that altitude is the most influential factor, altitude alone resulting in an accuracy of 80% of the 'conifer forest to broadleaf forest' sub-model. Most of the transitions from conifer plantation to broadleaf forests in Wales took place between altitudes of 100 and 250 m. Conversion was minimal close to sea level and above 275 m. Most of the land between 0 and 100 m of altitude is dedicated to agriculture and grasslands, while forests are less likely to occur above 275 m in Wales as land use above this altitude predominantly belongs to the Mountain, Heath and Bog category. In addition to altitude, the distance from roads made a notable contribution in explaining the conifer-to-broadleaf conversion between 2007 and 2015. Most of the conifers converted to broadleaves were located in areas 200–300 m from a road. Habitat expansion or restoration activity is more likely to be within 1 km of the road network as easy and frequent access is generally possible in this range [52].

One of the motivations for designing the EC scenario in this study was conservation of the 'Mountain, Heath and Bog' habitat. Heaths and peat bogs include all inland and coastal, dry and wet heaths and mires [58]. These are some of Britain's most scarce habitats having a unique ecological value as these habitat types support a range of animals, insects and plants and provide food and shelter to migrating birds [59]. Moreover, heath and peat bogs—which can be thousands of years old—contain a wealth of historical data on climate, landscape and biodiversity. A study in 1995 had indicated that around 20% of upland heather moorland present in England and Wales in the mid-1940s was lost by 1990, high grazing pressure being one of the chief reasons for this loss [59].

A recent study modelled species richness in heath and peat bog habitat in the UK and warned of major declines in this habitat by 2030 [58]. Our data show that 70% of Welsh heather moorland present in 1990s is 'at risk of change' in future. During 2007–2015, 40% of 'Mountain, Heath and Bog' was lost, three-quarters of the loss due to the conversion to 'Semi-Natural Grassland' category. Under the B-a-U scenario, 47% of the 2015 area under this LULC class is likely to be lost by 2030. Under the EC scenario—where we increased the probability of 'Mountain, Heath and Bog' to persist by 50%—we still saw a 38% loss. This indication of serious threats to 'Mountain, Heath and Bog' habitat suggests that major interventions are required to conserve this highly valuable and scarce habitat.

4.1. Applications of Future Land Use and Land Cover Maps for Ecosystem Services and Biodiversity Analysis in Wales

In addition to the utility as a decision support tool for broadleaf forest expansion in Wales, the output LULC maps of this study can be used for a range of habitat, ecosystem services and biodiversity analysis, some of which are discussed in the following.

4.1.1. Modelling the Abundance of Crop Pollinators

It is estimated that 20% of agricultural crops in the UK depend on pollinators; the economic value of pollinators to UK agriculture is estimated to be £690 million per year **[61].** The National Ecosystem Assessment showed that the abundance of wild pollinators in the UK has declined in the last 30 years and this trend is likely to continue [60]**.** In Wales, the declining abundance of pollinators is an increasingly important issue and several action plans have been proposed in the recent past to conserve pollinators [61][62]**.** The future LULC maps of Wales can be used to evaluate the likely effects of contrasting LULC scenarios on the future abundance of wild bees as pollinators for agricultural crops. The abundance of wild bees largely depends on factors like nesting site availability and flight range, and models based on current and future LULC maps can be used to estimate the number of wild bees visiting agricultural sites and identifying areas that are likely to gain the most benefits from wild pollination [47]**.**

4.1.2. Predicting Carbon Storage and Sequestration

The Welsh Government has a commitment to reduce annual carbon equivalent emissions by 3% per annum [63][64]. In this regard, monitoring the rates of carbon emissions and sequestration is a challenge. Carbon sequestration models are being used to estimate future carbon stocks and rates of sequestration [65]**.** The future LULC maps of Wales can be used to estimate future amounts of carbon stored in the landscape and sequestered over time. Current and future LULC maps along with rates of wood harvest, degradation rates of harvested products and carbon stocks in the current LULC classes can be used to calculate carbon storage and sequestration. Additionally, these maps can also be used to calculate the market value of sequestered carbon in current and future land cover of Wales [47].

4.1.3. Future Landscape Change Process Analysis

As stated in the State of Nature (2016) report for Wales, major changes in ecosystem services and abundance of species have occurred due to degradation and fragmentation of habitat in Wales [66]. Current and projected future LULC maps of Wales can be used to measure the nature of the change underway within each land use class under different policy scenarios of broadleaf forest expansion in Wales. In spatial analysis environments such as TerrSet, it is done by using a decision tree method that compares the land cover patches in each LULC category between the two time periods and calculates the changes in the perimeter and area of the corresponding patches [47]. The output map helps visualizing where in future a given LULC category is likely to experience persistence, fragmentation or aggregation of patches. In the context of Wales where there is a major drive to conserve and repair rare natural habitat such as bogs, this could be an important analysis as it would allow one to visualize the nature of landscape change that might occur under different future land use change scenarios.

4.1.4. Invasive Species Distribution Modelling in Wales

Invasive species are major drivers of ecosystem degradation in Wales costing the Welsh economy approximately £7 million per annum [67]. Predicting the future distribution of invasive species is key to effective invasive species management and planning [68]. Future distribution of invasive species is often governed by land cover type. Evidence suggests that in Wales the spread of invasive species such as *Rhododendron ponticum* is more sensitive to the land cover type than any other biophysical or climatic factor [68]. The projected future maps of our study can be used to run species distribution models of different invasive as well as any other species of interest. Contrasting the future scenarios may help understand how the different policy approaches are likely to affect the course of invasive species distribution in Wales.

4.2. Limitations of The Study

Explanatory variables used in land use change modelling studies are generally divided into three categories: biophysical, proximate and socio-economic variables [42]. In this study, we did not include socio-economic variables (e.g. GDP, population density, etc.) owing to the coarse resolution of available datasets. Instead, we preserved the fine spatial resolution of biophysical and proximate variables which are likely to be stronger determinants of land use change and reasonable proxies for the socio-economic variables. However, it is advisable to bear in mind that the resulting future projection does not directly represent the socio-economic landscape. Availability of fine-scale socio-economic and climatic variables may improve the modelling outputs in the future. Moreover, we used LULC maps generated by the Centre for Ecology & Hydrology, UK [41] which, to the best of our knowledge, are currently the most accurate, verified and finest-resolution LULC temporally repeated maps covering the UK. The fact that we used only two time points is a limitation of our study; we did not have a map of LULC after 2015 that could have been used for verification of the future projection. Although we adopted published protocols for future LULC projections [69][70], we suggest that the use of three or more historical LULC time points be considered for verification of projections. As we gather more archived LULC data, this approach should become the norm. Finally, a key limitation of this type of analysis is its ‘blindness’ to major shifts of socio-economic landscape and hence its inability to factor these into projections. A case in point is Brexit, where a set of self-imposed trade sanctions threatens a severe adjustment of existing drivers of land use.

CONCLUSION

This study reveals the changes in LULC in Wales from 2007 to 2015 by using a combined approach of GIS and land change prediction models. An integrated MLP–MCA method was applied to improve understanding of the scale and location of probable LULC changes under linear projection (B-a-U) and a policy-based future scenario (EC) up to 2030. Broadleaf forest expansion is likely to reach the targets set by the Welsh Government under the EC scenario. The study shows the potential of LULC predictions to test alternative policy aims and to generate evidence at a scale useful to local decision makers. This type of tool can contribute to sustainable development by providing an evidence-based spatial framework to support restoration and conservation of ecologically important habitats in Wales. Since land use and land cover change is a highly complex phenomenon affected by a range of ecological, political and socioeconomic factors, we contend that models incorporating the widest range of factors be used to test future LULC scenarios.

SUPPLEMENTARY DATA S1

Table S1. Actual and revised land use classes in the historical land use maps of Wales. Column 1 & 2 show the default legends of the land use maps acquired from Edina Digimap. Column 3 shows the harmonized/revised land use classes. Column 4 shows the finally selected land use classes for the model.

Land use Map 2015	**Land use Map 2007**	**Revised/Harmonized Land use Categories**	**Land use Categories Used in the Model**
Broadleaved woodland	Broadleaved, mixed and yew woodland	Broadleaved woodland	Broadleaved woodland
Coniferous woodland	Coniferous woodland	Coniferous woodland	Coniferous woodland
Arable and horticulture	Arable and horticulture	Arable and horticulture	Arable and horticulture
Improved grassland	Improved grassland	Improved grassland	Improved grassland
Neutral grassland	Rough grassland	Semi-Natural grassland	Semi-Natural grassland
Calcareous grassland	Neutral grassland		
Acid grassland	Calcareous grassland		
Fen, Marsh and Swamp	Acid grassland		
Heather	Fen, marsh and swamp	Mountain, Heath, Bog	Mountain, Heath, Bog
Heather grassland	Heather		
Bog	Heather grassland		
Inland rock	Bog		
Saltwater	Montane habitats	Water Bodies	*Category Excluded*
Freshwater	Inland rock		
Supra-littoral rock	Saltwater	Coastal	*Category Excluded*
Supra-littoral sediment	Freshwater		
Littoral rock	Supra-littoral rock		
Littoral sediment	Supra-littoral sediment		
Saltmarsh	Littoral rock		
Urban	Littoral sediment	Built Areas	*Category Excluded*
Suburban	Saltmarsh		
	Urban		
	Sub-Urban		

Table S2. Transition sub-models in the study. Accuracy rate determines the precision with which the sub models were trained and validated.

	Sub model	Accuracy Rate (%)
1	Broadleaf Forest to Conifer Forest	78.56
2	Broadleaf Forest to Arable Land	75.41
3	Broadleaf Forest to Improved Grassland	50.06
4	Broadleaf Forest to Semi Natural Grassland	50.07
5	Broadleaf Forest to Mountain, Heath & Bog	81.85
6	Conifer Forest to Broadleaf Forest	85.47
7	Conifer Forest to Improved Grassland	83.35
8	Conifer Forest to Semi Natural Grassland	70.27
9	Arable Land to Broadleaf Forest	76.81
10	Arable Land to Conifer Forest	93.29
11	Arable Land to Improved Grassland	68.4
12	Arable Land to Semi Natural Grassland	88.7
13	Arable Land to Mountain, Heath & Bog	78.4
14	Improved Grassland to Broadleaf Forest	70.35
15	Improved Grassland to Conifer Forest	80.02
16	Improved Grassland to Arable Land	69.3
17	Improved Grassland to Semi Natural Grassland	88.27
18	Improved Grassland to Mountain, Heath & Bog	75.74
19	Semi Natural Grassland to Broadleaf Forest	91.81
20	Semi Natural Grassland to Conifer Forest	72.28
21	Semi Natural Grassland to Arable Land	95.94
22	Semi Natural Grassland to Improved Grassland	89.33
23	Semi Natural Grassland to Mountain, Heath & Bog	68.87
24	Mountain Heath & Bog to Broadleaf Forest	93.75
25	Mountain Heath & Bog to Conifer Forest	78.88
26	Mountain, Heath & Bog to Arable Land	93.91
27	Mountain, Heath & Bog to Improved Grassland	92.74
28	Mountain, Heath & Bog to Semi Natural Grassland	65.13

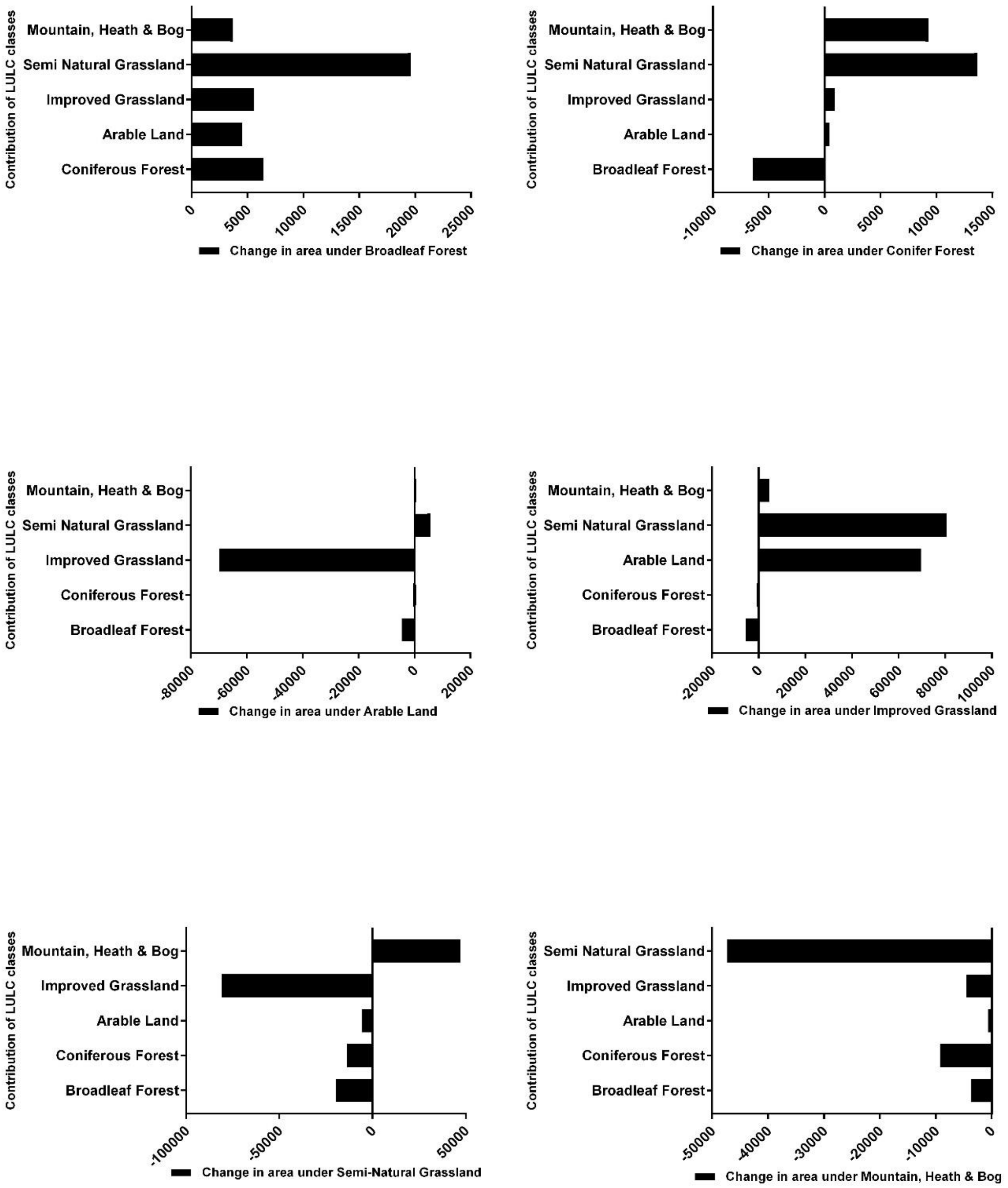

Figure 1. Contributions to net change in Broadleaf Forest, Coniferous Forests, Arable Land, Improved Grasslands, Semi Natural Grasslands and Mountain, Health & Bog in Wales, UK during 2007-2015 (hectares).

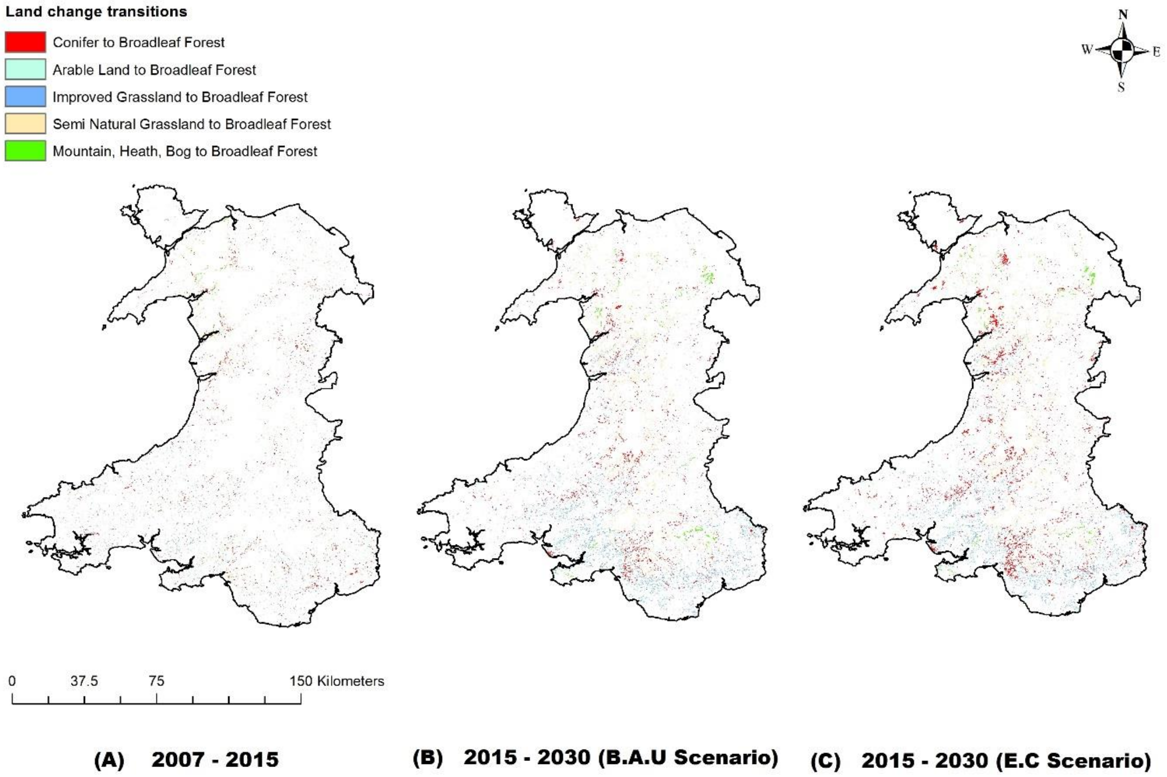

Figure 2. Historical land use transition maps for Wales between 2007 and 2015 (A), predicted land use transition from 2015 to 2030 under the Business-as-Usual scenario (B) and Ecosystem conservation scenario (C).

REFERENCES

1. Liu, Y.Y.; Van Dijk, A.I.J.M.; De Jeu, R.A.M.; Canadell, J.G.; McCabe, M.F.; Evans, J.P.; Wang, G. Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Chang.* **2015**, *5*, 470–474.
2. Lavorel, S.; Grigulis, K.; Leitinger, G.; Kohler, M.; Schirpke, U.; Tappeiner, U. Historical trajectories in land use pattern and grassland ecosystem services in two European alpine landscapes. *Reg. Environ. Chang.* **2017**, *17*, 2251–2264.
3. FAO Global Forest Resources Assessment 2010. *FAO For. Pap.* **2010**, *163*, 350 pp.
4. Forestry Commission NFI 2011 woodland map GB 2013.
5. Quine, C.P.; Bailey, S.A.; Watts, K. PRACTITIONER'S PERSPECTIVE: Sustainable forest management in a time of ecosystem services frameworks: Common ground and consequences. *J. Appl. Ecol.* **2013**, *50*, 863–867.
6. Blackstock, T.; Howe, E. a.; Stevens, J.; Howe, L.; Jones, P. Habitats of Wales: A Comprehensive Field Survey, 1979-1997 2010, 240.
7. Procter, D.S.; Cottrell, J.; Watts, K.; Robinson, E.J.H. Do non-native conifer plantations provide benefits for a native forest specialist, the wood ant Formica lugubris? *For. Ecol. Manage.* **2015**, *357*, 22–32.
8. Eşen, D.; Zedaker, S.M.; Kirwan, J.L.; Mou, P. Soil and site factors influencing purple-flowered rhododendron (*Rhododendron ponticum* L.) and eastern beech forests (Fagus orientalis Lipsky) in Turkey. *For. Ecol. Manage.* **2004**, *203*, 229–240.
9. Barsoum, N.; Henderson, L. Converting planted non-native conifer to native woodlands: a review of the benefits, drawbacks and experience in Britain. **2016**, 1–10.
10. Brandtberg, P.O.; Lundkvist, H.; Bengtsson, J. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. *For. Ecol. Manage.* **2000**, *130*, 253–264.
11. Crawford, R.M.M.; Jeffree, C.E.; Rees, W.G. Paludification and forest retreat in northern oceanic environments. *Ann. Bot.* **2003**, *91*, 213–226.
12. Morison, J.; Matthews, R.; Miller, G.; Perks, M.; Randle, T.; Vanguelova, E.; White, M.; Yamulki, S. *Understanding the carbon and greenhouse gas balance of forests in Britain.*; 2012; ISBN 9780855388553.
13. Gärtner, S.; Reif, A. The response of ground vegetation to structural change during forest conversion in the southern Black Forest. *Eur. J. For. Res.* **2005**, *124*, 221–231.
14. Sweeney, O.F.M.D.; Wilson, M.W.; Irwin, S.; Kelly, T.C.; O'Halloran, J. The influence of a native tree species mix component on bird communities in non-native coniferous plantations in Ireland. *Bird Study* **2010**, *57*, 483–494.
15. Brockerhoff, H.J. and E.G. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* **2007**, *10*, 835–848.
16. Haas, S.E.; Hooten, M.B.; Rizzo, D.M.; Meentemeyer, R.K. Forest species diversity reduces disease risk in a generalist plant pathogen invasion. *Ecol. Lett.* **2011**, *14*, 1108–1116.
17. Edwards, D.; Jay, M.; Jensen, F.S.; Lucas, B.; Marzano, M.; Montagné, C.; Peace, A.; Weiss, G. Public preferences for structural attributes of forests: Towards a pan-European perspective. *For. Policy Econ.* **2012**, *19*, 12–19.
18. Welsh Government Woodlands for Wales, The Welsh assembly government's startegy for woodlands and trees. **2009**, 57.
19. HM Government 25-Year-Environment-Plan. **2018**, 1–151.
20. Government, W.A. Climate Change Strategy for Wales. *Business* **2010**.
21. NRW A summary of the State of Natural Resources Report : **2016**.
22. Yanhui, W.; Bonell, M.; Feger, K.-H.; Pengtao, Y.; Wei, X.; Lihong, X. Changing Forestry Policy by Integrating Water Aspects into Forest/Vegetation Restoration in Dryland Areas in China. *Bull. Chinese Acad. Sci. Agric. Water Ecol. Bull. Chinese Acad. Sci. BCAS* **2012**, *2626*, 59–67.
23. Chappell, N.A. "Forests and floods: Moving to an evidence-based approach to watershed and integrated flood management" by Ian R. Calder (UK) and Bruce Aylward (USA). *Water Int.*

2006, *31*, 541–543.

24. Kamusoko, C.; Wada, Y.; Furuya, T.; Tomimura, S.; Nasu, M.; Homsysavath, K. Simulating Future Forest Cover Changes in Pakxeng District, Lao People's Democratic Republic (PDR): Implications for Sustainable Forest Management. *Land* **2013**, *2*, 1–19.
25. Soares-Filho, B.S.; Nepstad, D.C.; Curran, L.M.; Cerqueira, G.C.; Garcia, R.A.; Ramos, C.A.; Voll, E.; McDonald, A.; Lefebvre, P.; Schlesinger, P. Modelling conservation in the Amazon basin. *Nature* **2006**, *440*, 520–523.
26. Koomen, E.; Koekoek, A.; Dijk, E. Simulating Land-use Change in a Regional Planning Context. *Appl. Spat. Anal. Policy* **2011**, *4*, 223–247.
27. GoL Forestry Strategy to the Year 2020. *Vientiane Lao PDR* **2005**, 1–89.
28. Buenemann, M.; Martius, C.; Jones, J.W.; Herrmann, S.M.; Klein, D.; Mulligan, M.; Reed, M.S.; Winslow, M.; Washington-Allen, R.A.; Lal, R.; et al. Integrative geospatial approaches for the comprehensive monitoring and assessment of land management sustainability: Rationale, Potentials, and Characteristics. *L. Degrad. Dev.* **2011**, *22*, 226–239.
29. Mishra, V.N.; Rai, P.K. A remote sensing aided multi-layer perceptron-Markov chain analysis for land use and land cover change prediction in Patna district (Bihar), India. *Arab. J. Geosci.* **2016**, *9*.
30. Zhang, Q.; Ban, Y.; Liu, J.; Hu, Y. Simulation and analysis of urban growth scenarios for the Greater Shanghai Area, China. *Comput. Environ. Urban Syst.* **2011**, *35*, 126–139.
31. Nasiri, V.; Darvishsefat, A.A.; Rafiee, R.; Shirvany, A.; Hemat, M.A. Land use change modelling through an integrated Multi-Layer Perceptron Neural Network and Markov Chain analysis (case study: Arasbaran region, Iran). *J. For. Res.* **2018**.
32. Ahmed, B.; Ahmed, R. Modelling Urban Land Cover Growth Dynamics Using Multi-Temporal Satellite Images: A Case Study of Dhaka, Bangladesh. *ISPRS Int. J. Geo-Information* **2012**, *1*, 3–31.
33. Ozturk, D. Urban growth simulation of Atakum (Samsun, Turkey) using cellular automata-Markov chain and Multi-layer Perceptron-Markov chain models. *Remote Sens.* **2015**, *7*, 5918–5950.
34. Sleeter, B.M.; Sohl, T.L.; Bouchard, M.A.; Reker, R.R.; Soulard, C.E.; Acevedo, W.; Griffith, G.E.; Sleeter, R.R.; Auch, R.F.; Sayler, K.L.; et al. Scenarios of land use and land cover change in the conterminous United States : Utilizing the special report on emission scenarios at ecoregional scales. *Glob. Environ. Chang.* **2012**, *22*, 896–914.
35. *Statistical Bulletin: Annual Mid year Population Estimates: 2013*; 2014;
36. Swetnam, R.D.; Tweed, F.S. A tale of two landscapes: Transferring landscape quality metrics from Wales to Iceland. *Land use policy* **2018**, 0–1.
37. Forestry Commission Chapter 1: Woodland Areas and Planting. *For. Stat. 2017* **2017**, 37.
38. Research Service Natural Resources Wales Forestry in Wales Quick Guide. *For. Comm. For. Stat.* **2013**, 1–5.
39. Park, C.; Park, T. Review of Land Use Climate Change An assessment of the evidence base for climate change action in the agriculture , land use and wider foodchain sectors in Wales. **2014**.
40. Clark Labs TerrSet Tutorial; Clark Labs, Clark University: Worcester, MA, USA, 2015 2015.
41. Morton, D.; Rowland, C.; Wood, C.; Meek, L.; Marston, C.; Smith, G.; Wadsworth, R.; Simpson, I.C. Countryside Survey: Final Report for LCM2007 – the new UK Land Cover Map. *Countrys. Surv. Tech. Rep. No 11/07 NERC/Centre Ecol. Hydrol.* **2011**, 112 (CEH Project Number: C03259).
42. Verburg, P.H.; Schot, P.P.; Dijst, M.J.; Veldkamp, A. Land use change modelling: Current practice and research priorities. *GeoJournal* **2004**, *61*, 309–324.
43. Manzoor, S.A.; Griffiths, G.; Lukac, M. Species distribution model transferability and model grain size – finer may not always be better. *Sci. Rep.* **2018**, 1–9.
44. Hou, J.; Wu, W.; Lin, Y.; Wang, J.; Zhou, D.; Guo, J.; Gu, S.; He, M.; Ahmed, S.; Hu, J.; et al. Localization of cerebral functional deficits in patients with obsessive-compulsive disorder: A resting-state fMRI study. *J. Affect. Disord.* **2012**, *138*, 313–321.

45. Megahed, Y.; Cabral, P.; Silva, J.; Caetano, M. Land Cover Mapping Analysis and Urban Growth Modelling Using Remote Sensing Techniques in Greater Cairo Region—Egypt. *ISPRS Int. J. Geo-Information* **2015**, *4*, 1750–1769.
46. Verburg, P.H.; Ritsema van Eck, J.R.; de Nijs, T.C.M.; Dijst, M.J.; Schot, P. Determinants of land-use change patterns in the Netherlands. *Environ. Plan. B Plan. Des.* **2004**, *31*, 125–150.
47. Eastman, J.R. Guide to GIS and Image Processing. *Clark Univ. Worcester, MA, USA* **2006**, *1*, 87–131.
48. Laine, T.; Busemeyer, J. Comparing Agent-Based Learning Models of Land-Use Decision Making. In Proceedings of the Iccm; 2004; pp. 142–147.
49. Romano, G.; Abdelwahab, O.M.M.; Gentile, F. Modelling land use changes and their impact on sediment load in a Mediterranean watershed. *Catena* **2018**, *163*, 342–353.
50. Beygi Heidarlou, H.; Banj Shafiei, A.; Erfanian, M.; Tayyebi, A.; Alijanpour, A. Effects of preservation policy on land use changes in Iranian Northern Zagros forests. *Land use policy* **2019**, *81*, 76–90.
51. Dadhich, P.N.; Hanaoka, S. Markov Method Integration with Multi-layer Perceptron Classifier for Simulation of Urban Growth of Jaipur City. *6th Wseas Int. Conf. Remote Sens. , Iwate Prefect. Univ. Japan* **2010**, 118–123.
52. Iizuka, K.; Johnson, B.A.; Onishi, A.; Magcale-Macandog, D.B.; Endo, I.; Bragais, M. Modelling Future Urban Sprawl and Landscape Change in the Laguna de Bay Area, Philippines. *Land* **2017**, *6*, 26.
53. Forestry Commission *The UK Forestry Standard*; 2011; ISBN 9780855388300.
54. Wales, F. commission *Woodlands for Wales*; 2018; ISBN 9781473456464.
55. Warren-Thomas, Eleanor Henderson, E. Woodlands in Wales: a quick guide. **2017**.
56. Forestry Commission *Woodlands for Wales Indicators 2015-16*; 2016; ISBN 9781473456464.
57. Harmer, R.; Morgan, G. Storm damage and the conversion of conifer plantations to native broadleaved woodland. *For. Ecol. Manage.* **2009**, *258*, 879–886.
58. Stevens, C.J.; Payne, R.J.; Kimberley, A.; Smart, S.M. How will the semi-natural vegetation of the UK have changed by 2030 given likely changes in nitrogen deposition? *Environ. Pollut.* **2016**, *208*, 879–889.
59. Thompson, D.B.A.; MacDonald, A.J.; Marsden, J.H.; Galbraith, C.A. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biol. Conserv.* **1995**, *71*, 163–178.
60. Polce, C.; Termansen, M.; Aguirre-Gutiérrez, J.; Boatman, N.D.; Budge, G.E.; Crowe, A.; Garratt, M.P.; Pietravalle, S.; Potts, S.G.; Ramirez, J.A.; et al. Species Distribution Models for Crop Pollination: A Modelling Framework Applied to Great Britain. *PLoS One* **2013**, *8*.
61. Biodiversity and Nature Conservation Branch Welsh Government The Action Plan for Pollinators in Wales.; 2013; p. 28.
62. TACP *Green Infrastructure Action Plan for Pollinators in South-east Wales*; 2015;
63. Georgakaki, A.; Ghandi, K.; Eames, M.; Kerr, N.; Gouldson, A. Scenario Modelling for a Low Carbon Wales. **2013**.
64. Committee for Climate Change Building a low-carbon economy in Wales Setting Welsh carbon targets. **2017**.
65. Quijas, S.; Boit, A.; Thonicke, K.; Murray-Tortarolo, G.; Mwampamba, T.; Skutsch, M.; Simoes, M.; Ascarrunz, N.; Peña-Claros, M.; Jones, L.; et al. Modelling carbon stock and carbon sequestration ecosystem services for policy design: a comprehensive approach using a dynamic vegetation model. *Ecosyst. People* **2019**, *15*, 42–60.
66. State of Nature 2016. **2016**.
67. Snowdonia Rhododendron Partnership The Ecosystem Benefits of managing the invasive non–native plant *Rhododendron ponticum* in Snowdonia Snowdonia Rhododendron Partnership 2015 Rhododendron in Snowdonia. **2015**.
68. Manzoor, S.A.; Griffiths, G.; Iizuka, K.; Lukac, M. Land Cover and Climate Change May Limit

Invasiveness of *Rhododendron ponticum* in Wales. *Front. plant Sci. Pap.* **2018**, *9*.

69. Uddin, K.; Chaudhary, S.; Chettri, N.; Kotru, R.; Murthy, M.; Chaudhary, R.P.; Ning, W.; Shrestha, S.M.; Gautam, S.K. The changing land cover and fragmenting forest on the Roof of the World: A case study in Nepal's Kailash Sacred Landscape. *Landsc. Urban Plan.* **2015**, *141*, 1–10.
70. Ye, X.; Yu, X.; Yu, C.; Tayibazhaer, A.; Xu, F.; Skidmore, A.K.; Wang, T. Impacts of future climate and land cover changes on threatened mammals in the semi-arid Chinese Altai Mountains. *Sci. Total Environ.* **2018**, *612*, 775–7

EVIDENCE OF ECOLOGICAL NICHE SHIFT IN *RHODODENDRON PONTICUM* (L.) IN BRITAIN: HYBRIDIZATION AS A POSSIBLE CAUSE OF RAPID NICHE EXPANSION

ABSTRACT

Biological invasions threaten global biodiversity and natural resources. Anticipating future invasions is central to strategies for combating the spread of invasive species. Species distribution models are thus increasingly used to predict potential distribution of invasive species. A critical assumption in species distribution models is that the ecological niche of species is conserved. However, recent studies suggest that this assumption is not valid for all species. In this study, we compare ecological niches of *Rhododendron ponticum* in its native (Iberian Peninsula) and invasive (Britain) ranges**.** Here we test the conservation of ecological niche between invasive and native populations of *R. ponticum* using principal component analysis, niche dynamics analysis and MaxEnt-based reciprocal niche modelling. We show that the two niches and not equivalent and are dissimilar, leading us to conclude that this species has occupied novel environmental conditions in Britain. We then frame our results in the context of contradicting genetic evidence on possible hybridization of this invasive species in Britain.

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Ecological Niche Shift in Rhododendron

1. INTRODUCTION

Uncontrolled biological invasions by plants are among the most severe phenomena attributable to climate change and environmental disturbance by humans [1]. Invasive species replace native vegetation, which often leads to an alteration of ecosystem structure and function due to the simplification of plant community. Invasion may cause a disruption of nutrient cycles, reduction of soil health and a decrease of net primary productivity [2]. Understanding the factors that define the geographic range of a species, and prevent it from invading other environments, is one of the fundamental goals in ecology. Niche theory suggests that the area occupied by a species is defined by a set of biotic and abiotic factors and dispersal barriers. Successful biological invasions must thus be facilitated by a sequence of events. Breaching a dispersal barrier must be supported by climatic similarity between the native and invasive (also referred to as invaded, introduced or exotic) ranges and followed by attaining a competitive advantage against native species [1][3]. In most invasive species, however, the relative contribution of these factors to the shaping of range limits is not clearly understood [1]. A standard approach to studying invasive species' niche is to analyse the similarity of environmental conditions between the native and invasive ranges, as the correlation between the environment and the observed distribution of species is considered pivotal to species' introduction, establishment, and expansion in new environments [4][5].

Anticipating the spread of invasive species is central to the creation and application of effective management strategies [6]. Species distribution models (SDMs) are by far the most widely used predictive tool used to assess invasiveness of species [7]. The predictive power of SDMs rests upon the assumption that the relationship between a species and its ecological niche is conservative over space and time (i.e., the fundamental niche remains unchanged or changes very slowly due to evolution) [1][4][8]. This assumption, known as the niche conservatism hypothesis, implies that a species in the invasive range is likely to occupy environmental conditions similar to those typical for its native range [9]. Modern SDMs, and the increasing availability of species presence data, offer an opportunity to test this hypothesis. This endeavour is interesting for two reasons; (i) a significant violation of niche conservatism in a species is a strong indicator of adaptive [10] or evolutionary [11] changes during the invasion and (ii) in an era of rapid environmental change, improved understanding of if and when an environment suitable for an invasion will appear may be crucial to ecosystem management and conservation.

Recent studies on niche conservatism of species report conflicting results. While there is a plethora of evidence confirming spatial and temporal niche conservatism [9], this theory has been shown not to hold true for some insects [12], plants [13] and fish [14] either due to absence of natural enemies in the introduced range, availablity of unoccupied niches or adaptation to novel envrionmental conditions as a result of hybridization. Latter observations imply that some species can occupy different environmental niches in their invasive range, when compared to the niche they occupy in their native range. A mismatch between the native and the invasive environmental niche signifies either a shift in the fundamental niche (“the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions”[15]) or the realized niche (“the portion of the fundamental niche in which a species has positive population growth rates, given the constraining effects of biological interactions such as competition”[15]) [4]. Thus, a shift in the fundamental niche may be a consequence of evolutionary change (i.e. genetic drift and/or hybridization) [13]. A shift in the realized niche of a species may then be attributable to the availability of unoccupied niches in the invasive range or to a release from top-down regulators due to their absence in the new environment (i.e., predators or pathogens) [16].

Assuming that an invasive species occupies all suitable conditions in its native range, any difference between its niche in the native and invasive ranges can be attributed to three distinct processes: niche expansion (invasive species occupies new environmental conditions in the invasive range compared to its native range), niche unfilling (partial filling of the native niche in the invasive range) [9] and niche stability (proportion of native niche of an invasive species overlapping with its invasive niche) [4]. Two different hypotheses need to be tested to determine which of these processes drives niche differentiation for a given invasive species; niche equivalency (native and non-native niches are indistinguishable and interchangeable) and niche similarity (native and invasive niches are more similar than expected by chance) [17][18].

In addition to the spread of a species entirely novel to the invasive environmental space, biological invasion may also lead to hybridization if similar but historically isolated taxa come into contact. Hybridization of invasive species can produce genetically superior populations and, in some cases, new taxa [19][20][21]. Hybrids of invasive species are potentially better at exploiting new environmental conditions as compared to their parents [22], chiefly due to fast selection of new combinations of traits by the specific environment where hybridization occurs. Undetected hybridization of closely related species may thus lead to an apparent shift in fundamental niche of either or both parent species [23]. Despite the potentially large impact of rapid evolution of new species by hybridization, to date only a limited number of investigations have been made to explore the role of hybridization in niche occupancy [21][24].

In Great Britain, *Rhododendron ponticum* (L.) is a classic example of an invasive species that has spread at a massive scale and caused significant environmental and economic damage [25]. *R. ponticum* is an invasive plant species that was introduced to the British Isles as an ornamental plant from mainland Europe in the eighteenth century. It is a perennial, evergreen shrub that generally invades woodlands [26], although it is known to colonize other types of habitats too [2]. The success of the invasion of *R. ponticum* in Britain is attributed to its ecological and biological characteristics; it produces copious amounts of seeds and can tolerate shaded and nutrient-depleted soils [27]. Its growth prevents germination of native plant species by releasing allelochemicals into the soil [28][29].

The suitability of *R. ponticum* to the British environment and its invasiveness were first thought to result from a hybridization of *R. ponticum* with *Rhododendron catawbiense*, (a North American species), a process which supposedly lent frost hardiness to the British *R. ponticum* population [30]. However, this thesis was later rejected by other reports which did not find any genetic evidence of such hybridization [31]. The spread of *R. ponticum* thus represents an opportunity to test whether the current niche occupied in Britain corresponds to that in its native Iberia. To evaluate this, we tested two different hypotheses: a) the native and invaded niches are equivalent (species' native and invasive niches are interchangeable), and b) the native and invaded niches are similar (the native and invasive niches are more similar than expected by chance). Thus, in this study we examine the environmental niche of *R. ponticum* in its invasive and native ranges and interpret our findings in the context of contradicting reports on the hybridization if the British population of *R. ponticum.*

2. METHODOLOGY

2.1. Species Description and Geographic Ranges

The native range of *R. ponticum* covers the southern reaches of Spain, western Portugal and Georgia. However, the main ancestor of *Rhododendron* in Britain is reported to be the population of *R. ponticum* resident in southern Spain and western Portugal [27]. We thus consider the Iberian Peninsula as the native range *R ponticum*. We obtained distribution records of this species from the Global Biodiversity Information Facility (www.gbif.org/) using the dismo R package. These records were then complemented by a selection of background points (i.e. set of randomly sampled geographical locations that represent the environmental conditions available to an organism [32]). These points must cover the area where the species can easily disperse. In the absence of detailed information regarding the natural dispersal limits of *R. ponticum*, we used terrestrial ecoregions proposed by Oslon et al. [33] to define native and invaded range boundaries.

2.2. Variable Selection

Ideally, the selection of predictor variables in species distribution models should take into account the ecological requirements of the species under investigation [34]. However, like most invasive species, *R. ponticum* does not lend itself to the provision of autecological information, which makes it difficult to *a priori* select a specific set of biologically relevant predictors. Following a detailed literature review, we chose 19 bioclimatic variables to model the distribution of *R. ponticum* [2]. Current (1960–2000) climate data were downloaded from the WorldClim database [35] at a resolution of 30 arc-seconds, which was shown to provide optimal prediction of *R. ponticum* distribution [2]. The WorldClim database consists of 19 derived bioclimatic variables that represent climate average, extremes and variability.

Collinearity among predictor variables negatively impacts the model due to the substantial amount of information shared between variables, making it difficult to correctly interpret the relative contribution or importance of variables to model predictions [36]. Pearson correlation coefficient cut-off of $-0.75 \leq r \leq 0.75$ was applied to select bioclimatic variables to be used in the final model runs [36], chiefly to reduce the negative impact of multicollinearity and to conform to statistical assumptions [37]. Consequently, we selected four variables: annual mean temperature (Bio 1), minimum temperature of the coldest month (Bio 6), annual mean precipitation (Bio 12), and precipitation of the coldest month (Bio 14) for this study.

2.3. Climatic Niche Analysis

The Principal Component Analysis (PCA-env) approach proposed by Broennimann [38] was used to visualise the native and invaded niches of *R. ponticum* in a 2D climatic space. The PCA-env method compares the environmental conditions available for a species within the study area (background) with observed occurrences and calculates available environmental space defined by the first two axes from the PCA-env. This method corrects for sampling bias using a smooth kernel density function [38]. We estimated niche overlap between the two geographical ranges using Schoener's D index [39], which ranges from 0 to 1 (i.e. no to complete niche overlap). Niche shift was statistically tested as described by Broennimann [38].

2.3.1. Niche Equivalence Test

The niche equivalence test, as initially proposed by Graham et al. [40], asks whether niches under comparison are indistinguishable from each other. For this test, the occurrence points from both ranges were pooled together and then randomly split into two sets, maintaining the actual number of occurrences in each range. Niche equivalence was then determined by comparing the observed niche overlap values (D) to a null distribution of 1000 overlap values. Rejection of the niche equivalency hypothesis means that native and invaded niches are not environmentally identical (i.e. not equivalent) [18]. Thus, if the value of the observed niche overlap falls outside the 95% confidence intervals of the null distribution, the null hypothesis of the equivalency is rejected [38].

2.3.2. Niche Similarity Test

The niche similarity test examines whether the overlap between the observed native and invaded niches of *R. ponticum* is different from the overlap between the observed niche in one range and a randomly selected niche in the other range (based on 1000 repetitions). Rejection of the niche similarity hypothesis means that overlap of native and non-native niches is larger than random expectation, i.e. the environmental conditions occupied by the species in the non-native range are more similar to the conditions occupied in the native range than would be expected by chance [18]. Thus, for the niche similarity test, a p-value > 0.05 is considered to indicate that niches are no more similar than expected by chance. Niche similarity test was used in the current study to estimate niche divergence. Niche overlap value above 95% confidence interval of the null hypothesis indicates niche divergence [38].

Niche equivalence and similarity tests only verify whether niche shifts have occurred but do not address their causal mechanism [41]. To understand *R. ponticum* invasion process, we disentangled niche changes into the processes of niche stability (*S*, the overlap of invaded niche with native niche), unfilling (*U*, the non-overlapping part of native niche in the invaded niche) and expansion (*E*, the non-overlapping part of the invaded niche in the native niche) as described by Guisan et al. [5]. All analyses were done in the statistical software R, version 3.1.3 using the ecospat package [42].

2.4. Reciprocal Distribution Modelling

We used the Reciprocal Distribution Modelling approach [12] to estimate the potential distribution of *R. ponticum* in its invaded range. Following this approach, a model was first calibrated in the native range (Iberian Peninsula) and projected onto the invaded range (Great Britain). Then, a second model was calibrated in the invaded range and projected onto the native range. Furthermore, each model (native and invasive) was also projected in the same range and the degree of similarity between projected models (calibrated in the other range) and observed models (calibrated and projected in the same range) was assessed.

We used MaxEnt, a maximum-entropy based machine learning (presence/pseudo-absence) algorithm for distribution modelling. MaxEnt predicts the probability distribution of a species on the basis of a given set of predictor variables and presence-only species occurrence data [43]. We used a reasonably large sample size (79 in the Iberian Peninsula and 6579 in Britain) and applied the recommended screening and verification of occurrence records [34][44]. The complementary log-log output of MaxEnt was used to produce an estimate of occurrence probability for each model.

2.4.1. Model Complexity and Tuning

Various studies have confirmed that calibrating MaxEnt models with default settings frequently leads to highly complex models, a case-specific tuning of the model is thus recommended [45] (for details see [34]). To select the modelling parameters which give the best trade-off between model goodness of fit and complexity, we used ENMeval [46] to build models with all possible combinations of these parameters. We produced a total of 48 models using six combination of these feature classes (L, H, LQ, LQH, LQHP, LQHPT) and eight regularization multipliers (0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0) [32]. All models were built using 10,000 background points randomly selected within the calibration area (the Iberian Peninsula for the model calibrated with native records and Great Britain for the model calibrated with invasive records). We used the "block" method implemented in ENMeval to partition data into four geographically distinct calibration and evaluation datasets, in order to conduct spatially independent tests of model performance. Finally, we selected the most suitable model using the Akaike information criterion corrected for small sample sizes (ΔAICc< 2) [47].

2.4.2. Model Evaluation

Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) was used to test the performance of the model against actual observations in both the ranges [48]. An AUC value of 0.5 shows that the model does not predict any better than random chance, whereas a value closer to 1 indicates a better performance of the model [49]. Percentage of contribution and permutation importance contribution were used to assess the relative significance of predictor variables. In addition to AUC, we used Continuous Boyce Index (CBI) as an additional assessment tool. The Boyce index requires presence data only and measures by how much model predictions differ from a random distribution of observed presence across the prediction gradient (for details, see [34]). The continuous values of the Boyce index vary between -1 and +1. Positive values indicate a model where predictions are consistent with the distribution of actual presence data, values close to zero mean that the model is no different from a random model and negative values indicate counter predictions (e.g. predicting no occurrence in areas where actual presence is recorded) [47][50].

3. RESULTS

The climatic space occupied by *R. ponticum* in its native and invaded ranges is represented in Fig 1. The correlation circle in pane b shows that the first two PCA axes explained 95.51% of the variance in the set of four predictor variables. Annual mean temperature (Bio 1) and annual mean precipitation (Bio 12) were the most important variables in the first and second principal components. Niche overlap of *R. ponticum* between the Iberian Peninsula and Great Britain was very low (Schoener's D = 0.005) following the classification scheme of Rödder and Engler [78]. The test of equivalence between native and invaded realized niches of *R. ponticum* showed statistically significant differences, which are clearly visible in Fig. 2. Therefore, we reject the null hypothesis of niche equivalency and accept the alternative that the niches are ecologically distinct [17]. In addition, the similarity test results in a non-significant value of D, suggesting that the two niches are no more similar than random chance (Table 1). In other words, environmental conditions occupied by the species in the invasive range are no more similar to conditions occupied in the native range than would be expected by chance. Furthermore, given the low niche overlap and high expansion values (E = 0.996), the niche dynamics test suggests that *R. ponticum* currently occupies new environment in Britain. Similarly, a very high unfilling (U) value suggests that the conditions occupied by the species in the native range are still unoccupied in the invasive range. Furthermore, the results of the reciprocal distribution modelling suggest that the model calibrated in the native range failed to predict occurrence in the invasive range with reasonable accuracy, and vice versa (Fig. 3). The models calibrated and projected to the same range, however, predicted the distribution of *R. ponticum* reasonably well. The AUC and Boyce Index values for all combinations of projections are presented in Table 2.

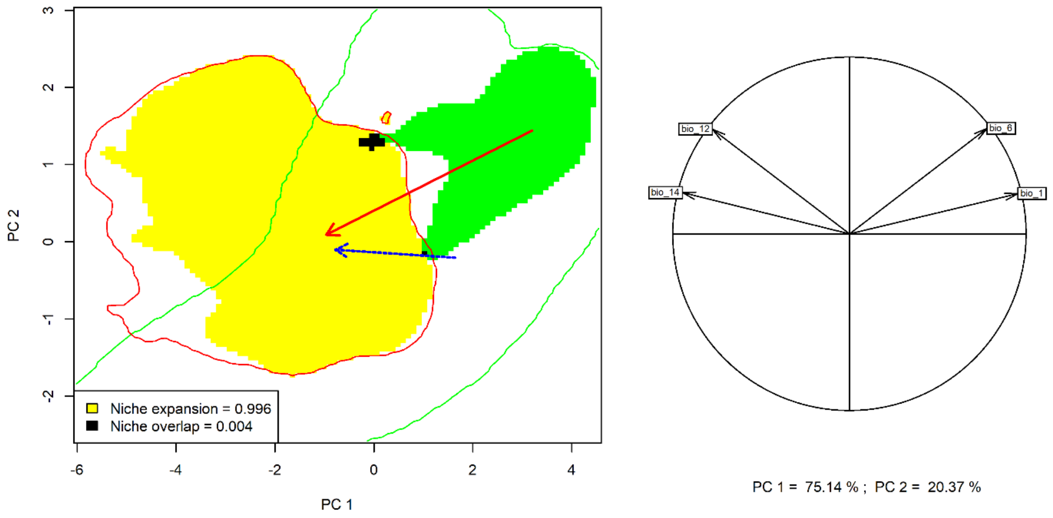

Figure. 1. (a) Principal component analysis of niche shift of *R. ponticum*. Green and red contour lines demarcate available niche in the native (Iberia) and invaded (GB) ranges, the blue arrow indicates a shift of the centroid of available niche. Green and yellow areas represent occupied niches in the native and invasive ranges, respectively. The red arrow links the centroid of the native and invasive distribution. (b) Correlation circle indicates the weight of each variable on the niche space as defined by the first two principal component axes.

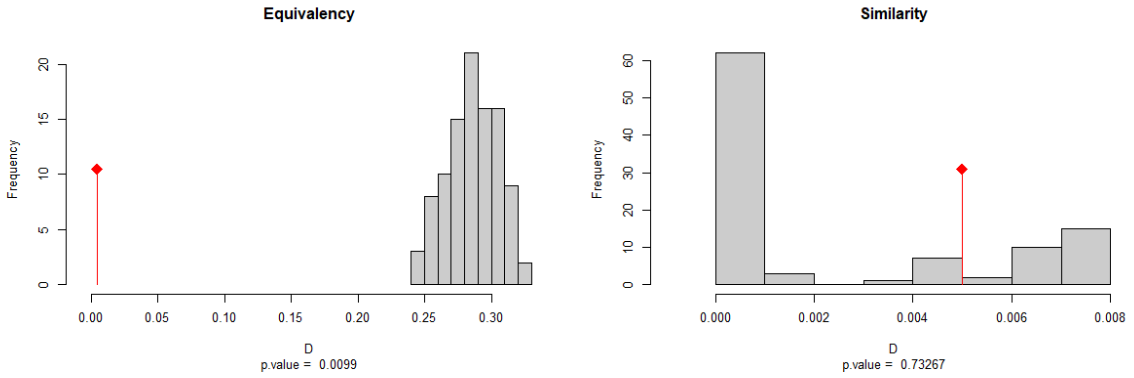

Figure 2. Niche equivalency and similarity test results comparing native and invaded ranges of *R. ponticum*. “D” denotes the Schoener's D index which takes values from 0 (none) to 1 (complete) niche overlap. Red lines indicate the value of observed overlap (D) compared to the simulated null distribution of 1000 random replicates to test for niche conservatism between native and invasive ranges.

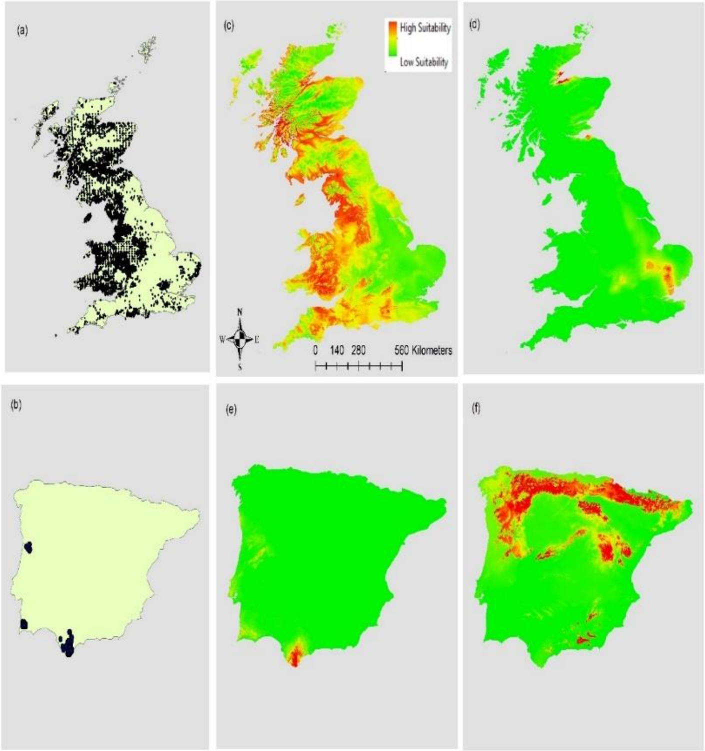

Figure 3. Current distribution of *R. ponticum* in a) Britain and, b) Iberian Peninsula. Predictive maps of *R. ponticum* distribution, based on models (c) trained in the invasive range and projected to the invasive range, (d) trained in the native range and projected to the invasive range, (e) trained in the native range and projected to the native range and finally (f) trained in the invasive range and projected the native range.

Table 1. Schoener's D values indicate niche overlap (corresponding *P* values show statistical significance). Expansion and Stability are proportions of non-overlapping and overlapping invasive niche compared to the native niche, respectively. Unfilling represents the proportion of the native niche available, but not occupied in the exotic niche.

Equivalence	**Similarity**		**Expansion**	**Stability**	**Unfilling**
	Native -> Native	**Native -> Invasive**			
D = 0.005	D = 0.005	0.005	0.9996	0.0003	0.9964
P = 0.009	*P* = 0.692	0.151			

Table 2. AUC and Boyce Index values showing indicating the accuracy of model transfer.

	Native -> Native	Native -> Invasive	Invasive -> Invasive	Invasive -> Native
AUC	0.952	0.4	0.7	0.52
Boyce Index	0.94	0.52	0.81	0.3

4. DISCUSSION

In this study, we compared the ecological niche of *R. ponticum* in its native and invasive ranges and tested the hypothesis of niche divergence. While previous studies have analysed the genetic material of *R. ponticum* populations to look for evidence of hybridization [31], our study is the first effort to model ecological niches and spatial distribution of this species in its native and invasive ranges by comparing niche differences in a gridded environmental space. We found a very limited niche overlap between *R. ponticum* populations in the Iberian Peninsula and Britain, as suggested by very high values of niche expansion and niche unfilling. Our results indicate that *R. ponticum* largely occupies novel niches in Britain. Conversely, large values of Unfilling (*U*) indicate that a large proportion of environmental conditions occupied in the native niche are available, but unoccupied in the invasive range [15]. The results of niche equivalency and niche similarity test show that the two niches are not equivalent and that the ecological niche of *R. ponticum* has shifted in the invasive range (i.e. the native niche is not conserved). We also show that MaxEnt-based reciprocal distribution models fail to predict species distribution in target ranges, confirming the earlier finding that environmental conditions occupied by *R. ponticum* in its native range differ from those occupied in the invasive range.

The pattern and the extent to which species' niches are conserved or shift over space and time is a key determinant of their response to local and global environmental change [51]. Predictive maps generated by reciprocal distribution models suggest that the current distribution of *R. ponticum* in Britain is mostly clustered in the western and northern parts which are the cooler and more humid parts of the country, whereas in its native range the species is present in the southern tips of Spain and southern and western parts of Portugal typical for milder temperature regime and less rainfall. Thus, the distribution model calibrated in Iberia incorrectly places the distribution to eastern Britain. This part of Britain is ecologically similar to conditions occupied by the species in the Iberian Peninsula, but it is not where the species is currently found. The actual distribution of *R. ponticum* in Britain is centred in Wales and the Scotland, areas with some of the lowest mean annual temperatures in the whole of Britain. This mismatch also explains the high value of niche expansion (E = 0.996), suggesting that *R. ponticum* in

Britain is present in locations where the environmental conditions are very different from those of its native range on the Iberian Peninsula. This type of invasive behaviour is very similar to that reported by a remarkable number of studies where hybridization fostered the emergence of successful invasive populations [52][53].

Although niche shift in terrestrial plants is rare [9], even large shifts in environmental niches such as the one observed in our study could potentially be a result of evolutionary changes. Hybridization of the invading species with a local or another introduced species has been shown to produce superior adaptive traits [52]. For example, the abundance of *R. ponticum* in Wales and Scotland is often attributed to the frost hardiness adaptation of this species, which, in turn, is considered a consequence of hybridization. Therefore, how significant a role does hybridization play in successful invasion and divergence of ecological niches?

4.1. The Role of Hybridization in Niche Expansion

Ecological niche expansion is often, but not exclusively, associated with hybridization [54]. This thesis rests on the proposition that under continuous presence of barriers to natural dispersal and establishment (e.g. climate, topography, predators, or competitors [55]), it is the species in question that must change in order to expand its range. Populations of a species that inhabit the leading edge of an expansion likely need genetic adaptions to colonise new environments, currently denied to them by barriers to dispersal [56][57]. One way to gain such adaptations is genetic mutations, followed by subsequent selection, however in most species this process operates at long timescales too long to explain the speed of observed biological invasions [58][59]. Alternatively, the population of a species at the leading edge may hybridize with an established native species or another introduced species to produce an advantageous combination of traits [54] and thus sustain the expanding population until new adaptive traits arise due to mutation [60]. Theoretically, a species may overcome its dispersal barriers to expand its geographic range by occupying microenvironments to which its ancestral populations are already adapted to certain extent [61]. However, this type of expansion is be different from that driven by hybridization. A key implication of the 'hybridization facilitates niche expansion' hypothesis is that the hybridizing population expands to environmental conditions where the native population does not occur [62]. Thus, rapid expansion into novel environments is a strong indication of hybridization.

4.2. Niche Expansion of *R. ponticum* in Great Britain – Evidence of Possible Hybridization

An early study of hybridization of *R. ponticum* in Britain reported on 260 naturalized accessions of *R. ponticum* and presented evidence that 89% of those accessions possessed a cpDNA haplotype occurring in the Spanish population of *R. ponticum,* while 10% of accessions had a haplotype unique to the Portuguese material [30]. Furthermore, rDNA or cpDNA evidence of hybridization from *R. catawbiense* - which is native to North America - was found only in 27 British accessions of *R. ponticum*. Interestingly, these 27 accessions were significantly more abundant in Britain's coldest regions. Since *R. catawbiense* is more resistant to frost than *R. potnicum*, the conclusion that suggests itself is that *R. ponticum* had acquired frost resistance genes from *R. catawbiencei,* leading to the expansion of its range into the western and north-western parts of Britain [63].

Our study, although focusing on climatic factors only and ignoring other critical ecological components such as interspecific competition, soil, and land cover composition, is compatible with the hypothesis that hybridization contributed to invasiveness of *R. ponticum* in the colder regions of Britain[52][53].

4.3. Hybridization *May Not* Be the Cause of Niche Expansion - A Counter-Narrative

A decade after the original '*R. ponticum* x *R. catawbiense*' hybridization explanation for the successful colonization of western Britain by *R. ponticum,* it was challenged by a study which sampled its populations in Ireland. The researchers used more advanced genetic analysis techniques and concluded that there is no evidence of Irish *R. ponticum* sharing either ecological or morphological traits with North American *R. catawbiense* [31]. Amplified Fragment Length Polymorphism (AFLP) data confirmed the distinctiveness of *R. ponticum* from its North American relative, leading the authors to reject the hybridization hypothesis presented in the earlier report [30]. Interestingly, increased frost tolerance – which is presented as evidence of hybridization - was also found in the Irish *R. ponticum* populations where the temperatures are mild, and therefore such a trait does not seem to have an adaptive value [31].

There is a plethora of evidence that hybridization and expansion into novel environments are strongly correlated, however hybridization may not be the driver of niche expansion in some cases [64][65][66]. The mere observation that a species has expanded its range into novel environments is not sufficient to claim that the range expansion was enabled by hybridization. Unless backed up with consolidated empirical evidence from genetic investigations of the native and invasive populations, it may not be correct to claim that niche expansion is explained by hybridization [62].

4.4. The Curious Case of *R. ponticum* Niche Expansion

We have shown that the native and invaded niches of *R. ponticum* are not equivalent and that they are no more similar than random chance (Fig. 2). Our analysis clearly shows that the population of *R. ponticum* in Britain has expanded and shifted its range to such an extent that using a model trained on its native range to predict it results in a complete mismatch. Given that the species was brought to the country about 200 years ago, such a shift would indicate genetic change caused by rapid introgression of genes rather than mutation. Both existing reports on the genetics of *R. ponticum* in Britain have limitations. Milne and Abbott (2000) posit that increased frost hardiness results from directional selection introgression but were limited by the lack of sufficient genetic analysis. The follow-up study of Erfmeier et al (2011) was limited only to the Irish population of *R. ponticum* and thus may not be generalizable for the Welsh and Scottish populations. Only a concerted testing of both an introgression by means of nuclear markers and the frost hardiness by means of experimental determination on a sample covering all populations from the British Isles may be able to identify the driver of *R. ponticum* expansion in Britain [31]. It is essential to keep in sight that the observed niche shift could either be due to an evolutionary process such as hybridization (changing fundamental niche hypothesis [67]) or it could be driven by a difference in the biotic environment between the native and invasive range (enemy-release hypothesis [19]), or indeed due to a combination of these reasons. The enemy release hypothesis is among the most widely proposed explanations for the dominance of exotic invasive species. In its native range, a species has co-evolved with pathogens, parasites and predators that limit its population. When it arrives in a new territory, it leaves these old enemies behind, while those in its introduced range are less effective at constraining them. The result is sometimes rampant growth that threatens native species and ecosystems.

Our niche shift and reciprocal modelling indicates a definitive shift in the environmental adaptation of *R. ponticum* in its invasive range, but a more comprehensive modelling approach using a wider set of environmental variables may be able to test causality rather than correlation. A future niche shift modelling exercise may combine data describing *R. ponticum* populations from North America and Iberian Peninsula (as native ranges) to predict observed niche shift. We based our analysis on the climatic factors only, however it is conceivable that in some instances these may only partially explain observed niche shift phenomena [11]. Other, more pertinent non-climatic factors such as soil properties, land cover, or land use type, may play a more decisive role in explaining niche dynamics [68]. Niche shift analysis is also sensitive to sample size. In our case, the sample describing the presence of *R. ponticum* in the Iberian Peninsula was small relatively to that describing Britain (although still the most comprehensive dataset available for Iberia).

CONCLUSION

Our study documented a substantial niche shift of *R. ponticum* in Great Britain. We show that in Britain the species occupies a niche that is entirely different from that in its native Iberia, both in terms of equivalence and similarity. On the basis of presented evidence, we believe that hybridization has driven the niche shift of *R. ponticum* in Britain, although we are not able to prove it conclusively. Observed expansion of species range may have been caused by biotic or abiotic factors not considered here. We suggest that a more comprehensive genetic analysis of *R. ponticum* populations in England, Scotland and Wales is needed to investigate any evidence of hybridization. Future development of ecological niche models that include a mechanistic approach for the species should be considered in order to study more accurately the niche differentiation of the species by hybridization and invasion.

REFERENCES

1. Tingley, R.; Vallinoto, M.; Sequeira, F.; Kearney, M.R. Realized niche shift during a global biological invasion. *Proc. Natl. Acad. Sci. U. S. A.* **2014**, *111*, 10233–10238.
2. Manzoor, S.A.; Griffiths, G.; Iizuka, K.; Lukac, M. Land Cover and Climate Change May Limit Invasiveness of *Rhododendron ponticum* in Wales. *Front. plant Sci. Pap.* **2018**, *9*.
3. Banerjee, A.K.; Mukherjee, A.; Dewanji, A. Potential distribution of Mikania micrantha Kunth in India – evidence of climatic niche and biome shifts. *Flora Morphol. Distrib. Funct. Ecol. Plants* **2017**, *234*, 215–223.
4. Pearman, P.B.; Guisan, A.; Broennimann, O.; Randin, C.F. Niche dynamics in space and time. *Trends Ecol. Evol.* **2008**, *23*, 149–158.
5. Jiménez-Valverde, A.; Peterson, A.T.; Soberón, J.; Overton, J.M.; Aragón, P.; Lobo, J.M. Use of niche models in invasive species risk assessments. *Biol. Invasions* **2011**, *13*, 2785–2797.
6. Minardo, J.D.; Heger, J.J.; Miles, W.M.; Zipes, D.P.; Prystowsky, E.N. Clinical characteristics of patients with ventricular fibrillation during antiarrhythmic drug therapy. *N. Engl. J. Med.* **1988**, *319*, 257–262.
7. Leung, B.; Lodge, D.M.; Finnoff, D.; Shogren, J.F.; Lewis, M.A.; Lamberti, G. An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proc. R. Soc. B Biol. Sci.* **2002**, *269*, 2407–2413.
8. Huntley, B.; Bartlein, P.J.; Prentice, I.C. Climatic Control of the Distribution and Abundance of Beech (Fagus L.) in Europe and North America. *J. Biogeogr.* **1989**, *16*, 551.
9. Petitpierre, B.; Kueffer, C.; Broennimann, O.; Randin, C.; Daehler, C.; Guisan, A. Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science (80-.).* **2012**, *335*, 1344–1348.
10. Klironomos, J.N. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **2002**, *417*, 67–70.
11. Lavergne, S.; Molofsky, J. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. U. S. A.* **2007**, *104*, 3883–3888.
12. Fitzpatrick, M.C.; Weltzin, J.F.; Sanders, N.J.; Dunn, R.R. The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? *Glob. Ecol. Biogeogr.* **2007**, *16*, 24–33.
13. Gallagher, R. V.; Beaumont, L.J.; Hughes, L.; Leishman, M.R. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *J. Ecol.* **2010**, *98*, 790–799.
14. Lauzeral, C.; Leprieur, F.; Beauchard, O.; Duron, Q.; Oberdorff, T.; Brosse, S. Identifying climatic niche shifts using coarse-grained occurrence data: A test with non-native freshwater fish. *Glob. Ecol. Biogeogr.* **2011**, *20*, 407–414.
15. Guisan, A.; Petitpierre, B.; Broennimann, O.; Daehler, C.; Kueffer, C. Unifying niche shift studies: Insights from biological invasions. *Trends Ecol. Evol.* **2014**, *29*, 260–269.
16. Broennimann, O.; Treier, U.A.; Müller-Schärer, H.; Thuiller, W.; Peterson, A.T.; Guisan, A. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* **2007**, *10*, 701–709.
17. Warren, D.L.; Glor, R.E.; Turelli, M. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution (N. Y).* **2008**, *62*, 2868–2883.
18. Strubbe, D.; Beauchard, O.; Matthysen, E. Niche conservatism among non-native vertebrates in Europe and North America. *Ecography (Cop.).* **2015**, *38*, 321–329.
19. Dietz, H.; Edwards, P.J. Recognition That Casual Processes Change During Plant Invasion Helps Explain Conflicts In Evidence. *Ecology* **2006**, *87*, 1359–1367.
20. Blaine Marchant, D.; Soltis, D.E.; Soltis, P.S. Patterns of abiotic niche shifts in allopolyploids relative to their progenitors. *New Phytol.* **2016**, *212*, 708–718.
21. Molina-Henao, Y.F.; Hopkins, R. Autopolyploid lineage shows climatic niche expansion but not divergence in Arabidopsis arenosa. *Am. J. Bot.* **2019**, *106*, 61–70.
22. Sheth, S.N.; Angert, A.L. The evolution of environmental tolerance and range size: A

comparison of geographically restricted and widespread Mimulus. *Evolution (N. Y).* **2014**, *68*, 2917–2931.

23. Parisod, C.; Broennimann, O. Towards unified hypotheses of the impact of polyploidy on ecological niches. *New Phytol.* **2016**, *212*, 540–542.
24. Mukherjee, A.; Williams, D.A.; Wheeler, G.S.; Cuda, J.P.; Pal, S.; Overholt, W.A. Brazilian peppertree (Schinus terebinthifolius) in Florida and South America: Evidence of a possible niche shift driven by hybridization. *Biol. Invasions* **2012**, *14*, 1415–1430.
25. Jackson, P. Rhododendron in Snowdonia and a strategy for its control. *Snowdownia Natl. Park Auth.* **2008**.
26. Tiedeken, E.J.; Stout, J.C. Insect-flower interaction network structure is resilient to a temporary pulse of floral resources from invasive *Rhododendron ponticum*. *PLoS One* **2015**, *10*, 1–19.
27. Dehnen-Schmutz, K.; Williamson, M. *Rhododendron ponticum* in Britain and Ireland: Social, economic and ecological factors in its successful invasion. *Environ. Hist. Camb.* **2006**, *12*, 325–350.
28. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–758.
29. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
30. Milne, R.I.; Abbott, R.J. Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. *Mol. Ecol.* **2000**, *9*, 541–556.
31. Erfmeier, A.; Tsaliki, M.; Roß, C.A.; Bruelheide, H. Genetic and phenotypic differentiation between invasive and native Rhododendron (Ericaceae) taxa and the role of hybridization. *Ecol. Evol.* **2011**, *1*, 392–407.
32. Obiakara, M.C.; Fourcade, Y. Climatic niche and potential distribution of Tithonia diversifolia (Hemsl.) A. Gray in Africa. *PLoS One* **2018**, *13*, 1–18.
33. Olson, D.M.; Dinerstein, E.; Wikramanayake, E.D.; Burgess, N.D.; Powell, G.V.N.; Underwood, E.C.; D'amico, J.A.; Itoua, I.; Strand, H.E.; Morrison, J.C.; et al. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience* **2001**, *51*, 933.
34. Manzoor, S.A.; Griffiths, G.; Lukac, M. Species distribution model transferability and model grain size – finer may not always be better. *Sci. Rep.* **2018**, 1–9.
35. Fick, S.E.; Hijmans, R.J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **2017**, *37*, 4302–4315.
36. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop.).* **2013**, *36*, 027–046.
37. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. *PLoS One* **2013**, *8*.
38. Broennimann, O.; Fitzpatrick, M.C.; Pearman, P.B.; Petitpierre, B.; Pellissier, L.; Yoccoz, N.G.; Thuiller, W.; Fortin, M.J.; Randin, C.; Zimmermann, N.E.; et al. Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob. Ecol. Biogeogr.* **2012**, *21*, 481–497.
39. Schoener, T.W. Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats Author (s): Thomas W . Schoener Published by : Wiley Stable URL : http://www.jstor.org/stable/1935376 REFERENCES Linked references are available on JSTOR for this article : You may need to log. *Ecology* **1970**, *51*, 408–418.
40. Graham, C.H.; Ron, S.R.; Santos, J.C.; Schneider, C.J.; Moritz, C. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution (N. Y).* **2004**, *58*, 1781–1793.

41. Sales, L.P.; Ribeiro, B.R.; Hayward, M.W.; Paglia, A.; Passamani, M.; Loyola, R. Niche conservatism and the invasive potential of the wild boar. *J. Anim. Ecol.* **2017**, *86*, 1214–1223.
42. Di Cola, V.; Broennimann, O.; Petitpierre, B.; Breiner, F.T.; D'Amen, M.; Randin, C.; Engler, R.; Pottier, J.; Pio, D.; Dubuis, A.; et al. ecospat: an R package to support spatial analyses and modelling of species niches and distributions. *Ecography (Cop.).* **2017**, *40*, 774–787.
43. Phillips SJ Dudik M, S.R.E. A maximum entropy approach to species distribution modelling. **2004**, 655–662.
44. Wisz, M.S.; Hijmans, R.J.; Li, J.; Peterson, A.T.; Graham, C.H.; Guisan, A.; Elith, J.; Dudík, M.; Ferrier, S.; Huettmann, F.; et al. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **2008**, *14*, 763–773.
45. Moreno-Amat, E.; Mateo, R.G.; Nieto-Lugilde, D.; Morueta-Holme, N.; Svenning, J.C.; Garc??a-Amorena, I. Impact of model complexity on cross-temporal transferability in Maxent species distribution models: An assessment using paleobotanical data. *Ecol. Modell.* **2015**, *312*, 308–317.
46. Muscarella, R.; Galante, P.J.; Soley-Guardia, M.; Boria, R.A.; Kass, J.M.; Uriarte, M.; Anderson, R.P. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for <scp>Maxent</scp> ecological niche models. *Methods Ecol. Evol.* **2014**, *5*, 1198–1205.
47. Boyce, M.S.; Vernier, P.R.; Nielsen, S.E.; Schmiegelow, F.K.A. Evaluating resource selection functions. *Ecol. Modell.* **2002**, *157*, 281–300.
48. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudik, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).* **2006**, *29*, 129–151.
49. Swets, J.A. Measuring the accuracy of diagnostic systems. *Science* **1988**, *240*, 1285–1293.
50. Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* **2006**, *199*, 142–152.
51. Thornton, D.H.; Murray, D.L. Influence of hybridization on niche shifts in expanding coyote populations. *Divers. Distrib.* **2014**, *20*, 1355–1364.
52. Ellstrand, N.C.; Schierenbeck, K.A. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc. Natl. Acad. Sci.* **2000**, *41*, 23–24.
53. Arrigo, N.; De La Harpe, M.; Litsios, G.; Zozomová-Lihová, J.; Španiel, S.; Marhold, K.; Barker, M.S.; Alvarez, N. Is hybridization driving the evolution of climatic niche in Alyssum montanum. *Am. J. Bot.* **2016**, *103*, 1348–1357.
54. Hedrick, P.W. Adaptive introgression in animals: Examples and comparison to new mutation and standing variation as sources of adaptive variation. *Mol. Ecol.* **2013**, *22*, 4606–4618.
55. Nasiri, V.; Darvishsefat, A.A.; Rafiee, R.; Shirvany, A.; Hemat, M.A. Land use change modelling through an integrated Multi-Layer Perceptron Neural Network and Markov Chain analysis (case study: Arasbaran region, Iran). *J. For. Res.* **2018**.
56. Sexton, J.P.; McIntyre, P.J.; Angert, A.L.; Rice, K.J. Evolution and Ecology of Species Range Limits. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 415–436.
57. Barrett, R.D.H.; Schluter, D. Adaptation from standing genetic variation. *Trends Ecol. Evol.* **2008**, *23*, 38–44.
58. Orr, H.A.; Unckless, R.L. Population extinction and the genetics of adaptation. *Am. Nat.* **2008**, *172*, 160–169.
59. Phillips, P.C. Waiting for a compensatory mutation: phase zero of the shifting-balance process. *Genet. Res.* **1996**, *67*, 271–283.
60. Drake, J.M. Heterosis, the catapult effect and establishment success of a colonizing bird. *Biol. Lett.* **2006**, *2*, 304–307.
61. Early, R.; Sax, D.F. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob. Ecol. Biogeogr.* **2014**, *23*, 1356–1365.

62. Pfennig, K.S.; Kelly, A.L.; Pierce, A.A. Hybridization as a facilitator of species range expansion. *Proceedings. Biol. Sci.* **2016**, *283*.
63. Erfmeier, A.; Bruelheide, H. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora - Morphol. Distrib. Funct. Ecol. Plants* **2004**, *199*, 120–133.
64. Melo-Ferreira, J.; Boursot, P.; Randi, E.; Kryukov, A.; Suchentrunk, F.; Ferrand, N.; Alves, P.C. The rise and fall of the mountain hare (Lepus timidus) during Pleistocene glaciations: Expansion and retreat with hybridization in the Iberian Peninsula. *Mol. Ecol.* **2007**, *16*, 605–618.
65. Orozco-Terwengel, P.; Andreone, F.; Louis, E.; Vences, M. Mitochondrial introgressive hybridization following a demographic expansion in the tomato frogs of Madagascar, genus D yscophus. *Mol. Ecol.* **2013**, *22*, 6074–6090.
66. Currat, M.; Ruedi, M.; Petit, R.J.; Excoffier, L. The hidden side of invasions: Massive introgression by local genes. *Evolution (N. Y).* **2008**, *62*, 1908–1920.
67. Society, B.E. Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants : A Hypothesis Author (s): Bernd Blossey and Rolf Notzold Source : Journal of Ecology , Vol . 83 , No . 5 (Oct ., 1995), pp . 887-889 Published by : British Ecological Society. *Society* **2009**, *83*, 887–889.
68. Broennimann, O.; Treier, U.A.; Müller-Schärer, H.; Thuiller, W.; Peterson, A.T.; Guisan, A. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* **2007**, *10*, 701–709

Chapter 6

LAND USE AND CLIMATE CHANGE INTERACTION TRIGGERS CONTRASTING TRAJECTORIES OF BIOLOGICAL INVASION

ABSTRACT

Global change drivers such as land use and climate changes are known to interact in their effects on biodiversity. The impact of these drivers on global biodiversity is increasingly evident in many forms including the spread of invasive species. Climate and land use changes affect introduction, colonization and spread of invasive species by affecting niche availability and dispersal potential. We tested the combined effects of land use and climate changes on the current and future habitat suitability of *Rhododendron ponticum* in Wales using a MaxEnt-based ecological niche model. We used two policy-driven land use change projections for Wales, in combination with two General Circulation Models and two Representative Concentration Pathways to derive eight different land use and climate change scenarios. In seven out of eight scenarios, the habitat suitability for *R. ponticum* is likely to reduce by 2030. However, in the eighth scenario representing an extreme where land use change and greenhouse gas emissions both accelerate, the interaction of land use and climate change forces an increase of habitat suitability of *R. ponticum*. The study highlights the importance of considering the combined effect of land use and climate change and including regional policy-based land use change projections to test the potential of an invasive species to expand or retreat in future.

THIS CHAPTER IS UNDER REVIEW IN "ECOLOGICAL INDICATORS

Land Use and Climate Change Interaction Triggers Contrasting Trajectories of Biological Invasion

1. INTRODUCTION

Global environmental change triggered by human activity represents an unprecedented threat to ecosystem function [1]. We know that the stability and functioning of all ecosystems on Earth is underpinned by biodiversity, represented by communities of species inhabiting individual ecosystems [2]. Each ecosystem function is dependent on a community with a specific composition, a change of species assemblage potentially leads to change of function [3]. Invasive species, defined as organisms that cause ecological or economic harm in a new environment where they are not native, contribute to global environmental change due to their increasing presence in all types of ecosystems [4]. Biological invasions increasingly threaten global biodiversity, economy, and even human health [5]. The success of invasive species is predominantly due to their ability to spread to new territories and due to the availability of unoccupied niches in the new area [6]. Niche availability may be altered by climate change and land-use change, both phenomena disturb existing ecosystem structure and create novel environments in the process [7]. Invasive species thus embody an example of a positive feedback; their invasiveness is aided by climate and land use change, while they themselves represent a factor of environmental change [8].

Climate change is predicted to significantly alter environmental conditions for most ecosystems [9]. Climate is a critical driver of biome distribution on Earth [10] and one of the most important drivers of biodiversity levels [11]. As well as altering the climatic envelope inhabited by species, extreme hydro-meteorological events such as floods or hurricanes may transport invasives to new regions [12]. Similarly, melting of icecaps is opening new Arctic shipping passages, an opportunity for many species to survive the journey and be introduced to a new region [13]. Most invasive species are opportunistic generalists with good dispersal potential, high population growth rates and a wide range of environmental tolerances [14]. Better capacity of invasives to adapt to new climates may potentially affect their interaction with native species, for example by rapidly increasing their population size or by affecting the extent of niche overlap between the native and invasive species [15]. Thus, climate change could potentially strengthen the invasive potential of these species [16].

At the same time, Land use and Land Cover (LULC) changes are critical to the introduction, establishment, and proliferation of invasives [17][18][19]. Changes in LULC create dispersal corridors and accelerate ecosystem disturbance (e.g., fragmentation), favouring the establishment of invasives [17][20]. LULC changes such as forest clearing for agriculture or pastureland, urban expansion, or field abandonment produce conditions suitable for biological invasions [20]. Interestingly, while LULC changes may create favourable conditions for some invasive species, they may inhibit the invasive potential of others [21][22]. Understanding the impact of LULC changes on niche availability is pivotal to forecasting invasion and to managing landscapes to reduce the spread of invasive species [18].

Climate change and LULC changes are often considered in isolation in current literature reporting on studies of ecosystem assemblage [23], overlooking the strong interaction between these two drivers of global change [24]. For example, forest degradation has been shown to reduce regional rainfall, thereby enhancing the impacts of climate change [25]. Similarly, populations with declining genetic diversity due to habitat degradation or fragmentation are less likely to adapt to climate change [26]. Although there is a wide range of future climate change and LULC scenarios available, there are several reasons why they have not been combined to project species' distribution. First, most of LULC data is available in coarse resolution and thus not able to reproduce ecological niches at finer scales [27]. Second, policy-based LULC projections are rarely available for most parts of the world [28].

Currently, one of the most efficient tools to predict the future spread of invasive species in a given area is the use of species distribution models (SDMs) [29]. SDMs correlate the presence of invasive species to environmental conditions and identify areas vulnerable to invasion, based on projected future conditions. Thus, it is critically important to feed SDMs with all variables that determine the spread of invasives and that reflect the impacts of anthropogenic activities over time [4]. Most existing SDM-based projections are based solely on climate variables and climate change scenarios [30][31][32]. Fewer studies use land cover for mapping the current distribution, but exclude this variable from future projections, making an assumption that either the species' future distribution is not sensitive to LULC changes, or the landscape composition remains constant in future [33]. However, it is no surprise that in a world dominated by humans, landscape patterns and ecosystem composition are rapidly changing, altering ecological ranges of species. Predictive models based on climatic data only may not represent the most plausible scenarios of species' future distribution [24]. There is a need to develop SDMs that combine climate change scenarios with policy-driven LULC projections and predict the distribution of ecologically important species using both of these synergistic factors [23].

In this study, we model the current and future distribution of an invasive species, *Rhododendron ponticum* (L.), in Wales using both climate and LULC projections for 2030. *R. ponticum* is an invasive plant species that was introduced to the British Isles as an ornamental plant from mainland Europe in the eighteenth century. It is a perennial, evergreen shrub that generally invades woodlands [34], although it is known to colonize other types of habitats too [29]. The novel contribution of this study is the use of current and future LULC maps at high spatial resolution (25 m), based on contrasting policies of forest management and land-use practice in Wales. Our previous work has shown that, a) land cover is the critical determinant of the distribution of *R. ponticum* [29], b) the distribution of *R. ponticum* can be best modelled at high spatial resolution (25 m) [35], and c) combinations of current policies of forest expansion and restoration of ecologically important habitats in Wales may lead to diverging patchwork of land use types in Wales by 2030 [36]. Thus, we aim to investigate the combined effect of climate change and LULC projections on future distribution of this invasive species in Wales. This study makes a theoretical contribution to the debate on combining climate change and LULC changes to predict species distribution and, at the same time, our observations are directly applicable to managing future invasion patterns of *R. ponticum* in Wales.

2. METHODOLOGY

4.5. Study Area and Species Records

Wales, a country in the UK, has an area of approximately 21000 km^2 and a population of over 3 million [37]. The country is characterized by a wide variety of landscapes, reflecting both its rugged topography and a long history of agricultural settlement and industrialization. A significant proportion of land (approx. 6000 km^2) is at an altitude above 300 m and considered mountainous. Welsh landscape contains a range of typical habitats; woodlands, semi-natural grasslands, arable agriculture, heathland, fens, bogs, coastal ecosystems including sand dunes and salt marshes, and a diverse range of upland and montane habitats [29][38].

We obtained distributional records for *R. ponticum* in Wales from the Global Biodiversity Information Facility (www.gbif.org/) by using the dismo R package [39]. We retrieved 8,764 presence records of *R. ponticum,* which we screened using recommended protocols [40]. Spatial uncertainty of all occurrence records was addressed by removing all duplicate or non-geo-referenced occurrence points. Occurrence records were spatially rarefied by eliminating all but one point within 1 km^2 of the study area to reduce clustering [35]. This resulted in a dataset of 1,280 presence records which were used in our modelling exercise.

4.6. Predictor Variables

We chose a set of 30 predictor variables based on a review of the literature [41][42][43][44], expert knowledge of the species and of the Welsh landscape, and the results of our earlier study on habitat suitability for *R. ponticum* [29]. We considered 19 bioclimatic variables (www.worldclim.org), 4 topographic variables (altitude, slope, hillshade and aspect, https://lta.cr.usgs.gov/SRTM1Arc), soil organic matter content (0-15 cm, https://soilgrids.org), land cover [36] and 5 proximate variables (distance from roads, watercourses, green spaces, motorway junctions and access points, https://digimap.edina.ac.uk). Based on the results presented in Chapter 3 of this thesis, all variables were resampled to 25 m spatial resolution as *R. ponticum* could be most accurately modelled at this scale [35]. We removed highly correlated variables to select the variable layers for use in final model runs by applying a Pearson correlation coefficient cut-off of $r \leq 0.70$ [45]. This step reduced the impact of multicollinearity and improved model conformity with statistical assumptions [46]. After omitting highly correlated variables, we were left with mean diurnal temperature range (bio 2), annual precipitation (bio 12), land cover, altitude, soil organic matter, distance from roads, and distance from motorway junctions.

4.7. Future Climate Change Scenarios

We used climate change scenarios for the year 2030 based on the IPCC 5th assessment report to model the effect of climate change on future distribution of *R. ponticum*. In an earlier investigation of the distribution of *R. ponticum* in Wales [29], we had tested future climate projections of six of the most recent General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, MIROC5, HadGEM2-ES, and MPI-ESM-LR. Three of these projections predicted a minor deviation from the current species distribution, whereas the other three GCMs depicted strong effects on the future distribution of this species. To account for this dichotomy, in the current study we use GISS-E2-R and MIROC5 to represent the high and low ends of the environmental conditions spectrum that may affect the distribution of *R. ponticum* in future. Furthermore, under each of the two GCMs, we consider two Representative Concentration Pathways (RCPs) - RCP 2.6 & RCP 8.6 to represent the best and the worst-case scenario of future GHG concentration [47]. In Chapter 2 of this thesis, I had used RCP 4.5 and 8.5, here, I chose RCP 2.6 as this trajectory of GHG concentration presents the best case scenario. The idea was to compare it with the worst case scenario (RCP 8.5) to increase the contrasting effects of climate change on the distribution of *R. ponticum*.

4.8. Future Land Use and Land Cover Change Scenarios

We used two *Land Use and Land Cover* (LULC) change projections for Wales for the year 2030 [36]. These projections were generated through the LULC modeling exercise presented in Chapter 4 of this thesis. The projections are based on contrasting policies of forest expansion and land management practice in Wales (see [36] for details). Both projections are informed by past LULC transitions (2007 – 2015). First, past LULC changes were explained by a suite of explanatory variables and then the trajectory of past LULC change was projected into the future using the Markov Chain and Multi-layer perceptron (MC-MLP) ensemble algorithms. The two future LULC scenarios, namely "**Business-as-Usual scenario**" and "**Ecosystem Conservation scenario**" (Supplementary Data S1, Figure 1) were motivated by the following storylines:

- The business-as-usual scenario (B-a-U) is the default scenario, which represents a linear projection of past trends (2007-2015) to 2030. This scenario assumes that the past trend and intensity of LULC change (e.g., new forest plantations, conversion of existing coniferous forests to broadleaf forests or the degradation of heath and bog) would continue until 2030.
- The ecosystem conservation scenario (E-C) is based on existing and proposed policies of the Welsh government and Natural Resources Wales on planting new woodlands, increasing the rate of conversion of coniferous forests to broadleaf forests, and improved conservation of heath and bog (see [36] for details). In the E-C scenario, the probability of Conifer-to-Broadleaf Forest conversion and the rate of conservation of heath and bog both increase by 50% as compared to the current rate. The scenario further assumes no deforestation of broadleaf forest until 2030. A detailed analysis of predicted LULC under both projections is presented in Supplementary Data S1 (Figure 2).

Thus, by combining the climate change and LULC change scenarios, we created eight future Land Use Land Cover and Climate (LULCC) change scenarios to model the effects of climate and land use change on the future distribution of *R. ponticum* in Wales (Table 1).

Table 1. Reference list of eight Land Use Land Cover & Climate (LULCC) Change scenarios for Wales in 2030, based on combinations of two Land Use & Land Cover (LULC) change scenarios, two General Circulations Models (GCMs) and two Representative Concentration Pathways (RCPs).

LULCC Change Scenarios	**LULC Scenario**	**Climate Change Scenarios**	
		GCMs	**RCPs**
1	B-a-U	GISS-E2-R	2.6
2	B-a-U	GISS-E2-R	8.5
3	B-a-U	MIROC5	2.6
4	B-a-U	MIROC5	8.5
5	E-C	GISS-E2-R	2.6
6	E-C	GISS-E2-R	8.5
7	E-C	MIROC5	2.6
8	E-C	MIROC5	8.5

4.9. Species Distribution Modelling Algorithm

We used MaxEnt, a maximum-entropy based machine learning (presence/pseudo-absence) algorithm to model the current and future distribution of *R. ponticum* (L.). MaxEnt predicts the distribution of a species on the basis of a given set of predictor variables and presence-only occurrence data [48]. We selected MAXENT primarily because it allows for the use of both continuous and categorical predictor variables [49], can handle complex interactions between predictor and response variables [50], and performs better than discriminative models while using presence-only records [49]. We used a reasonably large sample size [51] and applied the recommended screening and verification of occurrence records [35].

In MaxEnt, model complexity is primarily controlled by two factors: feature classes and regularization parameters [52]. Feature classes - Linear (L), Quadratic (Q), Hinge (H), Product (P), and Threshold (T) - transform predictor variables, whereas regularization multipliers penalize for overparameterization (for details, see [29]). MaxEnt-based models are prone to over-fitting due to their reliance on default options describing feature classes and regularization parameters [53][52]. Thus, an optimization of MaxEnt setting is recommended to avoid over-simplified or overly complex models [29]. To tune up the model, we used ENMeval [53] to create all possible combinations of selected parameters. We produced a total of 48 models using six combination of these feature classes (L, H, LQ, LQH, LQHP, LQHPT) and eight regularization multipliers (0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0) [54]. We then used corrected Akaike Information Criterion (AICc) to choose the best combination of feature class and regularization parameters.

We then ran MAXENT (version 3.4.1) with the default convergence threshold of 10^{-6} and with 5,000 iterations to allow the model a reasonable scope for convergence, thus reducing the risk of over-predicting or under-predicting the model relationships. The selected model used the “Linear,” “Quadratic” “Product,” and “Hinge” feature types and the regularization parameter of 2, as indicated by the lowest AICc value. We processed 25 model replications by bootstrap resampling, randomly allocating 80% of the occurrence records to calibration and 20% to validation. Habitat suitability maps under current and future LULCC change scenarios represent the average of the 25 replicate models.

MAXENT produces continuous suitability index in its output; 10 percentile training presence threshold was employed to convert this index into binary form (suitable or unsuitable habitat) [55].

4.10. Model Evaluation

We used the Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) to test the performance of the model against presence observations [50]. An AUC value of 0.5 shows that the model does not predict any better than random chance, whereas a value of 1 indicates a perfect performance of the model [56]. Percentage of contribution and permutation importance contribution were used to assess the relative significance of predictor variables. In addition to AUC, we used Continuous Boyce Index (CBI) as an additional assessment tool. The Boyce index requires presence data only and measures by how much model predictions differ from a random distribution of observed presence across the prediction gradient (for details, see [40]). The continuous values of the Boyce index vary between -1 and +1. Positive values indicate a model where predictions are consistent with the distribution of actual presence data, values close to zero mean that the model is no different from a random model and negative values indicate counter predictions (e.g., predicting no occurrence in areas where actual presence is recorded) [57][58].

5. RESULTS

3.1. Species Distribution Model Accuracy

We used 1280 presence points of *R. ponticum* and employed 6 least correlated variables to model the current and future distribution of this species in Wales under a range of LULCC change scenarios. The Maxent-based model with the lowest AICc showed encouraging predictive capacity: AUC_{train} = 81.8, AUC_{test} = 80.01, and CBI = 0.78. These results suggest that the predictor variables used during model calibration predicted the presence of *R. ponticum* in Wales with decent accuracy. Continuous and binary habitat suitability maps of the current distribution of *R. ponticum* in Wales are presented in Figure 1.

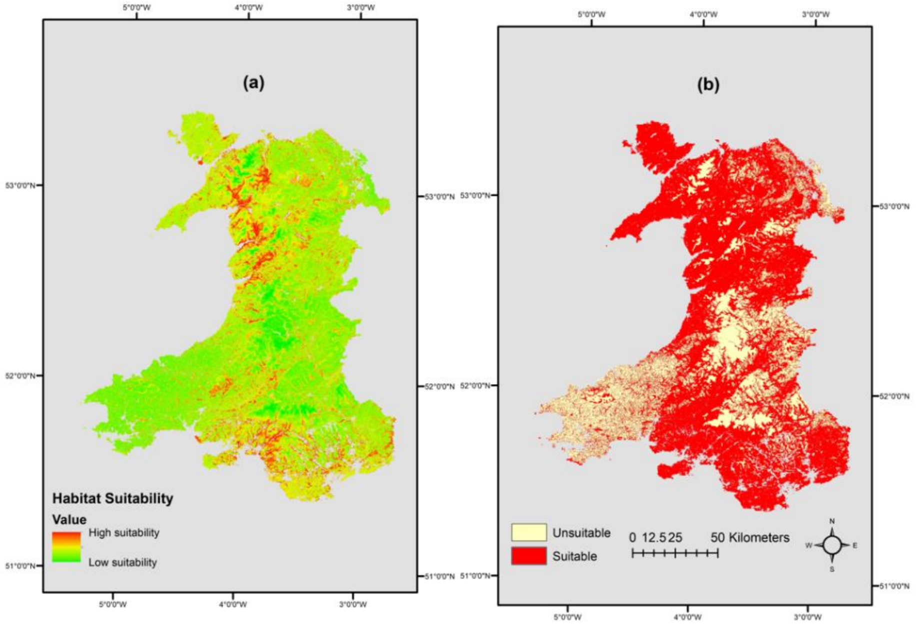

Figure 1. Present day continuous (a) and binary (b) habitat suitability maps of *R. ponticum* generated in MaxEnt-based *R. ponticum* distribution model.

3.2. Key Environment Variables

We used percentage contribution, permutation importance, and jack-knife test to assess the relative importance of environmental variables used to model the distribution of *R. ponticum* in Wales. As shown in Table 2, land cover has the highest contribution and permutation importance in predicting the distribution of *R. ponticum* whereas the distance from motorway junctions had the least percentage contribution and permutation importance. Furthermore, the Jack-knife test indicated that the land cover and distance from roads are the most significant variables, contributing the most to the models' predictive power (Figure 2).

Table 2. Percentage contribution and permutation importance of each variable for predicting the distribution of *R. ponticum* in Wales.

Variable	**Percent contribution**	**Permutation importance**
Land Cover	62.8	36.7
Distance from Roads	15.1	8.2
Altitude	5.6	27.9
bio_2	5.5	6.1
bio_12	5.4	5.7
Soil Organic Matter	4.2	14.1
Distance from Motorway Junction	1.5	1.3

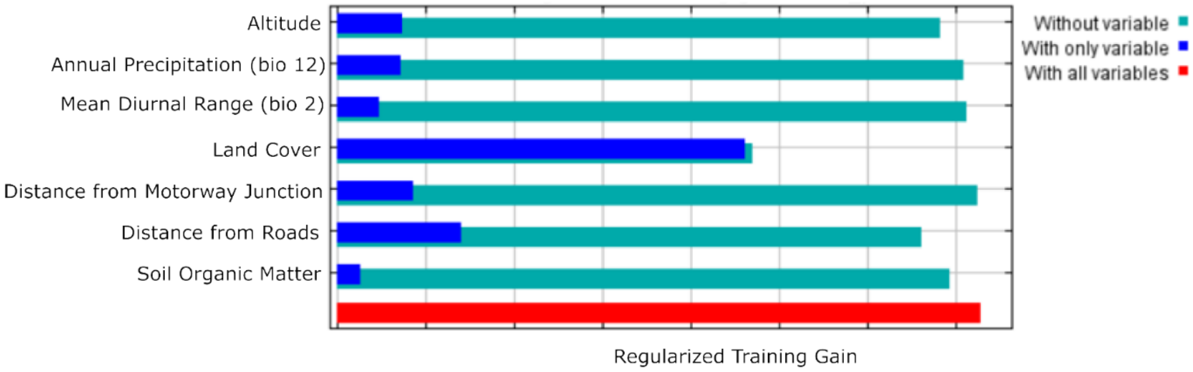

Figure 2. Jack-knife test of variable importance in the MaxEnt-based model for predicting the distribution of *R. ponticum* in Wales. Regularized training gain indicates how much better the MaxEnt distribution fits the present data compared to a uniform distribution. Dark blue bars indicate the gain from using each variable in isolation, light blue bars indicate the loss of gain by removing a single variable from the full model, the red bar indicates the gain using all variables.

Close inspection of individual response curves (Supplementary Data S2, Figure 3) shows logistic predictions by a specific variable, when the rest of the predictors are artificially kept at their average values. The response curve for land cover shows that land use category 1 and 2 (Broadleaf forest and coniferous forest, respectively) are the strongest predictors of *R. ponticum* distribution. Similarly, the response curves of distance from roads and distance from motorway junctions show that the invasive species is more likely to invade areas close to transportation networks. Furthermore, the presence of *R.*

ponticum is negatively associated with altitude. The response curves of bioclimatic variables (bio 2 and bio 12) show that its presence is lowest at extreme values of these variables.

3.3. Impact of LULCC Change on the Future Distribution of *R. ponticum*

Our models show that nearly 67 % or 1,396,607 ha is currently suitable for *R. ponticum* invasion, out of the total land area of 2,073,500 ha. Looking ahead on the basis of different LULCC change scenarios, the extent of habitat suitable for *R. ponticum* in Wales park is likely to contract under most of the LULCC change scenarios considered in this study (Figure 3).

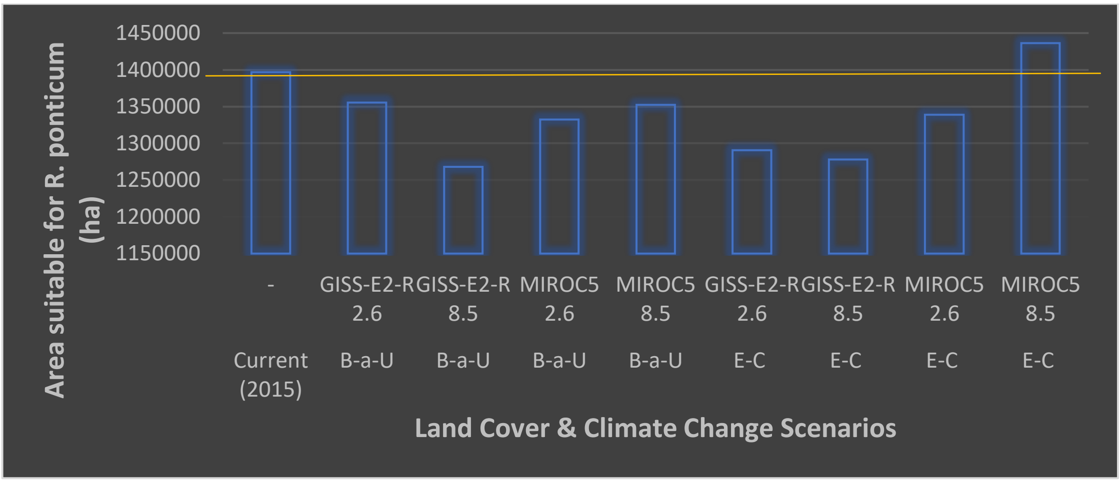

Figure 3. Area suitable for *R. ponticum* in Wales under eight LULCC change scenarios predicted for 2030. Recent Past refers to the baseline land cover and climatic conditions (2015), Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, Scenario 2: GISS-E2-R x RCP 8.5 x B-a-U, Scenario 3: MIROC5 x RCP 2.6 x B-a-U, Scenario 4: MIROC5 x RCP 8.5 x B-a-U, Scenario 5: GISS-E2-R x RCP 2.6 x E-C, Scenario 6: GISS-E2-R RCP 8.5 x E-C, Scenario 7: MIROC5 x RCP 2.6 x E-C, Scenario 8: MIROC5 x RCP 8.5 x E-C.

In all scenarios based on GCMs GISS-E2-R and GCM MIROC5 (Table 1), habitat suitability of *R. ponticum* is likely to decrease in future. The lowest habitat suitability is predicted by scenario 2 (B-a-U x GISS-E2-R x RCP 8.5), whereas the only instance of net expansion of habitat suitability is scenario 8 (E-C x MICROC5 x RCP 8.5). Binary habitat suitability maps of *R. ponticum* in Wales for all LULCC change scenarios are presented in Supplementary Data S1, Figure 5.

In all scenarios, including GCM GISS-E2-R (scenarios 1-2 & 5-6), new areas in the north-eastern and north-western edges of Wales are likely to become suitable for *R. ponticum* (Figure 4, a-b & e-f) and existing suitable areas of *R. ponticum* are likely to become unsuitable in the central and southern parts of Wales (Figure 5, a-b & e-f). In other scenarios, including GCM MIROC5 (3-4 & 7-8), new suitability spots are likely to emerge in the south-western coastal areas of Wales (Figure 4, c-d & g-h) whereas reduced suitability is likely along the eastern and northern parts of Wales (Figure 5, c-d & g-h).

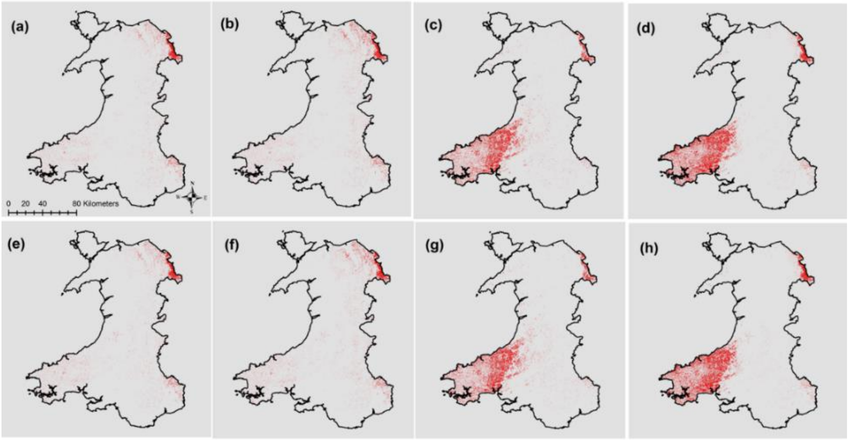

Figure 4. Maps showing areas of potential *R. ponticum* invasion in Wales by 2030 under future LULCC changes scenarios. a-h represent scenarios 1-8. (a) Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, (b) Scenario 2: GISS-E2-R x RCP 8.5 x B-a-U, (c) Scenario 3: MIROC5 x RCP 2.6 x B-a-U, (d) Scenario 4: MIROC5 x RCP 8.5 x B-a-U, (e) Scenario 5: GISS-E2-R x RCP 2.6 x E-C, (f) Scenario 6: GISS-E2-R RCP 8.5 x E-C, (g) Scenario 7: MIROC5 x RCP 2.6 x E-C, (h) Scenario 8: MIROC5 x RCP 8.5 x E-C.

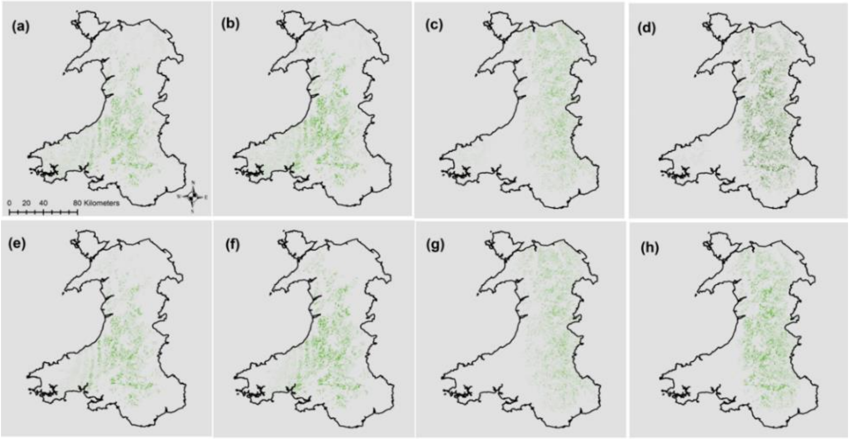

Figure 5. Maps showing areas in Wales which are likely to become unsuitable for *R. ponticum* by 2030 under future LULCC changes scenarios. a-h represent scenarios 1-8. Scenario a) Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, (b) Scenario 2: GISS-E2-R x RCP 8.5 x B-a-U, (c) Scenario 3: MIROC5 x RCP 2.6 x B-a-U, (d) Scenario 4: MIROC5 x RCP 8.5 x B-a-U, (e) Scenario 5: GISS-E2-R x RCP 2.6 x E-C, (f) Scenario 6: GISS-E2-R RCP 8.5 x E-C, (g) Scenario 7: MIROC5 x RCP 2.6 x E-C, (h) Scenario 8: MIROC5 x RCP 8.5 x E-C.

4. DISCUSSION

Accurate predictions of invasive species distribution and invasion trends are critical to understanding the impacts of global environmental change on terrestrial ecosystems and hence, pivotal to the development of global environmental change adaptation policy [59]. Such predictions are even more relevant in the contemporary world where the anthropogenic changes are likely to drive the sixth mass extinction event on Earth [60]. A considerable number of studies have looked at biological invasion, most however considering climate and LULC change - two key factors of global change - in isolation [61][62][63][64]. When considered together, the effect of climate and LULC change on ecosystems may be synergistic [65], leading to an under or overestimation of the effects of anthropogenic change on global ecosystems and biodiversity by the majority of the ecological models [66]. To the best of our knowledge, ours is one of the few investigations testing the combined effects of climate and LULC change and is the first attempt to model the distribution of an invasive species in Wales under these future scenarios.

4.1. Significance of Predictor Variables

Our results suggest that landscape features exert more influence than climate over the distribution of *R. ponticum* in Wales. Land cover is the most important variable determining its distribution, as it is often the critical variable limiting the distribution of a plant species [67]. LULC changes are closely associated with human population size and activity; invasive species are likely to take advantage of transportation networks and environments simplified by humans [68]. *R. ponticum* can invade a wide range of land cover classes, including forests, upland heaths and grasslands [69]. In Britain, forests represent the land cover class most susceptible to *R. ponticum* invasion [69]. In an earlier investigation of the distribution of *R. ponticum* in Snowdonia National Park, Wales, we found that this invasive species is most often found in “Mosaic Tree & Shrub” & “Needle Leaved Forest” [29]. This current study supports the earlier report by showing the preference of *R. ponticum* for conifer forests. A strong presence of *R. ponticum* in woodlands can be attributed to many reasons; environment suitable for seed germination [43], forest floor litter that supports *R. ponticum* growth [70] and shelter of woods that provides the necessary "cover" to spread without being eradicated [29].

In the current study, distance from roads is the second most important variable determining the distribution of *R. ponticum* in Wales. This is unsurprising, a number of studies have confirmed the strong relationship between road networks and the spread of invasive species [71][72][73]. In many ecosystems, roads facilitate biological invasions by providing the necessary corridors for the spread of invasives [72]. Roadsides are often typical for nutrient-rich soils and frequent disturbance [74]. Furthermore, surface permeability, increased exposure, and traffic on the roads affect the movement and direction of wind, water, and sometimes animals, which in turn affects the spread of invasive species [75][71]. Invasive species presence often declines with increasing distance from the road network; sometimes decreasing be a factor of 2 over tens of metres [72].

Land cover and distance from roads are followed by altitude and mean diurnal temperature range (bio 2) in terms of variable importance in the MaxEnt-based model in this study. The response curve (Supplementary Data S1, Figure 3) shows that the likelihood of *R. ponticum* presence is negatively correlated with altitude. Altitude may not have a direct effect on plant growth, but it is often considered a strong proxy for other variables important to species distribution. For example, exposure to sunlight, hydrology, soil physical and chemical properties, and wind speed may vary with increasing altitude, which in turn may be critical for the colonization by *R. ponticum* [76]. Earlier research has confirmed a strong relationship between mean diurnal temperature range ('bio 2' in the current study) and invasive plant species distribution [77]. Mean diurnal temperature range may affect biological invasion in many ways. For example, diurnal fluctuations in temperature increase seed germination and positively affect photosynthetic activity, especially in colder parts of the world [77]. Response curve (Supplementary Data S1, Figure 3) indicates that *R. ponticum* favours areas with higher values of 'bio 2', which is in agreement with earlier reports [77]. Furthermore, mean diurnal temperature range in Iberian Peninsula (the native range of *R. ponticum*) is ◦C 5.2 – 13.0 compared to the ◦C 5.4 – 7.0 (Table 3) in Wales which indicates that an increase in mean diurnal temperature range in Wales under future climate change scenarios is likely to improve habitat suitability for *R. ponticum* in Wales.

Table 3. Ranges of Bio 2 (mean diurnal range) and Bio 12 (mean annual precipitation) at present and under future climatic scenarios predicted for 2030.

		GISS-E2-R		**MIROC5**	
	Current	**RCP 2.6**	**RCP 8.5**	**RCP 2.6**	**RCP 8.5**
Bio 2 (◦C)	5.3 - 7.1	5.2 - 7.0	5.2 - 7.0	5.4 - 7.4	5.4 - 7.4
Bio 12 (mm)	718 - 1738	765 - 1783	790 - 1809	739 - 1757	788 – 1801

4.2. Effect of Climate and LULC Change Scenarios on Suitability of *R. ponticum* in Wales

Our analysis shows that the area suitable for *R. ponticum* is likely to contract in future. In our case, 7 out of the 8 LULCC change scenarios considered in this study indicate smaller suitable area than that at present. One of the main reasons for this could be the decline of coniferous forest cover from the current scenario under both B-a-U and E-C in future (Table 3). As shown by the response curves (Supplementary Data S1, Figure 3), presence of coniferous forests is the strongest predictor of *R. ponticum* occurrence, followed by the presence of broadleaf forest. *R. ponticum* favours acidic soils, coniferous forests may thus offer ideal growing conditions for this invasive species [78]. Existing UK Forestry Standard Guidelines on Biodiversity [79] and the UK Biodiversity Action Plan [36] both encourage large-scale conversion of coniferous forests to native broadleaf forests. This may benefit native species as native broadleaf woodland species would improve soil conditions for local flora and fauna, increase food availability and nesting opportunities for birds, reduce insect pests prevalence and enhance the overall aesthetics of the landscape [80][81][36]. Our model suggests that, alongside overall contraction, there is a possibility of an expansion in the *R. ponticum* habitat suitability in the southern-western and north-eastern parts of Wales. This could be attributed to increased forest cover in the south, which is likely to provide the required habitat, cover, and corridor for establishment and spread of *R.*

ponticum (Figure 6). In the north, appearance of new suitability hotspots could be due to expected change in the mean diurnal temperature range which may suit *R. ponticum* (Table 3, Figure 7). Evidence suggests that invasive species generally have higher energy demand for intense physiological activities; mean diurnal temperature range may affect species distribution.

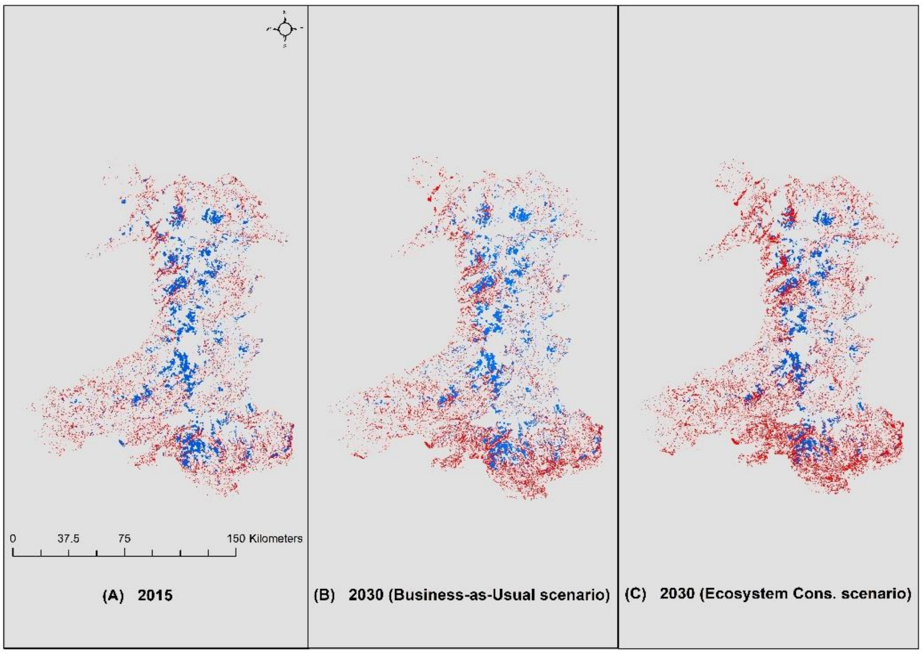

Figure 6. Spatial distribution of broadleaf (red pixels) and coniferous forests (blue pixels) in Wales under current (a) and future land use & land cover change scenarios (b and c).

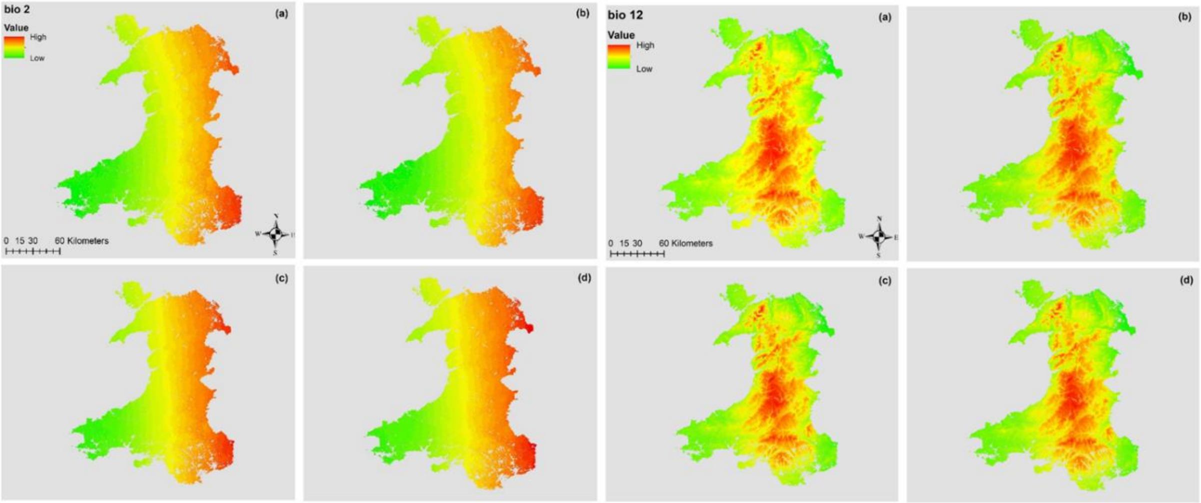

Figure 7. Spatial maps of bio 2 (mean diurnal range) and bio 12 (mean annual precipitation) under future climate change scenarios, a) GISS-E2-R x RCP 2.6, b) GISS-E2-R x RCP 8.5, c) MIROC5 x RCP 2.6, d) MIROC5 x RCP 8.5.

Land Use and Climate Change Interaction Triggers Contrasting Trajectories of Biological Invasion

The increase in future habitat suitability predicted by the GCM MIROC5 x RCP 8.5 x E-C scenario is very interesting. The E-C LULC change scenario depicts a future where overall forest cover will increase from the current 320,210 ha to 415,273 ha (Table 4). At the same time, RCP 8.5 indicates the highest projected GHG concentration pathway under which the mean diurnal temperature range will increase the most along the eastern foothills of Wales. It is possible that *R. ponticum* might take advantage of rapidly increasing forest cover and even though future forests are likely to be broadleaved and not conifers, their increasing extent will create an expanding niche for this invasive species. This observation underlines the importance of incorporating regional policy-driven LULC projections into invasive species distribution models. Extreme climate change and current plans for forest management may thus conspire to improve the future prospects of *R. ponticum* in Wales.

Table 4. Area under broadleaf, conifer and overall forest in Wales at present and under future business-as-usual (B-a-U) and ecosystem conservation (E-C) scenarios (data in hectares).

	Broadleaf forest	**Coniferous forest**	**Total Forest Cover**
Current	159951	160259	320210
B-a-U	203317	152780	356097
E-C	300367	114906	415273

4.3. Regional Policy-Driven LULC Change Scenarios Deserve More Attention

There is a strong consensus that models combining climate and LULC predictions are very good tools to predict species' distribution, usually far more accurate than climate-only models [82][83]. At fine spatial scales, land-use is often the factor driving the distribution and dispersal of species [4]. The interplay of climate and LULC changes may limit the spread of invasives in some cases, while promoting invasion in others [84][29][85][86]. To date, most invasive species distribution models have assumed homogenous and unchanging landscapes, mainly focussing on climate as the critical dynamic variable [87][62]. The attention has recently shifted towards considering landscape as a heterogenous variable that can affect the rate and trend of biological invasions [88]. This approach needs to be improved further because landscapes are not only heterogeneous but also subject to significant human pressure. Species distribution models cannot rely only on B-a-U projections to predict future species distributions, the trajectory and intensity of LULC change in the future is not likely to copy the past. The trajectory of change may vary, depending upon the socio-political and socio-economic factors of the region under study [89]. Researchers have considered global or continental LULC change scenarios to predict at local scale [82], we however argue that capturing the impact of local land management plans and policies is essential to develop realistic scenarios. One of the uses of the scenarios presented in our study is to relate the spread of *R. ponticum* or other invasive species to possible changes in both future landscapes and climate. A possible outcome of this type of modelling exercise is the design and targeting of land management policies to ecosystem conservation [90].

4.4. Implications for Landscape Management

Management of invasive species requires screening potential invasives through a process of risk assessment, which determines the likelihood that an invasive species would enter and inhabit a recipient area [82]. Most studies used in this type of screening of invasive species suggest either an increase [91] or a decrease in invasiveness [29]. We show that, for a single species in a well-defined area, expected LULC and climate changes may result in both an overall decrease or increase in future habitat suitability. If the purpose of the modelling exercise is to anticipate future trends of species distribution at fine spatial resolution, we suggest that (a) multiple regional change drivers should be considered, (b) future LULC change scenarios based on regional socio-economic and socio-political policies must be included, and (c) multiple combinations of climate and LULC change scenarios should be run to have confidence in predictions of future distribution of the species in question. We illustrate the use of this modelling framework against the backdrop of an invasive species spread, however its use to model distribution of all types of species can be easily envisaged. Alongside theoretical implications, our study has important traction for practical decisions on land management in Wales. We show that while the Welsh government aims to increase forest cover and cites biodiversity conservation as one of the reasons to do so, it is important to factor in and anticipate the spread of *R. ponticum* or other invasive species associated with woodlands. Specifically, a strategy combating the expansion of *R. ponticum* in the north-eastern and south-western regions should be considered. This is further discussed in Chapter 7 of this thesis.

CONCLUSION

This work demonstrates the need to understand and evaluate the combined effects of climate and policy-driven LULC scenarios on current and future distribution of *R. ponticum* in Wales. We show that the presence of *R. ponticum* is strongly associated with land cover but may be modified by strong climate change. Habitat suitability of *R. ponticum* is likely to decrease by 2030 in most future LULCC change scenarios we explore in this study, though its increase is plausible under a scenario that assumes substantial expansion of forest cover and rapid climate change. The study highlights the need for developing more detailed LULC scenarios, driven by regional policy developments in combination with a range of climate change scenarios. This approach may capture the heterogeneity of landscape and its changes that is exploited by *R. ponticum* and other invasive species.

SUPPLEMENTARY DATA S1

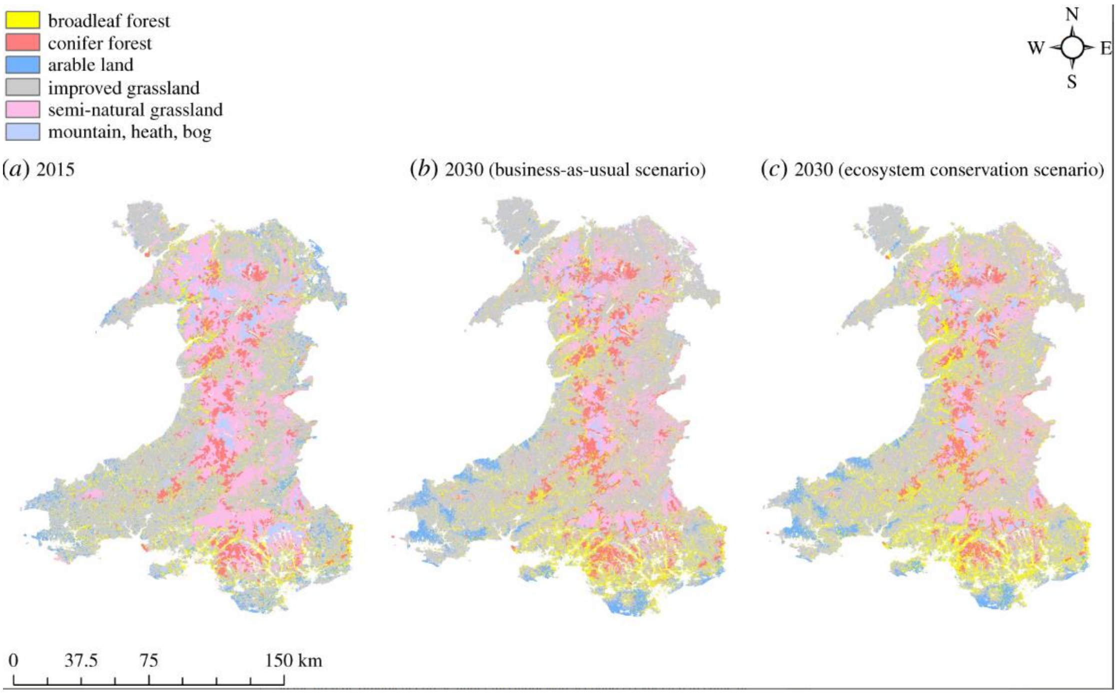

Figure S1. Current (*a*) and projected land use map of Wales, UK for the year 2030 under B-a-U (*b*) and EC (*c*) modelling scenarios. [36]

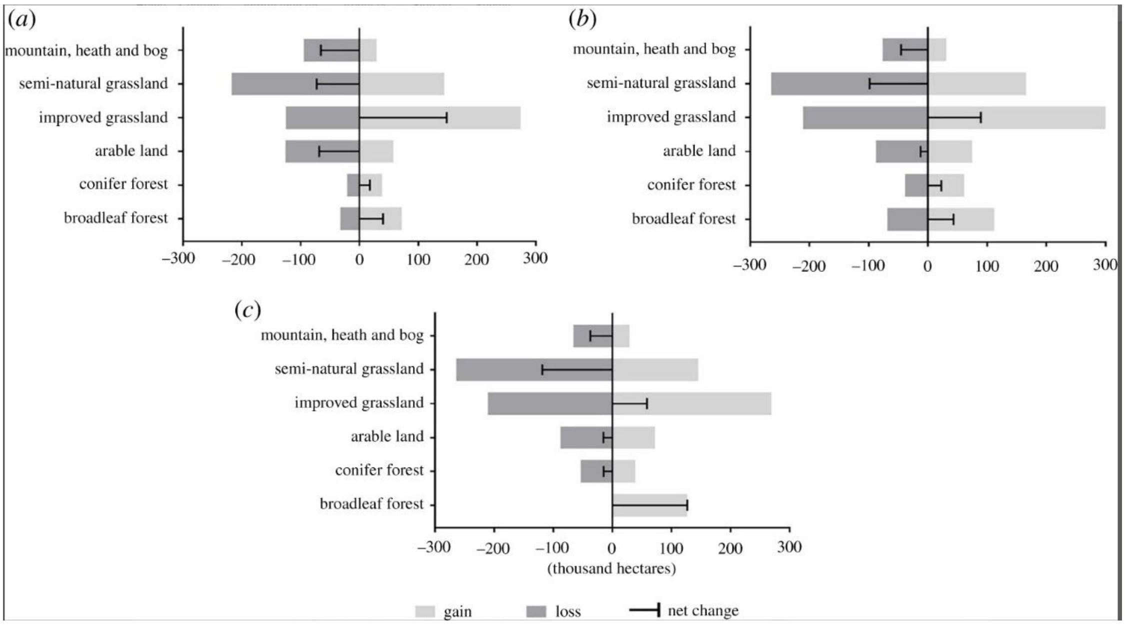

Figure S2. In Wales, UK, gains, losses and net changes between different LULC classes (hectares) during (*a*) 2007–2015, (*b*) 2015–2030 (B-a-U scenario) and (*c*) 2015–2030 (EC scenario) [36]

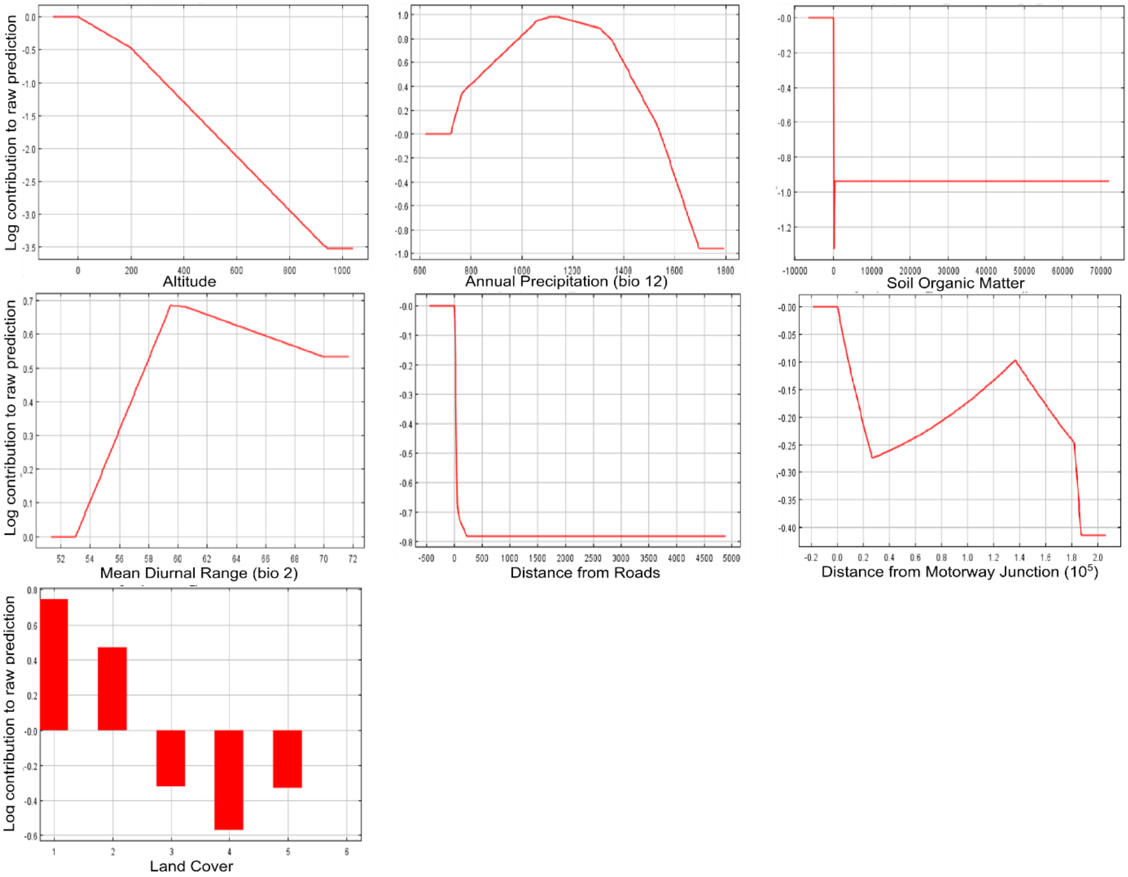

Figure S3. Response curves of environmental variables in the MaxEnt-based *R. ponticum* distribution model.

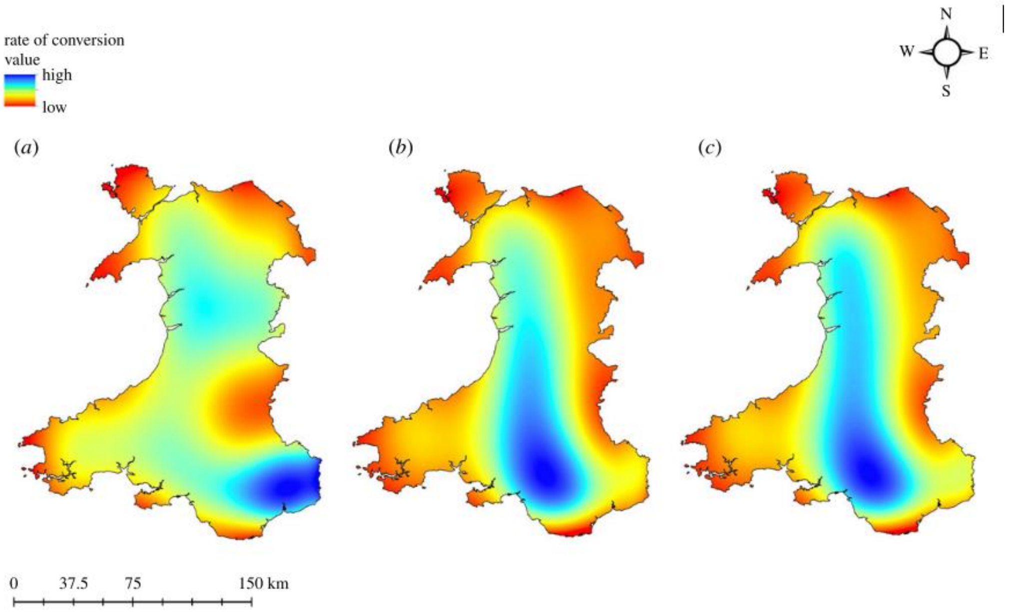

Figure S4. Heat map of large-scale trends of conifer to broadleaf forest conversion in Wales, UK during 2007–2015 (a), 2015–2030 B-a-U scenario (b) and 2015–2030 EC scenario (c). [36]

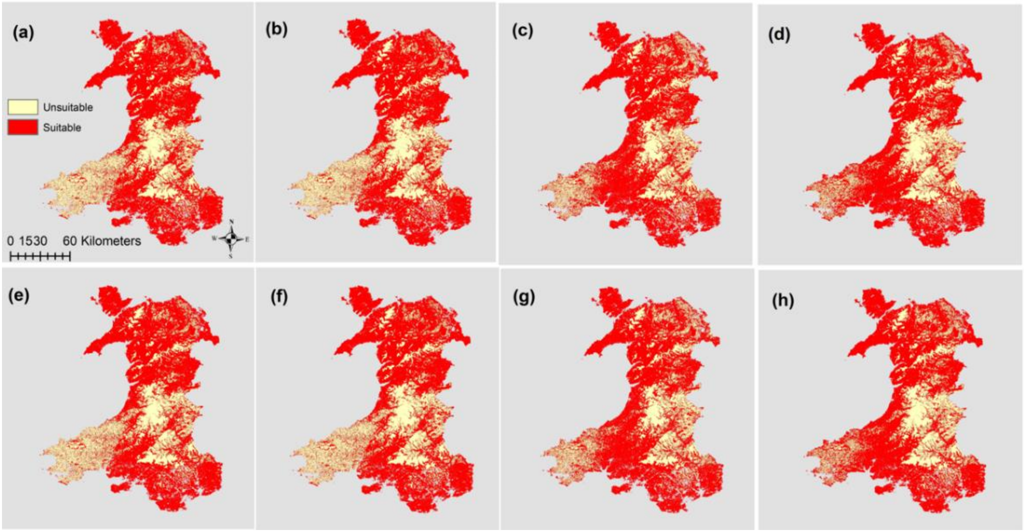

Figure S5. Binary habitat suitability maps of *R. ponticum* in Wales under future LULCC changes scenarios. a-h represent scenarios 1-8. Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, Scenario 2: GISS-E2-R x RCP 8.5 x B-a-U, Scenario 3: MIROC5 x RCP 2.6 x B-a-U, Scenario 4: MIROC5 x RCP 8.5 x B-a-U, Scenario 5: GISS-E2-R x RCP 2.6 x E-C, Scenario 6: GISS-E2-R RCP 8.5 x E-C, Scenario 7: MIROC5 x RCP 2.6 x E-C, Scenario 8: MIROC5 x RCP 8.5 x E-C.

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REFERENCE

1. Turner, B.L.; Lambin, E.F.; Reenberg, A. The emergence of land change science for global environmental change and sustainability. *Proc. Natl. Acad. Sci. U. S. A.* **2007**, *104*, 20666–20671.
2. Oliver, T.H.; Heard, M.S.; Isaac, N.J.B.; Roy, D.B.; Procter, D.; Eigenbrod, F.; Freckleton, R.; Hector, A.; Orme, C.D.L.; Petchey, O.L.; et al. Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* **2015**, *30*, 673–684.
3. Mace, G.M.; Norris, K.; Fitter, A.H. Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol. Evol.* **2012**, *27*, 19–26.
4. Ficetola, G.F.; Maiorano, L.; Falcucci, A.; Dendoncker, N.; Boitani, L.; Padoa-Schioppa, E.; Miaud, C.; Thuiller, W. Knowing the past to predict the future: Land-use change and the distribution of invasive bullfrogs. *Glob. Chang. Biol.* **2010**, *16*, 528–537.
5. Early, R.; Bradley, B.A.; Dukes, J.S.; Lawler, J.J.; Olden, J.D.; Blumenthal, D.M.; Gonzalez, P.; Grosholz, E.D.; Ibañez, I.; Miller, L.P.; et al. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* **2016**, *7*.
6. Bradley, B.A.; Blumenthal, D.M.; Wilcove, D.S.; Ziska, L.H. Predicting plant invasions in an era of global change. *Trends Ecol. Evol.* **2010**, *25*, 310–318.
7. Taylor, S.; Kumar, L.; Reid, N. Impacts of climate change and land-use on the potential distribution of an invasive weed: A case study of Lantana camara in Australia. *Weed Res.* **2012**, *52*, 391–401.
8. Mainka, S.A.; Howard, G.W. Climate change and invasive species: Double jeopardy. *Integr. Zool.* **2010**, *5*, 102–111.
9. Mooney, H.; Larigauderie, A.; Cesario, M.; Elmquist, T.; Hoegh-Guldberg, O.; Lavorel, S.; Mace, G.M.; Palmer, M.; Scholes, R.; Yahara, T. Biodiversity, climate change, and ecosystem services. *Curr. Opin. Environ. Sustain.* **2009**, *1*, 46–54.
10. Salazar, L.F.; Nobre, C.A.; Oyama, M.D. Climate change consequences on the biome distribution in tropical South America. *Geophys. Res. Lett.* **2007**, *34*, 2–7.
11. Kerr, J.T.; Pindar, A.; Galpern, P.; Packer, L.; Potts, S.G.; Roberts, S.M.; Rasmont, P.; Schweiger, O.; Colla, S.R.; Richardson, L.L.; et al. Climate change impacts on bumblebees converge across continents. *Science (80-.).* **2012**, *349*, 177–180.
12. Bhattarai, G.P.; Cronin, J.T. Hurricane activity and the large-scale pattern of spread of an invasive plant species. *PLoS One* **2014**, *9*.
13. Pyke, C.R.; Thomas, R.; Porter, R.D.; Hellmann, J.J.; Dukes, J.S.; Lodge, D.M.; Chavarria, G. Current practices and future opportunities for policy on climate change and invasive species. *Conserv. Biol.* **2008**, *22*, 585–592.
14. Diez, J.M.; D'Antonio, C.M.; Dukes, J.S.; Grosholz, E.D.; Olden, J.D.; Sorte, C.J.B.; Blumenthal, D.M.; Bradley, B.A.; Early, R.; Ibáñez, I.; et al. Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* **2012**, *10*, 249–257.
15. Lankau, R.A. Rapid Evolutionary Change and the Coexistence of Species. *Annu. Rev. Ecol. Evol. Syst.* **2011**, *42*, 335–354.
16. Alexander, J.M.; Levine, J.M. Earlier phenology of a nonnative plant increases impacts on native competitors. *Proc. Natl. Acad. Sci. U. S. A.* **2019**, *116*, 6199–6204.
17. With, K.A. The landscape ecology of invasive spread. *Conserv. Biol.* **2002**, *16*, 1192–1203.
18. Wang, W.; Zhang, C.; Allen, J.M.; Li, W.; Boyer, M.A.; Segerson, K.; Silander, J.A. Analysis and prediction of land use changes related to invasive species and major driving forces in the state of Connecticut. *Land* **2016**, *5*.
19. Álvarez-Berríos, N.L.; Redo, D.J.; Aide, T.M.; Clark, M.L.; Grau, R. Land change in the Greater Antilles between 2001 and 2010. *Land* **2013**, *2*, 81–107.
20. Vilà, M.; Ibáñez, I. Plant invasions in the landscape. *Landsc. Ecol.* **2011**, *26*, 461–472.
21. Degasperis, B.G.; Motzkin, G. Windows of opportunity: Historical and ecological controls on

Berberis thunbergii invasions. *Ecology* **2007**, *88*, 3115–3125.

22. Mosher, E.S.; Silander, J.A.; Latimer, A.M. The role of land-use history in major invasions by woody plant species in the northeastern north american landscape. *Biol. Invasions* **2009**, *11*, 2317–2328.
23. Betts, M.G.; Gutiérrez Illán, J.; Yang, Z.; Shirley, S.M.; Thomas, C.D. Synergistic Effects of Climate and Land-Cover Change on Long-Term Bird Population Trends of the Western USA: A Test of Modeled Predictions. *Front. Ecol. Evol.* **2019**, *7*, 1–11.
24. Opdam, P.; Wascher, D. Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* **2004**, *117*, 285–297.
25. Lawrence, D.; Vandecar, K. Effects of tropical deforestation on climate and agriculture. *Nat. Clim. Chang.* **2015**, *5*, 27–36.
26. Holt, R.D.; Keitt, T.H. Alternative causes for range limits: A metapopulation perspective. *Ecol. Lett.* **2000**, *3*, 41–47.
27. Wiens, J.A. Spatial Scaling in Ecology Published by : British Ecological Society Stable URL : https://www.jstor.org/stable/2389612 Spatial scaling in ecology1. *Funct. Ecol.* **1989**, *3*, 385–397.
28. Shirley, S.M.; Yang, Z.; Hutchinson, R.A.; Alexander, J.D.; Mcgarigal, K.; Betts, M.G. Species distribution modelling for the people: Unclassified landsat TM imagery predicts bird occurrence at fine resolutions. *Divers. Distrib.* **2013**, *19*, 855–866.
29. Manzoor, S.A.; Griffiths, G.; Iizuka, K.; Lukac, M. Land Cover and Climate Change May Limit Invasiveness of *Rhododendron ponticum* in Wales. *Front. plant Sci. Pap.* **2018**, *9*.
30. Xiaojun, K.; Qin, L.; Shirong, L. High-resolution bioclimatic dataset derived from future climate projections for plant species distribution modelling. *Ecol. Inform.* **2011**, *6*, 196–204.
31. Conrad, K.F.; Woiwod, I.P.; Perry, J.N. Long-term decline in abundance and distribution of the garden tiger moth (Arctia caja) in Great Britain. *Biol. Conserv.* **2002**, *106*, 329–337.
32. Roy, D.B.; Rothery, P.; Moss, D.; Pollard, E.; Thomas, J.A. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *J. Anim. Ecol.* **2008**, *70*, 201–217.
33. Bosso, L.; Luchi, N.; Maresi, G.; Cristinzio, G.; Smeraldo, S.; Russo, D. Predicting current and future disease outbreaks of Diplodia sapinea shoot blight in Italy: species distribution models as a tool for forest management planning. *For. Ecol. Manage.* **2017**, *400*, 655–664.
34. Tiedeken, E.J.; Stout, J.C. Insect-flower interaction network structure is resilient to a temporary pulse of floral resources from invasive *Rhododendron ponticum*. *PLoS One* **2015**, *10*, 1–19.
35. Manzoor, S.A.; Griffiths, G.; Lukac, M. Species distribution model transferability and model grain size – finer may not always be better. *Sci. Rep.* **2018**, *8*, 7168.
36. Manzoor, S.A.; Griffiths, G.; Latham, J.; Lukac, M. Scenario-led modelling of broadleaf forest expansion in Wales. *R. Soc. Open Sci.* **2019**, *6*.
37. *Statistical Bulletin: Annual Mid year Population Estimates: 2013*; 2014;
38. Swetnam, R.D.; Tweed, F.S. A tale of two landscapes: Transferring landscape quality metrics from Wales to Iceland. *Land use policy* **2018**, 0–1.
39. Hijmans, R.J.; Phillips, S.; Leathwick, J.; Elith, J. Dismo: Species Distribution Modelling 2011.
40. Manzoor, S.A.; Griffiths, G.; Lukac, M. Species distribution model transferability and model grain size – finer may not always be better. *Sci. Rep.* **2018**, 1–9.
41. Harris, C.M.; Stanford, H.L.; Edwards, C.; Travis, J.M.J.; Park, K.J. Integrating demographic data and a mechanistic dispersal model to predict invasion spread of *Rhododendron ponticum* in different habitats. *Ecol. Inform.* **2011**, *6*, 187–195.
42. Erfmeier, A.; Bruelheide, H. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. *Flora - Morphol. Distrib. Funct. Ecol. Plants* **2004**, *199*, 120–133.
43. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–

758.

44. Eşen, D.; Zedaker, S.M.; Kirwan, J.L.; Mou, P. Soil and site factors influencing purple-flowered rhododendron (*Rhododendron ponticum* L.) and eastern beech forests (Fagus orientalis Lipsky) in Turkey. *For. Ecol. Manage.* **2004**, *203*, 229–240.
45. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop.).* **2013**, *36*, 027–046.
46. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. *PLoS One* **2013**, *8*.
47. Moss, R.H.; Edmonds, J.A.; Hibbard, K.A.; Manning, M.R.; Rose, S.K.; Van Vuuren, D.P.; Carter, T.R.; Emori, S.; Kainuma, M.; Kram, T.; et al. The next generation of scenarios for climate change research and assessment. *Nature* **2010**, *463*, 747–756.
48. Phillips SJ Dudik M, S.R.E. A maximum entropy approach to species distribution modelling. **2004**, 655–662.
49. Elith, J.; Phillips, S.J.; Hastie, T.; Dudík, M.; Chee, Y.E.; Yates, C.J. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **2011**, *17*, 43–57.
50. Elith, J.; Graham, C.H.; Anderson, R.P.; Dudik, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.).* **2006**, *29*, 129–151.
51. Wisz, M.S.; Hijmans, R.J.; Li, J.; Peterson, A.T.; Graham, C.H.; Guisan, A.; Elith, J.; Dudík, M.; Ferrier, S.; Huettmann, F.; et al. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **2008**, *14*, 763–773.
52. Moreno-Amat, E.; Mateo, R.G.; Nieto-Lugilde, D.; Morueta-Holme, N.; Svenning, J.C.; Garc??a-Amorena, I. Impact of model complexity on cross-temporal transferability in Maxent species distribution models: An assessment using paleobotanical data. *Ecol. Modell.* **2015**, *312*, 308–317.
53. Muscarella, R.; Galante, P.J.; Soley-Guardia, M.; Boria, R.A.; Kass, J.M.; Uriarte, M.; Anderson, R.P. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for <scp>Maxent</scp> ecological niche models. *Methods Ecol. Evol.* **2014**, *5*, 1198–1205.
54. Obiakara, M.C.; Fourcade, Y. Climatic niche and potential distribution of Tithonia diversifolia (Hemsl.) A. Gray in Africa. *PLoS One* **2018**, *13*, 1–18.
55. Rebelo, H.; Jones, G. Ground validation of presence-only modelling with rare species: A case study on barbastelles Barbastella barbastellus (Chiroptera: Vespertilionidae). *J. Appl. Ecol.* **2010**, *47*, 410–420.
56. Swets, J.A. Measuring the accuracy of diagnostic systems. *Science* **1988**, *240*, 1285–1293.
57. Boyce, M.S.; Vernier, P.R.; Nielsen, S.E.; Schmiegelow, F.K.A. Evaluating resource selection functions. *Ecol. Modell.* **2002**, *157*, 281–300.
58. Hirzel, A.H.; Le Lay, G.; Helfer, V.; Randin, C.; Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* **2006**, *199*, 142–152.
59. Titeux, N.; Henle, K.; Mihoub, J.B.; Regos, A.; Geijzendorffer, I.R.; Cramer, W.; Verburg, P.H.; Brotons, L. Global scenarios for biodiversity need to better integrate climate and land use change. *Divers. Distrib.* **2017**, *23*, 1231–1234.
60. Barnosky, A.D.; Matzke, N.; Tomiya, S.; Wogan, G.O.U.; Swartz, B.; Quental, T.B.; Marshall, C.; McGuire, J.L.; Lindsey, E.L.; Maguire, K.C.; et al. Has the Earth's sixth mass extinction already arrived? *Nature* **2011**, *471*, 51–57.
61. Mamun, M.; Kim, S.; An, K.G. Distribution pattern prediction of an invasive alien species largemouth bass using a maximum entropy model (MaxEnt) in the Korean peninsula. *J. Asia-Pacific Biodivers.* **2018**, *11*, 516–524.
62. Xu, D.; Zhuo, Z.; Wang, R.; Ye, M.; Pu, B. Modelling the distribution of Zanthoxylum armatum in China with MaxEnt modelling. *Glob. Ecol. Conserv.* **2019**, *19*, e00691.

63. Yan, H.; Feng, L.; Zhao, Y.; Feng, L.; Zhu, C.; Qu, Y.; Wang, H. Predicting the potential distribution of an invasive species, Erigeron canadensis L., in China with a maximum entropy model. *Glob. Ecol. Conserv.* **2020**, *21*, e00822.
64. Yan, H.; Feng, L.; Zhao, Y.; Feng, L.; Wu, D.; Zhu, C.; Ecology, G. Prediction of the spatial distribution of Alternanthera philoxeroides in China based on ArcGIS and MaxEnt. **2019**.
65. Anteau, M.J.; Wiltermuth, M.T.; van der Burg, M.P.; Pearse, A.T. Prerequisites for Understanding Climate-Change Impacts on Northern Prairie Wetlands. *Wetlands* **2016**, *36*, 299–307.
66. Stanton, J.C.; Pearson, R.G.; Horning, N.; Ersts, P.; Reşit Akçakaya, H. Combining static and dynamic variables in species distribution models under climate change. *Methods Ecol. Evol.* **2012**, *3*, 349–357.
67. Yang, X.Q.; Kushwaha, S.P.S.; Saran, S.; Xu, J.; Roy, P.S. Maxent modelling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in Lesser Himalayan foothills. *Ecol. Eng.* **2013**, *51*, 83–87.
68. McKinney, M.L. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **2006**, *127*, 247–260.
69. Dehnen-Schmutz, K.; Williamson, M. *Rhododendron ponticum* in Britain and Ireland: Social, economic and ecological factors in its successful invasion. *Environ. Hist. Camb.* **2006**, *12*, 325–350.
70. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
71. Flory, S.L.; Clay, K. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecol.* **2006**, *184*, 131–141.
72. Tyser, R.W.; Worley, C.A.; Tyser, R.W.; Worley, C.A. Society for Conservation Biology Alien Flora in Grasslands Adjacent to Road and Trail Corridors in Glacier National Park , Published by : Wiley for Society for Conservation Biology Alien Flora in Grasslands Adjacent to Road and Trail Corridors in Glacier . **2016**, *6*, 253–262.
73. Gelbard, J.L.; Belnap, J. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conserv. Biol.* **2003**, *17*, 420–432.
74. Trombulak, S.C.; Frissell, C.A. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* **2000**, *14*, 18–30.
75. Myers, J.A.; Vellend, M.; Gardescu, S. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* **2004**, *139*, 35–44.
76. Körner, C. The use of “altitude” in ecological research. *Trends Ecol. Evol.* **2007**, *22*, 569–574.
77. Chen, B.M.; Gao, Y.; Liao, H.X.; Peng, S.L. Differential responses of invasive and native plants to warming with simulated changes in diurnal temperature ranges. *AoB Plants* **2017**, *9*.
78. Jones, G.L.; Tomlinson, M.; Owen, R.; Scullion, J.; Winters, A.; Jenkins, T.; Ratcliffe, J.; Gwynn-Jones, D. Shrub establishment favoured and grass dominance reduced in acid heath grassland systems cleared of invasive *Rhododendron ponticum*. *Sci. Rep.* **2019**, *9*, 1–10.
79. Barsoum, N.; Henderson, L. Converting planted non-native conifer to native woodlands: a review of the benefits, drawbacks and experience in Britain. **2016**, 1–10.
80. Brandtberg, P.O.; Lundkvist, H.; Bengtsson, J. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. *For. Ecol. Manage.* **2000**, *130*, 253–264.
81. Crawford, R.M.M.; Jeffree, C.E.; Rees, W.G. Paludification and forest retreat in northern oceanic environments. *Ann. Bot.* **2003**, *91*, 213–226.
82. Di Febbraro, M.; Menchetti, M.; Russo, D.; Ancillotto, L.; Aloise, G.; Roscioni, F.; Preatoni, D.G.; Loy, A.; Martinoli, A.; Bertolino, S.; et al. Integrating climate and land-use change scenarios in modelling the future spread of invasive squirrels in Italy. *Divers. Distrib.* **2019**, *25*,

644–659.
83. Marshall, L.; Biesmeijer, J.C.; Rasmont, P.; Vereecken, N.J.; Dvorak, L.; Fitzpatrick, U.; Francis, F.; Neumayer, J.; Ødegaard, F.; Paukkunen, J.P.T.; et al. The interplay of climate and land use change affects the distribution of EU bumblebees. *Glob. Chang. Biol.* **2018**, *24*, 101–116.
84. Dukes, J.S.; Mooney, H.A. Does global change increase the success of biological invaders? **1999**, *14*, 135–139.
85. Bellard, C.; Thuiller, W.; Leroy, B.; Genovesi, P.; Bakkenes, M.; Courchamp, F. Will climate change promote future invasions? *Glob. Chang. Biol.* **2013**, *19*, 3740–3748.
86. Bezeng, B.S.; Morales-Castilla, I.; Van Der Bank, M.; Yessoufou, K.; Daru, B.H.; Davies, T.J. Climate change may reduce the spread of non-native species. *Ecosphere* **2017**, *8*.
87. Hastings, A.; Cuddington, K.; Davies, K.F.; Dugaw, C.J.; Elmendorf, S.; Freestone, A.; Harrison, S.; Holland, M.; Lambrinos, J.; Malvadkar, U.; et al. The spatial spread of invasions: New developments in theory and evidence. *Ecol. Lett.* **2005**, *8*, 91–101.
88. O'Reilly-Nugent, A.; Palit, R.; Lopez-Aldana, A.; Medina-Romero, M.; Wandrag, E.; Duncan, R.P. Landscape Effects on the Spread of Invasive Species. *Curr. Landsc. Ecol. Reports* **2016**, *1*, 107–114.
89. Falcucci, A.; Maiorano, L.; Boitani, L. Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landsc. Ecol.* **2007**, *22*, 617–631.
90. van Vuuren, D.P.; Isaac, M.; Kundzewicz, Z.W.; Arnell, N.; Barker, T.; Criqui, P.; Berkhout, F.; Hilderink, H.; Hinkel, J.; Hof, A.; et al. The use of scenarios as the basis for combined assessment of climate change mitigation and adaptation. *Glob. Environ. Chang.* **2011**, *21*, 575–591.
91. Bradley, B.A.; Wilcove, D.S.; Oppenheimer, M. Climate change increases risk of plant invasion in the Eastern United States. *Biol. Invasions* **2010**, *12*, 1855–1

GENERAL DISCUSSION

1. Determinants of *R. ponticum* Distribution

In order to explore the environmental predictors that determine the distribution of *R. ponticum* in the UK, I considered Wales as a case study since this region is one of the hotspots of *R. ponticum* invasion in the UK. For the analysis presented in the first two chapters of this study, I selected Snowdonia and Brecon Beacons National parks to map current distribution, project future distribution and understand the species distribution model performance and transferability. These two parks were selected because a) *R. ponticum* invasion is widespread in here and, b) reliable presence data of *R. ponticum* is available for these national parks.

The following variables were found responsible for determining the distribution of *R. ponticum*.

1.1. Land Cover

Land use has repeatedly been shown to be the critical predictor determining plant species distribution [1]. *R. ponticum* can invade a range of land cover categories, including natural to semi-natural, upland heaths, and occasionally grasslands. In Britain, earlier studies reporting on its occurrence suggest that woodland is the land cover type most affected by the invasion of *R. ponticum* [2]. The results of Chapter 2 of this study are in agreement with these reports; *R. ponticum* has the highest probability of occurrence in land cover categories representing "Mosaic Tree & Shrub" and "Needle Leaved Forest." There are numerous reasons why *R. ponticum* favours woodland in Wales, for example, the availability of a microenvironment suitable for seed germination [3] or growing under tree canopies to spread "under-cover" and thus avoid eradiation likely play a role. Crucially, the presence of dead plant material or moss cover may be critical to *R. ponticum* establishment [4]. In this study, Mosaic Tree & Shrub and Forests were the land cover categories that are likely to contain these substrates in the understory.

1.2. Topography

Among the topographic variables, aspect made a significant contribution to the model presented in Chapter 1 of this study. *R. ponticum* favours the northern aspect for its establishment and growth.

North-facing slopes at the latitude of Wales are likely to offer greater soil moisture, in addition to lower direct insulation intensity. The results show that the probability of occurrence of *R. ponticum* in Snowdonia National Park is negatively correlated with slope. Earlier studies suggested that shallow-slope areas are typically those with high soil moisture and nutrient availability, thus offering a more favourable microenvironment for plant proliferation [5]. Altitude, another important topographic variable, explained a minor share of the variation in the training set of occurrence observations in this study. Even though altitude is considered an indirect variable since it has no direct effect on plant growth and physiology, it acts as a very good proxy of other un-measured or un-used variables such as hydrology, exposure to light, wind speed, soil type and others which are not included in my model.

1.3. Climate

Both temperature and precipitation related variables made a significant contribution to model prediction (Chapter 2), which is in agreement with earlier studies which posit that the future distribution of *R. ponticum* in Wales may be affected by climatic predictors [5]. Under all GCMs considered, habitat suitability range decreases from the current situation. Increasing temperature and changes in precipitation are likely to impact species distribution [6]. However, existing investigations paint a mixed picture; plant species may experience an increase or a decrease in their current range [7][8]. A study investigating potential changes in the future distribution of 100 of the world's worst invasive species concluded that the potential range of the majority of these species would increase [9]. Contrary to this, there is evidence of a range reduction of over 80 invasive species in South Africa under varying climate change scenarios [6].

1.4. Distance from Roads

Distance from roads is another important variable determining the distribution of *R. ponticum* in Wales. This is unsurprising as a number of studies have confirmed the strong relationship between road networks and the spread of invasive species [7][8][9]. In many ecosystems, roads facilitate biological invasions by providing the necessary corridors for the spread of invasives [7]. Roadsides are often typical for nutrient-rich soils and frequent disturbance [9]. Furthermore, surface permeability, increased exposure, and traffic on the roads affect the movement and direction of wind, water, and sometimes animals, which in turn affects the spread of invasive species [9][10]. Invasive species presence often declines with increasing distance from the road network; sometimes decreasing be a factor of 2 over tens of metres [7].

An important point to consider is the correlation cut-off value to drop the highly correlated variables. In literature, different values (i.e. 0.85, 0.75, 0.7) are reported. In Chapter 2 I used 0.85 and in subsequent chapters I used 0.75 and 0.7. The most widely accepted value is 0.70 and should be used as a threshold in future studies.

2. Ecological Niche Shift in *R. ponticum*

The fact that *R. ponticum* is an alien invasive species is an important aspect of this study. One of the ways to build a species distribution model is to use climatic data and occurrence records from the native range of the invasive species under consideration and to project it to the invaded region [10]. This is because the ecological niche of species is assumed to be conserved while developing species distribution models. However, invasives are a good example of species with the potential to expand their range beyond the climatic envelope defined in their native range [11]. Several studies have confirmed this idea by concluding that invaded locations cannot necessarily be predicted from native distribution records of invasive species [12]. In the case of *R. ponticum*, there was absence of any evidence on whether the ecological niche of *R. ponticum* is conserved. The results of Chapter 5 present evidence that the ecological niche of *R. ponticum* is not conserved in its invaded region, and therefore it is not advisable to train models in its native range if the objective is to map its distribution in the invaded region.

2.1. Evidence of Niche Shift in Britain

In this study (Chapter 5), I compared the ecological niche of *R. ponticum* in its native and invasive ranges and tested the hypothesis of niche divergence. While previous studies have analysed the genetic material of *R. ponticum* populations to look for evidence of hybridization [13], this study is the first effort to model ecological niches and spatial distribution of this species in its native and invasive ranges by comparing niche differences in a gridded environmental space. I found a minimal niche overlap between *R. ponticum* populations in the Iberian Peninsula and Britain. The results indicate that *R. ponticum* largely occupies novel niches in Britain. Also, the MaxEnt-based reciprocal distribution models fail to predict species distribution in target ranges, confirming that the environmental conditions occupied by *R. ponticum* in its native range differ from those occupied in the invasive range. The pattern and the extent to which species' niches are conserved or shift over space and time is a key determinant of their response to local and global environmental change [14]. Predictive maps generated by reciprocal distribution models suggest that the current distribution of *R. ponticum* in Britain is mostly clustered in the western and northern parts which are the cooler and more humid parts of the country, whereas in its native range the species is present in the southern tips of Spain and southern and western parts of Portugal typical for milder temperature regime and less rainfall. Thus, the distribution model calibrated in Iberia incorrectly places the distribution to eastern Britain. This part of Britain is ecologically similar to conditions occupied by the species in the Iberian Peninsula, but it is not where the species is currently found. The actual distribution of *R. ponticum* in Britain is centred in Wales and the Scotland, areas with some of the lowest mean annual temperatures in the whole of Britain.

2.2. Hybridization May Have Caused Rapid Niche Expansion of *R. ponticum* in Britain

The analysis (Chapter 5) shows that the population of *R. ponticum* in Britain has expanded and shifted its range to such an extent that using a model trained on its native range to predict it results in a complete mismatch. It is essential to keep in sight that the observed niche shift could either be due to an evolutionary process such as hybridization (changing fundamental niche hypothesis [15]) or it could be driven by a difference in the biotic environment between the native and invasive range (enemy-release hypothesis [16]), or indeed due to a combination of these reasons.

Given that the species was brought to the country about 200 years ago, such a shift would indicate genetic change caused by rapid introgression of genes rather than mutation. There are contradicting reports on whether the *R. ponticum* population in Britain has undergone hybridization. However, both existing reports on the genetics of *R. ponticum* in Britain have limitations. Milne and Abbott in 2000 [17] posit that increased frost hardiness results from directional selection introgression but were limited by the lack of sufficient genetic analysis. The follow-up study of Erfmeier et al. in 2011 [13] which claimed absence of any evidence of hybridization in *R. ponticum* population of Britain was limited only to the Irish population of *R. ponticum* and thus may not be generalizable for the Welsh and Scottish populations. Only a concerted testing of both an introgression by means of nuclear markers and the frost hardiness by means of experimental determination on a sample covering all populations from the British Isles may be able to identify the driver of *R. ponticum* expansion in Britain.

3. Determining the Optimum Grain Size for *R. ponticum* Distribution Modelling

At this stage, I had identified the key determinants of *R. ponticum* distribution (Chapter 2) and found evidence of ecological niche shift, implying that the models of this invasive should be trained within its invaded range to project future distribution in Britain. The next step was to identify the optimum grain size for developing accurate species distribution models. A number of studies have highlighted the fact that coarse grain size of predictor variables in SDMs may obscure effects of biotic interactions, small-scale heterogeneity of abiotic factors and micro habitat of species [18][19]. A review of 149-peer reviewed publications concluded that the choice of grain size is a highly neglected aspect in species distribution modelling and is a factor that significantly impacts modelling outcomes [20]. In this study (Chapter 3), species distribution models were built using different grain sizes (50m, 300m and 1000 m) and model performance and transferability was evaluated.

3.1. Model Performance in the Training Area

The results from this study show that MAXENT model predictions in the training area are likely to improve with smaller grain size of predictor variables. It has been claimed that too coarse a grain size in SDMs leads to spatial smoothing and thus obscures the connection between, for example, land cover types and species occurrence [21]. This occurs by homogenizing the dominant land types within a grid cell resulting in the loss of useful information for accurate modelling [22]. In accordance with this assertion, the accuracy of model predictions in my study improved with decreasing grain size of the predictor variables, possibly as the result of capturing small-scale ecological interactions critical for species distribution being maximized at a finer grain size [19][23]. As grain size becomes finer, the number of mixed pixels decreases, leading to an increase in 'distinct' pixels which clearly separate different land cover, topographical or environmental units (or classes) and thus enables the algorithm to build more accurate species-habitat relationships [24]. This improvement becomes more relevant when the species being modelled is a habitat specialist. Since *R. ponticum* is considered one such species – in Wales it has a high preference for woodlands – better performance of models using small grain size data can be explained by improving representation of this community type.

3.2. Model Performance in the Transfer Area

After assessing model performance in the training area, the second goal of the study was to test the effects of grain size on the spatial transferability of the model (i.e. training the model in Snowdonia National Park and transferring model to Brecon Beacons National Park). The results suggest that a coarse grain size (1000 m) produced the poorest model transferability while a medium grain size (300 m) resulted in the most accurate transfer of the model. The poor model transferability at 1 km grain size may be explained by the fact that key environmental factors, which in this case were land cover and topography, are 'averaged out' at coarser grain size both in the training and the transfer areas [18]. I expected the best model transferability when using data with the finest grain size. This was not the case; the transferred model had the best predictive power at medium grain size. A possible explanation is that Snowdonia National Park (training area) and Brecon Beacons National Park (transfer area) differ in the range and the character of topographical features. Since topography and land cover are best represented at small grain size, a discrepancy in the typography of landscape features between the two areas will negatively affect model transferability. Similarly, it has been shown that species occurrence data needs to be highly accurate when modelled at very fine grain size as any location [25][26] errors in the survey data may impact model performance.

3.3. Bioclimatic Variables in SDMs – An Inevitable Choice?

In the context of our results it appears that unnecessary or 'customary' use of bioclimatic variables without considering the species' ecology negatively affects the predictive potential of an SDM. Including these bioclimatic variables almost always comes at a cost of reducing the grain size of other variables, such as topography and land cover. However, as climate is likely to be one of the determinants of a species' fundamental niche, I suggest that expert knowledge of species' ecology and an extensive review of the literature should be carried out before deciding whether or not to include climatic variables in a SDM. Naturally, when modelling large-scale distributions (continental or global) or if the objective is a temporal prediction, perhaps to account for climate change, there currently may not be many alternatives to a 1 km grain size bioclimatic variables at a global scale. Choice of predictor variables is also a matter of the research question. If researches are strictly interested in estimating climatic suitability or sensitivity, then the climatic variables become an appropriate choice. Our results strictly refer to cases where researchers might be interested in mapping species' distribution with high accuracy using the best possible combination of all the available predictor variables.

Accuracy of presence/occurrence point is also critical in developing useful SDMs. A number of studies emphasize the significance of reliable occurrence data [20][31][35]. Especially when SDMs are run at high spatial resolution (100 m or higher), special attention should be paid to the quality of occurrence data as most global databases have occurrence records with accuracy of 500 m or 1 km.

4. Combined Effects of Land Use and Climate Change

Accurate predictions of invasive species distribution and invasion trends are critical to understanding the impacts of global environmental change on terrestrial ecosystems and hence, pivotal to the development of global environmental change adaptation policy [27]. Such predictions are even more relevant in the contemporary world where the anthropogenic changes are likely to drive the sixth mass extinction event on Earth [28]. A considerable number of studies have looked at biological invasion, most however considering climate and LULC change - two key factors of global change - in isolation [29][30][31][32]. When considered together, the effect of climate and LULC change on ecosystems may be synergistic [33], leading to an under or overestimation of the effects of anthropogenic change on global ecosystems and biodiversity by the majority of the ecological models [34].

4.1. *R. ponticum* Distribution in Wales in 2030

In order to assess the combined effects of climate and LULC change on future distribution of *R. ponticum* in Wales, I projected LULC change of Wales to 2030 (Chapter 4) and then used the climate and LULC data for 2030 to model the distribution of *R. ponticum* in Wales (Chapter 6). The LULC projections included a Business-as-Usual (B-a-U) scenario and a regional policy-based scenario called as Ecosystem Conservation (E-C) scenario. The results suggested that most of the future LULC and climate change scenarios are likely to decrease the potential distribution of *R. ponticum* in Wales, though I found evidence of increasing range in only one of the future LULC and climate change scenarios.

There is a strong consensus that models combining climate and LULC predictions are very good tools to predict species' distribution, usually far more accurate than climate-only models [35][36]. At fine spatial scales, land-use is often the factor driving the distribution and dispersal of invasive species [37]. The interplay of climate and LULC changes may limit the spread of invasives in some cases, while promoting invasion in others [38][39][9][6]. To date, most invasive species distribution models have assumed homogenous and unchanging landscapes, mainly focusing on climate as the critical dynamic variable [40][30]. The attention has recently shifted towards considering landscape as a heterogenous variable that can affect the rate and trend of biological invasions [41]. This approach needs to be improved further, for that landscapes are not only heterogeneous but also subject to significant human pressure. Species distribution models cannot rely only on B-a-U projections to predict future species distributions, the trajectory and intensity of LULC change in the future is not likely to copy the past. The trajectory of change may vary, depending upon the socio-political and socio-economic factors of the region under study [42]. Researchers have considered global or continental LULC change scenarios to predict at local scale [35], I however argue that capturing the impact of local land management plans and policies is essential to develop realistic scenarios. One of the uses of the scenarios presented in my study is to relate the spread of *R. ponticum* or other invasive species to possible changes in both future landscapes and climate. A possible outcome of this type of modelling exercise is the design and targeting of land management policies to ecosystem conservation [43].

5. Linking Results to Research Objectives and Hypotheses

The research presented in this thesis was aimed to a) test the effects of bioclimatic, topographic and anthropogenic (proximate) factors on the distribution of *R. ponticum* in Wales, b) test if the ecological niche of *R. ponticum* is conserved in its invaded range (UK) as compared to its native range (Iberian Peninsula), c) generate policy-driven land use change scenarios for Wales, and, d) test the combined effects of future climate and land use change on the future distribution of *R. ponticum* in Wales. These research objectives were comprehensively met in Chapters 2-6 of this thesis.

The results presented in Chapter 5 reject the first hypothesis that 'ecological niche of *R. ponticum* is conserved in its invaded niche.' This implies that any ecological model for this species must be trained and projected within its invaded range (UK) if the aim of the study is to predict its future spread in the invaded range. Evidence generated in Chapter 1 and 5 suggest that 'land cover is a more important determinant of the distribution of *R. ponticum* as compared to climate.' This implies that any modelling exercise aimed at predicting future distribution of *R. ponticum* (and other species of similar nature) must include a future projection of LULC, preferably driven by regional land management policies. Moreover, the third hypothesis 'species distribution models improve with decreasing grain size of predictor variables', was supported by the results presented in Chapter 3. This implies that the choice of variables for ecological models should be based on ecological requirements of the species under question and finer grain size of more important variables should not be compromised to match the coarser resolution of frequently available 'bioclimatic' variables. Finally, the last hypothesis, 'climate and land use change will enhance *R. ponticum* invasion in the UK' was largely rejected by the evidence presented in Chapter 6 of this thesis as invasiveness of *R. ponticum* reduced in most of the future land cover and climate change scenarios. This suggests that species distribution models should not conclude results based on one or two future scenarios, rather a range of future land use and climate change scenarios must be investigated.

6. Limitations of the Current Study and Recommendations for Future Research

The series of experiments presented in this study is the first comprehensive attempt to model the distribution of *R. ponticum* in Britain under future climate and land use change scenarios. Although the results suggest good accuracy of the models developed, there are some limitations of these studies which are important to be kept in sight while interpreting the results. In the following sections, I discuss the limitations of the current study and the new research questions for future research that arise from identifying these limitations.

6.1. Comprehensive Selection of Variables and Climate Change Scenarios for SDMs

The first objective of this study was to use correlative ecological modelling exercise to test the assumption that land cover and climatic variables have a dominant role in current and future distribution of *R. ponticum* (Chapter 2). Although the results suggest an acceptable model performance, there are some limitations of this study which, I recommend, should be considered in future studies. **First**, given that 14 out of 19 climatic variables originally considered for this study were excluded due to high correlation with variables chosen for the best performing model, an in-depth analysis of the sensitivity of *R. ponticum* distribution to the remaining variables may reveal interesting insights. **Second**, I made use of only six GCMs and two RCPs scenarios for the sake of simplicity, but further studies including more numerous GCMs and RCPs may prove useful for improved prediction of future distribution and a better understanding of the sensitivity of *R. ponticum* to climate change. **Third**, distribution models may be improved by the inclusion of high resolution variables derived from remote sensing and lidar (canopy height, cover, vertical distribution ratio etc.), variables such as vegetation density or stand height have been shown to significantly improve SDMs [1][44].

6.2. Determining Optimum Grain Size for SDMs – Important Considerations

One of the objectives of this study was to test the effect of grain size on the accuracy of ecological niche models. The results (Chapter 3) suggest that a grain size smaller than 1 km should be preferred in SDM studies; however, I recommend some precautions while using fine-resolution predictors in SDMs. **First**, it is important to note that models using finer grain size data should be trained and validated with carefully validated occurrence records. Training a model with predictor variables at very small grain size leads to a very specific species-habitat relationship and thus needs to be verified with accurate presence records. **Second**, this study modelled the distribution of *R. ponticum*, a habitat specialist species that showed a clear response to the changes in grain size. By contrast, generalist species may not be as sensitive to changes in grain size. **Third**, my results suggest that there may not be a 'gold standard' for the grain size of predictor variables when it comes to model transferability across space. Ideally, transferring the model to another area requires the identification of optimum grain size by considering a range of grain sizes, perhaps on a sub-set of available occurrence data. **Fourth,** I considered only a small area for model training and transferability which possibly explains why climatic variables contributed the least in the models. For SDMs over large spatial scale, climatic variables may have greater effect in determining the distribution of species. **Fifth,** I only used two evaluation tools (AUC & CBI). For future studies I recommend applying more robust statistics to evaluate the significance of difference between modelling scenarios.

6.3. Improved Dataset for Projecting LULC Changes

An important objective of this study was to project LULC changes in Wales to 2030 in order to test the effects of land use and climate change on the future distribution of *R. ponticum* (Chapter 4). The results indicate a reasonable accuracy of transition sub-models run in the study. However, it is important to acknowledge a few limitations of this study which could form interesting research questions for future research. **First,** explanatory variables used in land use change modelling studies are generally divided into three categories: biophysical, proximate and socio-economic variables [45]. In this study, I did not include socio-economic variables owing to the coarse resolution of available datasets. Instead, I preserved the fine spatial resolution of biophysical and proximate variables which are likely to be stronger determinants of land use change and reasonable proxies for the socio-economic variables. However, it is advisable to bear in mind that the resulting future projection does not directly represent the socio-economic landscape. Availability of fine-scale socio-economic (e.g. human influence index, population density, etc.) and climatic variables may improve the modelling outputs in the future.

Second, I used LULC maps generated by the Centre for Ecology & Hydrology, UK [46] which, to the best of my knowledge, are currently the most accurate, verified and finest-resolution temporally repeated maps covering the UK. The fact that I used only two time points is a limitation of our study; I did not have a map of LULC after 2015 that could have been used for verification of the future projection. Thus, although I adopted published protocols for future LULC projections [47][48], I suggest that the use of three or more historical LULC time points be considered for verification of projections. As we gather more archived LULC data, this approach should become the norm. It is important to note that the LULC maps used in this study come with some inaccuracies as well; for example, LULC map of 2007 has an accuracy of 83% (compared against 9127 ground reference polygons in the UK). In future, availability of more accurate LULC maps could help refining the projections. **Third,** a key limitation of this type of analysis is its 'blindness' to major shifts of socio-economic landscape and hence its inability to factor these into projections. A case in point is Brexit, where a set of self-imposed trade sanctions threatens a severe adjustment of existing drivers of land use. Thus, I recommend LULC change model of Wales driven by regional policies, especially post-Brexit scenarios.

6.4. Choice of Predictors, Native Range and Sample Size for Niche Shift Analysis

The niche shift and reciprocal modelling (Chapter 5) indicates a definitive shift in the environmental adaptation of *R. ponticum* in its invasive range. However, there are three limitations of this study, which I recommend as research questions for future studies. **First**, my analysis of niche shift is primarily based on bioclimatic variables only, however a more comprehensive modelling approach using a wider set of environmental variables may be able to test causality rather than correlation. Other, more pertinent non-climatic factors such as soil properties, land cover, or land use type, may play a more decisive role in explaining niche dynamics [49]. **Second**, in this study I considered Iberian Peninsula as the native range of *R. ponticum*, however, a future niche shift modelling exercise may combine data describing *R. ponticum* populations from North America and Iberian Peninsula (as native ranges) to predict observed niche shift. This would help test the claim that the British population of *R. ponticum* is a hybrid of Iberian and North American Rhododendron populations. **Third**, niche shift analysis is sensitive to sample size.

In this study, the sample describing the presence of *R. ponticum* in the Iberian Peninsula was small relatively to that describing Britain (although still the most comprehensive dataset available for Iberia). A future study with a more comprehensive sample size from the native range could be interesting.

6.5. Individual and Combined Effects of Climate and LULC Change on Invasive Species Distribution Modelling

Management of invasive species requires screening potential invasives through a process of risk assessment, which determines the likelihood that an invasive species would enter and inhabit a recipient area [35]. Most studies used in this type of screening of invasive species suggest either an increase [7] or a decrease in invasiveness [39]. This study (Chapter 6) shows that, for a single species in a well-defined area, expected LULC and climate changes may result in both an overall decrease or an increase in future habitat suitability. If the purpose of the modelling exercise is to anticipate future trends of species distribution at fine spatial resolution, I suggest that **(a)** multiple regional change drivers should be considered, **(b)** future LULC change scenarios based on regional socio-economic and socio-political policies must be included, and **(c)** multiple combinations of climate and LULC change scenarios should be run to have confidence in predictions of future distribution of the species in question. Furthermore, the current study only tests the combined effects of land use and climate change on future distribution of *R. ponticum*. I recommend future studies testing the effects of these two drivers individually and analyse the comparative effects of these two drivers to further broaden the understanding of the key drivers of invasive species distribution.

6.6. Process-based Modelling – The Way Forward

In this study, the distribution of *R. ponticum* has been modelled using MaxEnt algorithm which employs a correlative approach to model species distribution. Correlative modelling is the most commonly applied approach to predict the impacts of global change drivers on biodiversity. This is largely because correlative species distribution models have minimal data requirement such as current presence records and coarse climate data [50]. Thus, despite being the most frequently used approach for ecological modelling, correlative models are often criticized since they do not account for the critical processes determining species ranges (i.e., biotic interactions, dispersal limits, etc.) [50][51]. Correlative models assume that the effects of factors determining species' range will remain fixed in time and space. However, it is reasonable to argue that future environmental conditions are likely to present novel set of abiotic and biotic variables and that the said species will evolve, resulting in a new situation that may fall outside of the range of parameters used to train the models [50]. I therefore suggest future studies to use mechanistic species distribution modelling approach that incorporates process-based variables in the modelling process and to link the extrapolated changes in climate with the processes that determine range of species (for example, physiological limitations, dispersal range, etc.) [51]. Process-based (mechanistic) models can extrapolate beyond known conditions and isolate traits that determine biogeography [52]. Several authors have also pointed out that the use of different types of models, such as both correlative and mechanistic, provides independent lines of evidence that may confer accuracy to projections where they converge [53][54].

7. Policy Implications

This thesis presents a range of modelling exercises aimed at understanding the niche dynamics of *R. ponticum*, main drivers of its distribution in the UK and projecting its future distribution under several climate and land use change scenarios. Whereas some of the results presented in this thesis are of value to species' ecological knowledge (Chapter 1 & Chapter 4) and improving species distribution modeling parameterization (Chapter 3), the results presented in Chapter 5 and Chapter 6 are of direct relevance of land management and control of *R. ponticum* in Wales. The following paragraphs briefly discuss what are the implications of the results for the government and regional bodies policy in Wales.

7.1. Achieving the forest cover target by 2030

As discussed in Chapter 4 of this thesis, the Welsh Government committed to increasing the overall forest area in Wales as its contribution to sustainable development. In 2010, the Welsh Assembly Government's Climate Change Strategy recommended that woodland establishment rates be increased to 5000 ha per year for 20 years as an option for meeting Welsh carbon emission reduction targets. This figure was subsequently adopted by the Welsh Government as a policy target in the form of planting

100 000 ha of new, primarily broadleaved, woodland by 2030. However, actual planting levels over the following years were insufficient to meet this. The Welsh Government then retrospectively reduced the target, first to 50 000 ha, and eventually to the current commitment to plant at least 2000 ha of woodland a year between 2020 and 2030. The B-a-U scenario (Chapter 4) finds that if the current rate (2007-2015) of change continues, the total forest area in Wales by 2030 is likely to increase from current 15 to 17% (i.e. an increase of 35000 hectares). However, in the EC scenario where the rates of afforestation and conversion to broadleaf are prioritized, future forest cover could reach the original target: 19% of the total Welsh area (i.e. 95,000 hectares). The scenario can be used by policymakers to taylor the target expansion rate and to use it as evidence in the debate about the actual effects of such policy. The future projections of land use change indicate suitable sites for expansion under both scenarios. Since these projections are available at very fine spatial resolution (i.e. 25 m), these maps could point to potential sites in Wales where broadleaf expansion or conifer-to-broadleaf forest expansion could occur as a result of a change of policy, or as specific areas to be targeted as 'the lowest hanging fruit' when trying to stimulate expansion of woodland in Wales.

7.2. Improved Monitoring of Future Invasion & Reducing Cost of Control

The results presented in Chapter 6 clearly indicate that an increase in temperature and forest cover are critical for the potential spread of *R. ponticum* in Wales. Under most future climate change scenarios, the eastern belt of Wales will experience warming. Invasive species have generally higher energy requirements than natives due to unusually high rates of metabolism and growth. Interestingly, an increase in temperature is not likely to increase the invasion of *R. ponticum,* an increased forest cover in in combination with warmer climate would provide the necessary corridor and cover for the growth of *R. ponticum*. As suggested by the results presented in Chapter 4, most of the forest expansion would occur between 100-300 m altitude and between 0-200 meters distance from roads, potentially narrowing the extent of the monitoring zones for future invasion of *R. ponticum*. Since invasive species are most likely to be eradicated if detected in the early stages of invasion, monitoring the eastern and south western parts of Wales in areas where the altitude and distance from roads are within the susceptible range could help reduce the cost of monitoring and increase the efficiency of monitoring campaigns. Currently, a range of control methods are being used in Scotland and Wales, for example, mechanical eradication, stem control injections, spraying herbicides, etc. These methods involve labour, cost, and time. With improved monitoring of the spread of species and early detection, significant cost and time could be saved.

7.3. LULC Change in the post-Brexit UK – A Wider Implication of PhD research

The methods of LULC projections presented in Chapter 4 of this thesis can be used to generate national-scale future LULC maps of Wales in context of important socio-economic and socio-political scenarios such as Brexit. The UK voted to leave the European Union in June 2016, culminating with her official departure on January 31st, 2020. During its membership, the EU's Common Agricultural Policy (CAP) was the primary driver of agricultural intensification as it guided UK's approach to agriculture. Post-Brexit, Wales is developing its own suite of agricultural policies as agriculture is a devolved issue in the UK. Despite devolution, however, the outcome of UK-EU negotiations and the nature of UK future trading relationships with the bloc and the rest of the world (RoW) is very likely to influence LULC in Wales, with the potential to enact significant changes to the landscape. Since its inception, Brexit has represented a wide range of potential outcomes – ranging from a 'soft' departure (Brexit in name only) to a 'hard' reset of all regulation and trading agreements, including those pertinent to agriculture. I suggest modelling exercise of LULC change based on Brexit-related scenarios on LULC in Wales to 2030. Existing information on agricultural and environmental policy can be used, together with a range of future trading arrangements to modify recently observed LULC change trends and use change demand modelling to predict their impact on LULC in Wales.

REFERENCES

1. Yang, X.Q.; Kushwaha, S.P.S.; Saran, S.; Xu, J.; Roy, P.S. Maxent modelling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in Lesser Himalayan foothills. *Ecol. Eng.* **2013**, *51*, 83–87.
2. Dehnen-Schmutz, K.; Perrings, C.; Williamson, M. Controlling *Rhododendron ponticum* in British Isles: An economic analysis. *J. Environ. Manage.* **2004**, *70*, 323–332.
3. Stephenson, C.M.; MacKenzie, M.L.; Edwards, C.; Travis, J.M.J. Modelling establishment probabilities of an exotic plant, *Rhododendron ponticum*, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecol. Modell.* **2006**, *193*, 747–758.
4. Cross, J.R. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods , S . W . Ireland Author (s): J . R . Cross Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2259638 JSTOR is a not-for-profit service that helps scho. *J. Ecol.* **1981**, *69*, 807–824.
5. Kang, W.; Minor, E.S.; Lee, D.; Park, C.R. Predicting impacts of climate change on habitat connectivity of Kalopanax septemlobus in South Korea. *Acta Oecologica* **2016**, *71*, 31–38.
6. Bezeng, B.S.; Morales-Castilla, I.; Van Der Bank, M.; Yessoufou, K.; Daru, B.H.; Davies, T.J. Climate change may reduce the spread of non-native species. *Ecosphere* **2017**, *8*.
7. Bradley, B.A.; Wilcove, D.S.; Oppenheimer, M. Climate change increases risk of plant invasion in the Eastern United States. *Biol. Invasions* **2010**, *12*, 1855–1872.
8. Midgley, G.; Hannah, L. Extinction risk from climate change. *Biodivers. Clim. Chang. Transform. Biosph.* **2019**, 294–296.
9. Bellard, C.; Thuiller, W.; Leroy, B.; Genovesi, P.; Bakkenes, M.; Courchamp, F. Will climate change promote future invasions? *Glob. Chang. Biol.* **2013**, *19*, 3740–3748.
10. Kaplan, H.; Van Zyl, H.W.F.; Le Roux, J.J.; Richardson, D.M.; Wilson, J.R.U. Distribution and management of Acacia implexa (Benth.) in South Africa: A suitable target for eradication? *South African J. Bot.* **2012**, *83*, 23–35.
11. Rödder, D.; Lötters, S. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (Hemidactylus turcicus). *Glob. Ecol. Biogeogr.* **2009**, *18*, 674–687.
12. Fernandez, M.; Hamilton, H. Ecological niche transferability using invasive species as a case study. *PLoS One* **2015**, *10*, 1–17.
13. Erfmeier, A.; Tsaliki, M.; Roß, C.A.; Bruelheide, H. Genetic and phenotypic differentiation between invasive and native Rhododendron (Ericaceae) taxa and the role of hybridization. *Ecol. Evol.* **2011**, *1*, 392–407.
14. Thornton, D.H.; Murray, D.L. Influence of hybridization on niche shifts in expanding coyote populations. *Divers. Distrib.* **2014**, *20*, 1355–1364.
15. Society, B.E. Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants : A Hypothesis Author (s): Bernd Blossey and Rolf Notzold Source : Journal of Ecology , Vol . 83 , No . 5 (Oct ., 1995), pp . 887-889 Published by : British Ecological Society. *Society* **2009**, *83*, 887–889.
16. Dietz, H.; Edwards, P.J. RECOGNITION THAT CAUSAL PROCESSES CHANGE DURING PLANT INVASION HELPS EXPLAIN CONFLICTS IN EVIDENCE. *Ecology* **2006**, *87*, 1359–1367.
17. Milne, R.I.; Abbott, R.J. Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. *Mol. Ecol.* **2000**, *9*, 541–556.
18. Baniya, C.B.; Solhøy, T.; Gauslaa, Y.; Palmer, M.W. Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. *Folia Geobot.* **2012**, *47*, 135–151.
19. Özesmi, U.; Mitsch, W.J. A spatial habitat model for the marsh-breeding red-winged blackbird

(Agelaius phoeniceus L.) in coastal Lake Erie wetlands. *Ecol. Modell.* **1997**, *101*, 139–152.
20. Mayer, A.L.; Cameron, G.N. Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landsc. Urban Plan.* **2003**, *65*, 201–217.
21. Lawes, M.J.; Piper, S.E. There is less to binary maps than meets the eye: The use of species distribution data in the southern African sub-region. *S. Afr. J. Sci.* **1998**, *94*, 207–210.
22. Saura, S. Effects of minimum mapping unit on land cover data spatial configuration and composition. *Int. J. Remote Sens.* **2002**, *23*, 4853–4880.
23. Ödland, A.; Birks, H.J.B. The altitudinal gradient of vascular plant richness in Anrland, western Norway. *Ecography (Cop.).* **1999**, *22*, 548–566.
24. Gottschalk, T.K.; Aue, B.; Hotes, S.; Ekschmitt, K. Influence of grain size on species-habitat models. *Ecol. Modell.* **2011**, *222*, 3403–3412.
25. Hanberry, B.B. Finer grain size increases effects of error and changes influence of environmental predictors on species distribution models. *Ecol. Inform.* **2013**, *15*, 8–13.
26. Guisan, A.; Thuiller, W. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* **2005**, *8*, 993–1009.
27. Titeux, N.; Henle, K.; Mihoub, J.B.; Regos, A.; Geijzendorffer, I.R.; Cramer, W.; Verburg, P.H.; Brotons, L. Global scenarios for biodiversity need to better integrate climate and land use change. *Divers. Distrib.* **2017**, *23*, 1231–1234.
28. Barnosky, A.D.; Matzke, N.; Tomiya, S.; Wogan, G.O.U.; Swartz, B.; Quental, T.B.; Marshall, C.; McGuire, J.L.; Lindsey, E.L.; Maguire, K.C.; et al. Has the Earth's sixth mass extinction already arrived? *Nature* **2011**, *471*, 51–57.
29. Mamun, M.; Kim, S.; An, K.G. Distribution pattern prediction of an invasive alien species largemouth bass using a maximum entropy model (MaxEnt) in the Korean peninsula. *J. Asia-Pacific Biodivers.* **2018**, *11*, 516–524.
30. Xu, D.; Zhuo, Z.; Wang, R.; Ye, M.; Pu, B. Modelling the distribution of Zanthoxylum armatum in China with MaxEnt modelling. *Glob. Ecol. Conserv.* **2019**, *19*, e00691.
31. Yan, H.; Feng, L.; Zhao, Y.; Feng, L.; Zhu, C.; Qu, Y.; Wang, H. Predicting the potential distribution of an invasive species, Erigeron canadensis L., in China with a maximum entropy model. *Glob. Ecol. Conserv.* **2020**, *21*, e00822.
32. Yan, H.; Feng, L.; Zhao, Y.; Feng, L.; Wu, D.; Zhu, C.; Ecology, G. Prediction of the spatial distribution of Alternanthera philoxeroides in China based on ArcGIS and MaxEnt. **2019**.
33. Anteau, M.J.; Wiltermuth, M.T.; van der Burg, M.P.; Pearse, A.T. Prerequisites for Understanding Climate-Change Impacts on Northern Prairie Wetlands. *Wetlands* **2016**, *36*, 299–307.
34. Stanton, J.C.; Pearson, R.G.; Horning, N.; Ersts, P.; Reşit Akçakaya, H. Combining static and dynamic variables in species distribution models under climate change. *Methods Ecol. Evol.* **2012**, *3*, 349–357.
35. Di Febbraro, M.; Menchetti, M.; Russo, D.; Ancillotto, L.; Aloise, G.; Roscioni, F.; Preatoni, D.G.; Loy, A.; Martinoli, A.; Bertolino, S.; et al. Integrating climate and land-use change scenarios in modelling the future spread of invasive squirrels in Italy. *Divers. Distrib.* **2019**, *25*, 644–659.
36. Marshall, L.; Biesmeijer, J.C.; Rasmont, P.; Vereecken, N.J.; Dvorak, L.; Fitzpatrick, U.; Francis, F.; Neumayer, J.; Ødegaard, F.; Paukkunen, J.P.T.; et al. The interplay of climate and land use change affects the distribution of EU bumblebees. *Glob. Chang. Biol.* **2018**, *24*, 101–116.
37. Ficetola, G.F.; Maiorano, L.; Falcucci, A.; Dendoncker, N.; Boitani, L.; Padoa-Schioppa, E.; Miaud, C.; Thuiller, W. Knowing the past to predict the future: Land-use change and the distribution of invasive bullfrogs. *Glob. Chang. Biol.* **2010**, *16*, 528–537.
38. Dukes, J.S.; Mooney, H.A. Does global change increase the success of biological invaders? **1999**, *14*, 135–139.
39. Manzoor, S.A.; Griffiths, G.; Iizuka, K.; Lukac, M. Land Cover and Climate Change May Limit Invasiveness of *Rhododendron ponticum* in Wales. *Front. plant Sci. Pap.* **2018**, *9*.

40. Hastings, A.; Cuddington, K.; Davies, K.F.; Dugaw, C.J.; Elmendorf, S.; Freestone, A.; Harrison, S.; Holland, M.; Lambrinos, J.; Malvadkar, U.; et al. The spatial spread of invasions: New developments in theory and evidence. *Ecol. Lett.* **2005**, *8*, 91–101.
41. O'Reilly-Nugent, A.; Palit, R.; Lopez-Aldana, A.; Medina-Romero, M.; Wandrag, E.; Duncan, R.P. Landscape Effects on the Spread of Invasive Species. *Curr. Landsc. Ecol. Reports* **2016**, *1*, 107–114.
42. Falcucci, A.; Maiorano, L.; Boitani, L. Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landsc. Ecol.* **2007**, *22*, 617–631.
43. van Vuuren, D.P.; Isaac, M.; Kundzewicz, Z.W.; Arnell, N.; Barker, T.; Criqui, P.; Berkhout, F.; Hilderink, H.; Hinkel, J.; Hof, A.; et al. The use of scenarios as the basis for combined assessment of climate change mitigation and adaptation. *Glob. Environ. Chang.* **2011**, *21*, 575–591.
44. Ackers, S.H.; Davis, R.J.; Olsen, K.A.; Dugger, K.M. The evolution of mapping habitat for northern spotted owls (Strix occidentalis caurina): A comparison of photo-interpreted, Landsat-based, and lidar-based habitat maps. *Remote Sens. Environ.* **2015**, *156*, 361–373.
45. Verburg, P.H.; Schot, P.P.; Dijst, M.J.; Veldkamp, A. Land use change modelling: Current practice and research priorities. *GeoJournal* **2004**, *61*, 309–324.
46. Morton, D.; Rowland, C.; Wood, C.; Meek, L.; Marston, C.; Smith, G.; Wadsworth, R.; Simpson, I.C. Countryside Survey: Final Report for LCM2007 – the new UK Land Cover Map. *Countrys. Surv. Tech. Rep. No 11/07 NERC/Centre Ecol. Hydrol.* **2011**, 112 (CEH Project Number: C03259).
47. Uddin, K.; Chaudhary, S.; Chettri, N.; Kotru, R.; Murthy, M.; Chaudhary, R.P.; Ning, W.; Shrestha, S.M.; Gautam, S.K. The changing land cover and fragmenting forest on the Roof of the World: A case study in Nepal's Kailash Sacred Landscape. *Landsc. Urban Plan.* **2015**, *141*, 1–10.
48. Ye, X.; Yu, X.; Yu, C.; Tayibazhaer, A.; Xu, F.; Skidmore, A.K.; Wang, T. Impacts of future climate and land cover changes on threatened mammals in the semi-arid Chinese Altai Mountains. *Sci. Total Environ.* **2018**, *612*, 775–787.
49. Broennimann, O.; Treier, U.A.; Müller-Schärer, H.; Thuiller, W.; Peterson, A.T.; Guisan, A. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* **2007**, *10*, 701–709.
50. Evans, T.G.; Diamond, S.E.; Kelly, M.W. Mechanistic species distribution modelling as a link between physiology and conservation. *Conserv. Physiol.* **2015**, *3*, 1–16.
51. Kearney, M.; Porter, W. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **2009**, *12*, 334–350.
52. Cuddington, K.; Fortin, M.J.; Gerber, L.R.; Hastings, A.; Liebhold, A.; O'connor, M.; Ray, C. Process-based models are required to manage ecological systems in a changing world. *Ecosphere* **2013**, *4*, 1–12.
53. Hijmans, R.J.; Graham, C.H. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Chang. Biol.* **2006**, *12*, 2272–2281.
54. Morin, X.; Thuiller, W. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* **2009**, *90*, 1301–1313

CONCLUSION

This study presents the results of correlative ecological modelling of *R. ponticum* in Britain, specifically focusing on Wales. Future distribution range of *R. ponticum* in Snowdonia National Park (taken as a case study area in Wales), may decrease as a result of projected climate and land use changes. Land cover is the most important variable determining the distribution of *R. ponticum.* The study also confirms a substantial niche shift of *R. ponticum* in Great Britain as the species occupies a niche in Britain that is entirely different from that in its native Iberia, both in terms of equivalence and similarity. It is argued that hybridization may have driven the niche shift of *R. ponticum* in Britain. Thus, it is concluded that the species distribution models aimed at predicting potential distributional range of *R. ponticum* in the UK should be trained in its invaded range (UK) and the future distribution of *R. ponticum* will be primarily determined by the future LULC changes in the UK.

Grain size smaller than 1 km should be preferred in SDM studies; however, models using finer grain size data should be trained and validated with carefully validated occurrence records. Training a model with predictor variables at very small grain size leads to a very specific species-habitat relationship and thus needs to be verified with accurate presence records. The distribution of *R. ponticum*, a habitat specialist species that showed a clear response to the changes in grain size. It is concluded that there may not be a 'gold standard' for the grain size of predictor variables when it comes to model transferability across space. Ideally, transferring the model to another area requires the identification of optimum grain size by considering a range of grain sizes.

Combined effects of climate and policy driven LULC scenarios should be considered to determine the current and future distribution of invasive species. The results of LULC change modelling (Chapter 4) concluded that the current level of expansion and restoration of broadleaf forest in Wales is sufficient to deliver on existing policy goals; LULC projection modelling has the potential to test alternative policy aims and generate evidence at a scale useful to local decision makers. When I combined the LULC change projection with the future climate change projections for Wales, I concluded that the presence of *R. ponticum* is strongly associated with land cover but may be modified by strong climate change (Chapter 6). Habitat suitability of *R. ponticum* in Wales is likely to decrease by 2030 in most future LULCC change scenarios explored in this study, though its increase is plausible under a scenario that assumes substantial expansion of forest cover and rapid climate change. The study highlights the need for developing more detailed LULC scenarios, driven by regional policy developments in combination with a range of climate change scenarios. This approach may capture the heterogeneity of landscape and its changes that is exploited by *R. ponticum* and other invasive species.

This thesis contributes to the theoretical improvement of species distribution modelling by providing evidence of the importance of grain size (spatial resolution) of predictor variable and significance of the combined effect of climate and policy-based land use change projections to predict the future distribution of species. The thesis also, for the first time, presents a national-scale future LULC change projections of Wales based on contrasting set of policies. Besides theoretical contributions, this study has produced various invasion risk maps showing hotspots of projected invasion of *R. ponticum* in Wales, which may aid in devising management plans to combat further spread of this invasive species

SUMMARY

In Chapter 2, I made use of MAXENT modelling environment to develop a current distribution model of *R. ponticum* and assessed the likely effects of land cover and climatic conditions on the future distribution of this species in the Snowdonia National park in Wales. Six general circulation models (GCMs) and two representative concentration pathways (RCPs), together with a land cover simulation for 2050 were used to investigate species' response to future environmental conditions. Having considered a range of environmental variables as predictors, I found that under all land cover and climatic conditions considered in this study, the range of *R. ponticum* in Wales is likely to contract in the future. Land cover and topographic variables were found to be the most important predictors of the distribution of *R. ponticum*.

Based on the results of Chapter 2, I designed experiments to answer following **four key questions**:

i. Does grain size (spatial resolution) of predictors affect species distribution models and what is the optimum grain size to develop national-scale species distribution model?

ii. Since future LULC changes are going to be critical for the spread of *R. ponticum*, what could be the possible trajectories of LULC change in Wales under contrasting set of land management policies?

iii. If the aim is to project future distribution of *R. ponticum* in the UK, should the SDM be trained in the UK or Iberian Peninsula? i.e. has *R. ponticum* shifted or conserved its niche in its invaded range (UK) compared to its native range (Iberian Peninsula)?

iv. Given that LULC change is the most important determinant of *R. ponticum* distribution, how would current land management policies in Wales affect potential future distribution of this invasive in the country? And, how future LULC and climate change scenarios are likely to impact the distribution of *R. ponticum* in Wales when modelled at high spatial resolution?

In Chapter 3, I attempted to answer the first question by testing the effect of grain size of predictor variables on the accuracy and transferability of SDMs. Choice of grain size is often dependent on the type of predictor variables used and the selection of predictors sometimes rely on data availability. I employed MaxEnt to investigate the effect of the grain size on model transferability for an invasive plant species. I modelled the distribution of *R. ponticum* in Wales and tested model performance and transferability by varying grain size (50 m, 300 m, and 1 km). The results suggest that model accuracy is likely to increase with decreasing grain size. However, successful model transferability may require optimization of model grain size.

In Chapter 4 - to answer the second question that came out of Chapter 2 - I projected future LULC changes in Wales to year 2030 under contrasting set of policies. I quantified changes in different LULC classes in Wales between 2007 and 2015 and used a multi-layer perceptron–Markov chain ensemble modelling approach to project the state of Welsh forests in 2030 under the current and an alternative policy scenario, i.e. Ecosystem Conservation Scenario. Results suggest that the current level of expansion and restoration of broadleaf forest in Wales is sufficient to deliver on existing policy goals. In a key finding, the highest intensity of broadleaf expansion is likely to shift from south-eastern to more central areas of Wales.

A critical assumption in species distribution models is that the ecological niche of species is conserved. However, recent studies suggest that this assumption is not valid for all species. In Chapter 5, I compared ecological niches of *Rhododendron ponticum* in its native (Iberian Peninsula) and invasive (Britain) ranges address the fourth question based on the results of Chapter 2. I tested the conservation of ecological niche between invasive and native populations of *R. ponticum* using principal component analysis, niche dynamics analysis and MaxEnt-based reciprocal niche modelling. Results show that the two niches and not equivalent and are dissimilar, leading us to conclude that this species has occupied novel environmental conditions in Britain.

In Chapter 6 of this thesis, I tested the combined effects of land use and climate changes on the current and future habitat suitability of *R. ponticum* in Wales using a MaxEnt-based SDM. I used two policy-driven land use change projections for Wales (Chapter 4), in combination with two General Circulation Models and two Representative Concentration Pathways to derive eight different land use and climate change scenarios. In seven out of eight scenarios, the habitat suitability for *R. ponticum* is likely to reduce by 2030. However, in the eighth scenario representing an extreme where land use change and greenhouse gas emissions both accelerate, the interaction of land use and climate change forces an increase of habitat suitability of *R. ponticum*. The results of this study highlighted the importance of considering the combined effect of land use and climate change and including regional policy-based land use change projections to test the potential of an invasive species to expand or retreat in future.

In the general discussion (Chapter 7), I bring all the findings presented earlier together and wrap up with recommendations for future studies.

LIST OF PUBLICATIONS

1. Manzoor, S.A.; Griffiths, G.; Iizuka, K.; Lukac, M. Land Cover and Climate Change May Limit Invasiveness of *Rhododendron ponticum* in Wales. *Front. plant Sci.* **2018**, *9*.
2. Manzoor, S.A.; Griffiths, G.; Lukac, M. Species distribution model transferability and model grain size – finer may not always be better. *Sci. Rep.* **2018**, *8*, 7168.
3. Manzoor, S.A.; Griffiths, G.; Latham, J.; Lukac, M. Scenario-led modelling of broadleaf forest expansion in Wales. *R. Soc. Open Sci.* **2019**, *6*.
4. Manzoor, S.A.; Griffiths, G.; Obiakara, M.C.; Esparza-Estrada, C.E.; Lukac, M. Evidence of ecological niche shift in *Rhododendron ponticum* (L.) in Britain: Hybridization as a possible cause of rapid niche expansion. *Ecol. Evol.* **2020**, 2040–2050.
5. Manzoor, S.A.; Griffiths, G.; Lukac, M. Land cover and climate change interaction triggers contrasting trajectories of biological invasion. Ecological Indicators. (Under Review).
6. Manzoor, S.A.; Malik, A.; Zubair, M.; Griffiths, G.; Lukac, M. Linking Social Perception and Provision of Ecosystem Services in a Sprawling Urban Landscape: A Case Study of Multan, Pakistan. *Sustainability* **2019**, *11*, 654.
7. Zubair, M.; Jamil, A.; Lukac, M.; Manzoor, S.A. Non-timber forest products collection affects education of children in forest proximate communities in northeastern Pakistan. *Forests* **2019**, *10*, 1–13.
8. Khan, F.Z.A.; Manzoor, S.A.; Akmal, M.; Imran, M.U.; Taqi, M.; Manzoor, S.A.; Lukac, M.; Gul, H.T.; Joseph, S. Modelling pesticide use intention in Pakistani farmers using expanded versions of the theory of planned behaviour. *Hum. Ecol. Risk Assess. An Int. J.* **2020**, *0*, 1–21.

LIST OF TRAININGS ATTENDED

1. **The importance of environmental sustainability in development.** Warwick Business School, University of Warwick, UK. 10th May 2018.
2. **Science communication skills: Talk about your research in an engaging and accessible way.** CSC Workshop Series, London, UK. June 22nd, 2018.
3. **An Introduction to Programming in R.** School of Agriculture, Policy & Development, University of Reading, UK, 5-8th November 2018.
4. **How to Write Highly Cited Papers.** Centre for Ecology & Hydrology, Wallingford, UK. 5th February 2019.
5. **Ecological Niche Modelling using R.** PR Statistics, Glasgow, UK. 11–15th March 2019.
6. **Trade-Offs in Ecosystem Services and Varying Stakeholder Preferences: Evaluating Conflicts, Obstacles, and Opportunities.** Queens College, University of Cambridge, UK. 27-28th March 2019.
7. **Structural Equation Modelling Workshop.** University of Kent, UK. 1st April 2019
8. **Video Production For Social Media Training.** British Ecological Society, University College London, UK. 26th April 2019.
9. **Species Distribution Modelling: Fundamentals and the Future.** British Ecological Society, University of Nottingham, UK. 7–9th May 2019.
10. **Phase 1 Habitat Survey & QGIS Course.** Acer Ecology Ltd, Wales. 23rd June 2019.
11. **Agent-based Modelling With NetLogo**. . Department of Ecosystem Modelling, University of Gottingen, Germany. 26th – 30th August 2019.
12. **Structural Equation Models, Path Analysis, Causal Modelling and Latent Variable Models Using R.** PR Statistics, Glasgow, UK. 16–20th September 2019.
13. **Structural Equation Modelling in R.** The Psychometrics Centre Cambridge Judge Business School, 11-13th March 2020.