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

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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

Keywords: biological invasion; climate change; invasive species; land use change; Rhododendron.

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 climate change 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 ecological niche models (ENMs) [29]. ENMs 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 ENMs with all variables that determine the spread of invasives and that reflect the impacts of anthropogenic activities over time [4]. Most existing ENM-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 ENMs 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 species has caused economic and ecological losses by affecting soil health, inhibiting the regeneration of native flora and posing risk to pollinators [35][36]. 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) [37], 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 [38]. 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

2.2. Study Area and Species Records

Wales, a country in the UK, has an area of approximately 21000 km^2 and a human population of over 3 million [39]. 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][40].

We obtained distributional records for *R. ponticum* in Wales from the Global Biodiversity Information Facility (www.gbif.org/) by using the dismo R package [41]. We retrieved 8,764 presence records of *R. ponticum,* which we screened using recommended protocols [42]. 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 [37]. This resulted in a dataset of 1,280 presence records which were used in our modelling exercise.

2.3. Predictor Variables

We chose a set of 24 predictor variables based on a review of the literature [43][44][45][46], 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) and land cover (consisted of 6 classes namely, 'broadleaf forest', 'conifer forest', 'arable land', 'improved grassland', 'semi-natural grassland', 'mountain, heath & bog') [38]. For the ease of interpretation, land cover was converted into 6 continuous variables by calculating Euclidian distances of each land cover class to each pixel in the study area.

The default spatial resolution of variables was, bioclimatic: ~ 1km, topographic variables: 25 m, and land cover: 25 m. All variables were resampled to 25 m spatial resolution since our earlier investigation on habitat suitability modelling of *R. ponticum* confirmed that the species could be most accurately modelled at this scale [37]. Furthermore, in an earlier investigation we demonstrated that it is useful to conserve the high resolution of land cover and topography when the species being modelled is more sensitive to these variables as compared to bioclimatic variables [42]. 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 $r \leq 0.70$ [47]. This step reduced the impact of multicollinearity and improved model conformity with statistical assumptions [48]. After omitting highly correlated variables, we were left with mean diurnal temperature range (bio 2), annual precipitation (bio 12), minimum temperature of the coldest month (bio 6), distance to broadleaf forests, distance to conifer forests, distance to arable land, distance to mountain, heath & bog, altitude and aspect. All raster variables were projected using 'British National Grid' projected coordinate system.

2.4. 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 Global 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 [49].

2.5. **Future Land Use & Land Cover Change Scenarios**

We used two *Land Use and Land Cover* (LULC) change projections for Wales for the year 2030 [38]. The projections were derived using a Multi-Layer-Perceptron and Markov Chain ensemble algorithms. The projections based on contrasting policies of forest expansion and land management practice in Wales (see [38] 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, 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 [38] 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 (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 Global 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

2.6. Ecological Niche Modelling Algorithm

We used MaxEnt, a maximum-entropy based machine learning (presence/background) 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 [50]. We selected MAXENT primarily because it allows for the use of both continuous and categorical predictor variables [51], can handle complex interactions between predictor and response variables [52], and performs better than discriminative models while using presence-only records [51]. We used a reasonably large sample size [53] and applied the recommended screening and verification of occurrence records [37].

In MaxEnt, model complexity is primarily controlled by two factors; feature classes and regularization parameters [54]. 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 [55][54]. 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 [55] 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) [56]. 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) [57]. We used Cloglog output format.

We trained the model in Britain and not in the Iberia (the native range of R. ponticum) as one of our earlier investigations suggested that this invasive species has shifted its niche in Britain [58].

2.7. Model Evaluation

We used the Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) to test the performance of the model against presence observations [52]. 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 [59]. 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 [42]). 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) [60][61]. In addition, we calculated a set of null models [62] by generating 100 random datasets, each equalling the actual number of presence points. We then calculated a Maxent model for each dataset and used a Kruskal-Wallis test to compare the training AUC values of the species models with null models.

3. Results

3.1. Ecological niche model accuracy

The Maxent-based model with the lowest AICc showed encouraging predictive capacity: AUC_{train} = 79.8, AUC_{test} = 77.21, and CBI = 0.81. These results suggest that the predictor variables used during model calibration predicted the presence of *R. ponticum* in Wales with decent accuracy. Moreover, our model performed significantly better than null models (Kruskal-Wallis with p-values < 0.001).

Continuous and binary habitat suitability maps of the current distribution of *R. ponticum* in Wales are presented in Figure 1.

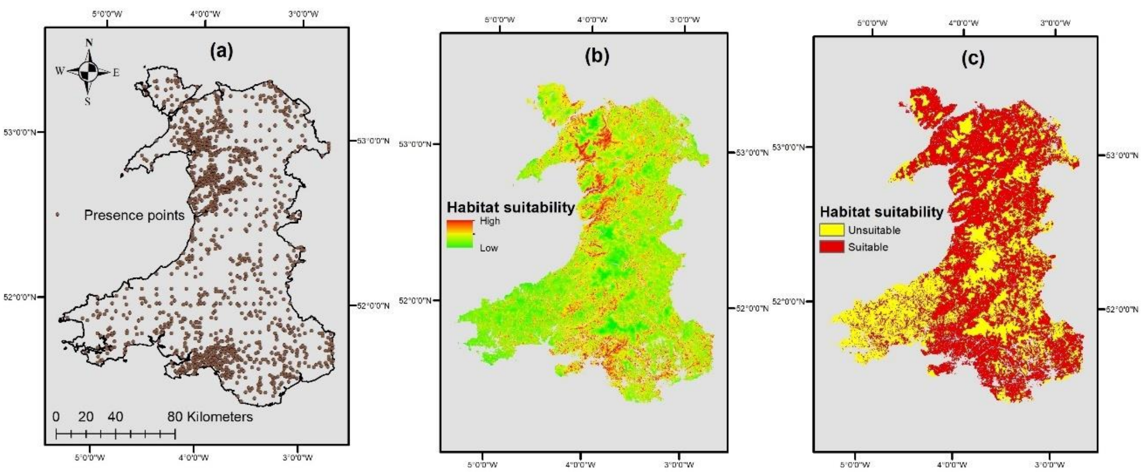

Figure 1. Distribution of presence points (a), present day continuous (b) and binary (c) habitat suitability maps of *R. ponticum* generated in MaxEnt-based *R. ponticum* distribution model.

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 & Figure 2, land cover (distance from broadleaf and conifer forests) has the highest contribution and permutation importance in predicting the distribution of *R. ponticum*.

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

Variable	Percent contribution	Permutation importance
Distance from broadleaf forest	60.6	39
Distance from conifer forests	21.3	23.8
Altitude	7.5	17.5
bio_2	3.7	7.3
Distance from mountain, heath, bog	3.2	7.1
Distance from arable land	2.6	2.4
bio_12	0.4	1.7
Aspect	0.4	0.8
bio_6	0.3	0.5

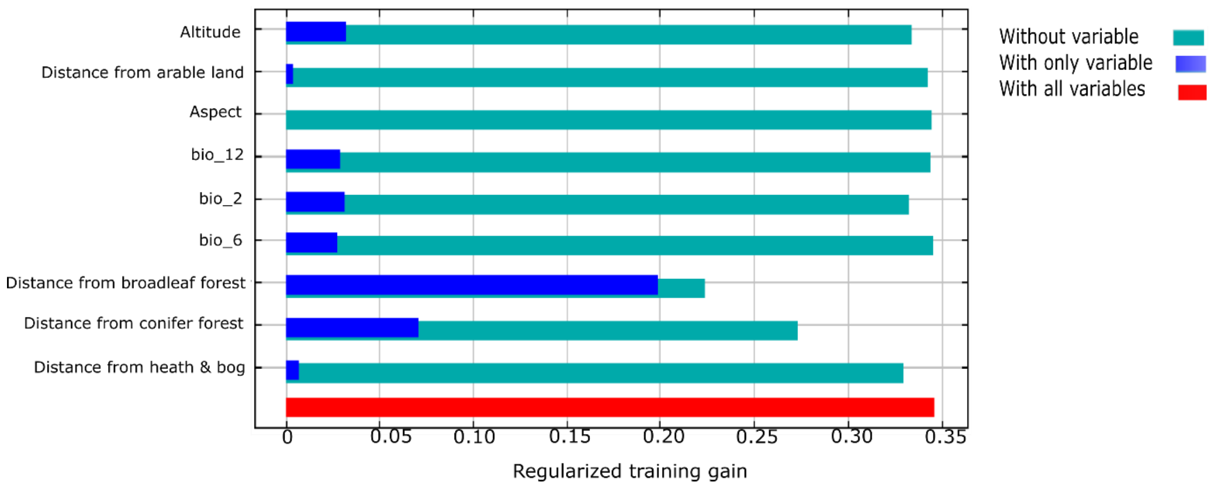

Figure 2. Jack-knife test of variable importance in the MaxEnt-based model for predicting the distribution of *R. ponticum* in Wales. Regularized training gain indicates how much better the MaxEnt distribution fits the present data compared to a uniform distribution. Dark blue bars indicate the gain 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, 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 *R. ponticum* favours broadleaf and conifer forests. Furthermore, the presence of *R. ponticum* is negatively associated with altitude. The response curves of bio 2 bio 6 show that its presence is lowest at extreme values of these variables.

Impact of LULCC change on the future distribution of *R. ponticum*

Our models show that nearly 52 % or 1081582 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).

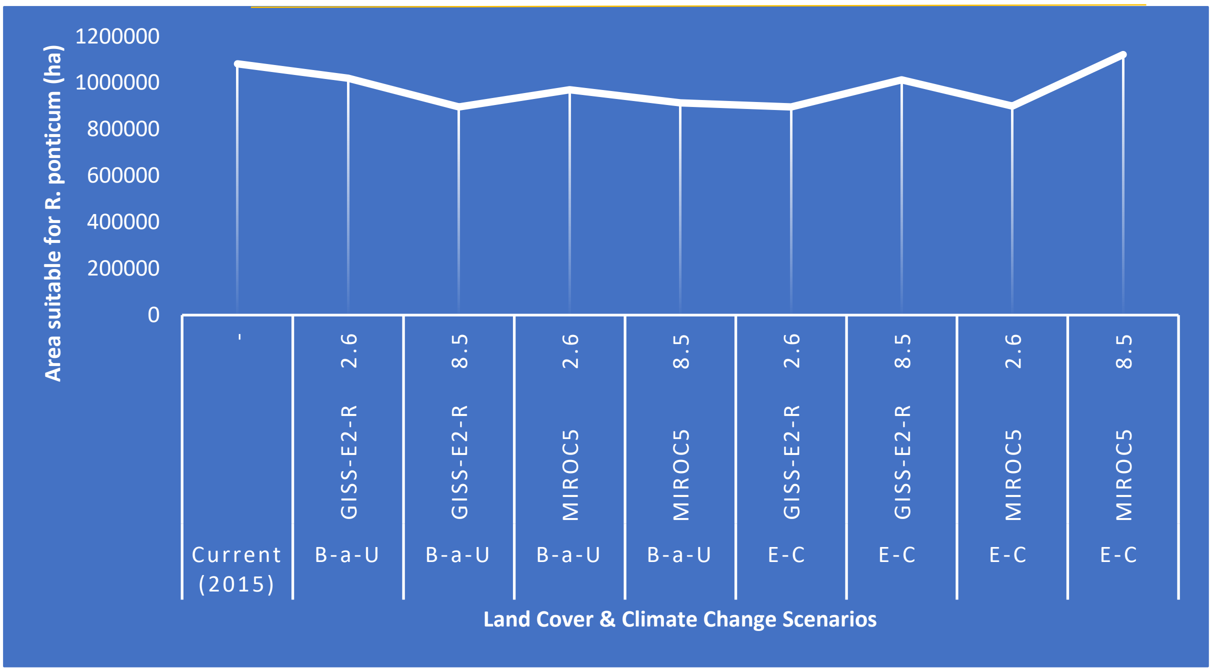

Figure 3. Area suitable for *R. ponticum* in Wales under eight LULCC change scenarios predicted for 2030. Recent Past refers to the baseline land cover and climatic conditions (2015), Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, Scenario 2: GISS-E2-R x RCP 8.5 x B-a-U, Scenario 3: MIROC5 x RCP 2.6 x B-a-U,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

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, red pixels) and existing suitable areas of *R. ponticum* are likely to become unsuitable in the central and southern parts of Wales (Figure 4, a-b & e-f, green pixels). 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) whereas reduced suitability is likely along the eastern and northern parts of Wales (Figure 4).

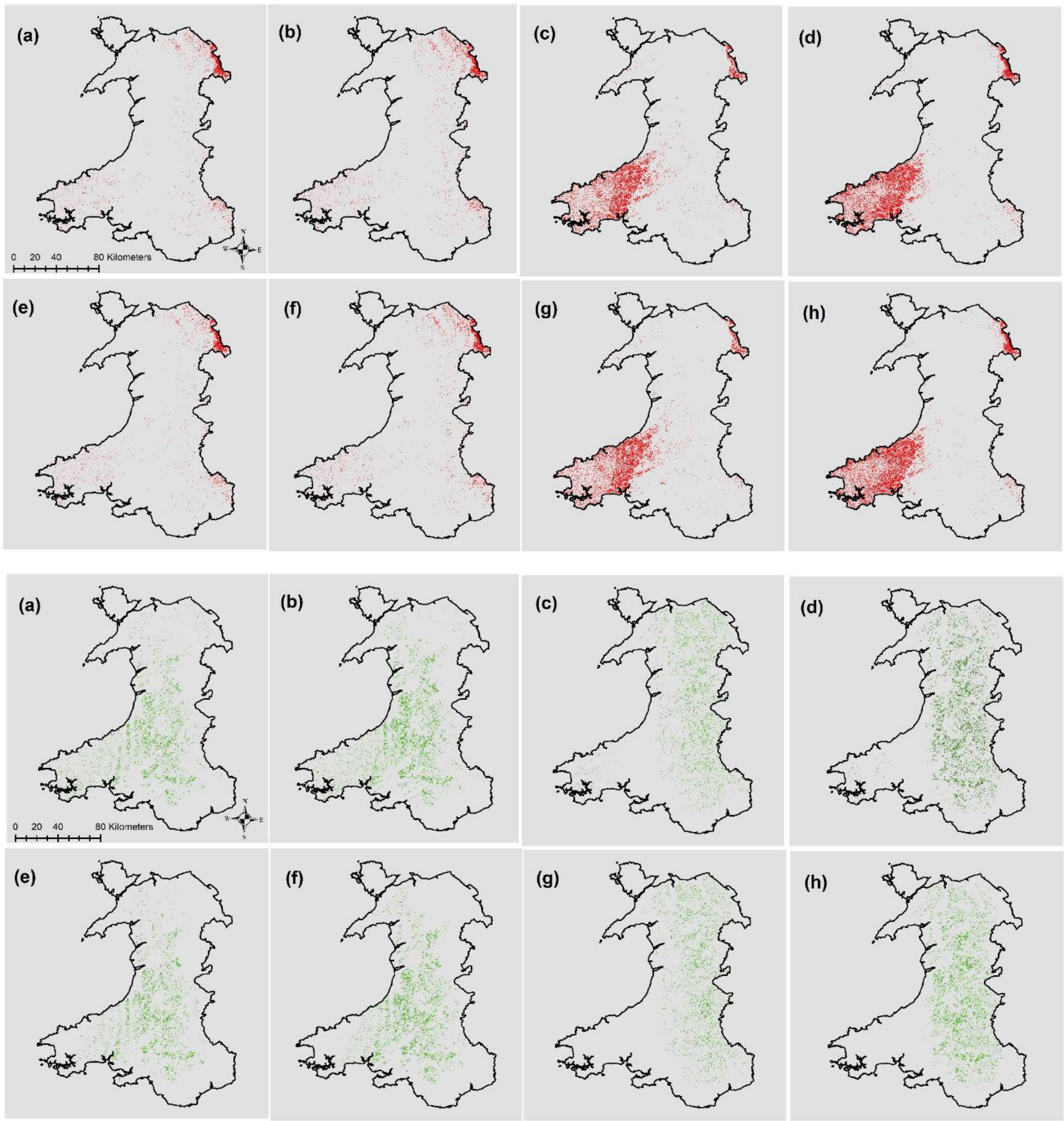

Figure 4. Maps showing areas in Wales which are likely to become suitable (shown in red) and unsuitable (shown in green) for *R. ponticum* by 2030 under future LULCC changes scenarios. a-h represent scenarios 1-8. Scenario a) Scenario 1: GISS-E2-R x RCP 2.6 x B-a-U, (b) Scenario 2: GISS-E2-R x RCP 8.5 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 [63]. 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 [64]. 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 [65][66][67][68]. When considered together, the effect of climate and LULC change on ecosystems may be synergistic [69], leading to an under or overestimation of the effects of anthropogenic change on global ecosystems and biodiversity by the majority of the ecological models [70]. 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 [71]. 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 [72]. *R. ponticum* can invade a wide range of land cover classes, including forests, upland heaths and grasslands [73]. In Britain, forests represent the land cover class most susceptible to *R. ponticum* invasion [73]. 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 [45], forest floor litter that supports *R. ponticum* growth [74] and shelter of woods that provides the necessary "cover" to spread without being eradicated [29].

Land cover is 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, 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* [75]. Earlier research has confirmed a strong relationship between mean diurnal temperature range ('bio 2' in the current study)and invasive plant species distribution [76]. 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 [76]. Response curve (Supplementary Data, Figure 3) indicates that *R. ponticum* favours areas with higher values of 'bio 2', which is in agreement with earlier reports [76]. 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 (Supplementary data, Table S1) 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.

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 conifer forest cover from the current scenario under both B-a-U and E-C in future (Supplementary data, Table S1). As shown by the response curves (Supplementary Data, Figure 3), *R. ponticum* is most likely to occur in conifer forests. *R. ponticum* favours acidic soils, coniferous forests may thus offer ideal growing conditions for this invasive species [77]. Existing UK Forestry Standard Guidelines on Biodiversity [78] and the UK Biodiversity Action

Plan [38] 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 [79][80][38]. 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*. 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* (Supplementary Data, Table S1 & Figure S5). Evidence suggests that invasive species generally have higher energy demand for intense physiological activities; mean diurnal temperature range may affect species distribution.

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 (Supplementary data, Table S2). 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 ecological niche models. Extreme climate change and current plans for forest management may thus conspire to improve the future prospects of *R. ponticum* in Wales.

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 [81][82]. At fine spatial scales, land-use is often the factor driving the distribution and dispersal of invasive species [4]. The interplay of climate and LULC changes may limit the spread of invasives in some cases, while promoting invasion in others [83][29][84][85]. To date, most invasive ecological niche models have assumed homogenous and unchanging landscapes, mainly focussing on climate as the critical dynamic variable [86][66]. The attention has recently shifted towards considering landscape as a heterogenous variable that can affect the rate and trend of biological invasions [87]. This approach needs to be improved further, for that landscapes are not only heterogeneous but also subject to significant human pressure. Ecological niche 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 [88]. Researchers have considered global or continental LULC change scenarios to predict at local scale [81], we however argue that capturing the impact of local land management plans and policies is essential to develop realistic scenarios. One of the used 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 [89].

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 [81]. Most studies used in this type of screening of invasive species suggest either an increase [90] 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 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, 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.

Our model predicts future habitat suitability of *R. ponticum* in Wales under a set of climate and land use change scenarios. However, dispersion of *R. ponticum* to these newly suitable habitats will depend on dispersal potential of the invasive, dispersal barriers and corridors as well as biotic factors (i.e. competitors or predators). We recommend the future habitat suitability maps produced in this study should overlaid with road and water networks as these two channels are most likely to facilitate dispersion of invasives to new areas.

In this study, we resampled the climate variables to 25 m to conserve the spatial resolution of topography and land cover as suggested by our earlier studies on *R. ponticum* [37]. However, resampling climate to finer resolution might influence the climate-species relationship. Therefore, we recommend future studies to resample climate variable while considering the spatial scale of study, ecological sensitivity of the species to different abiotic factors and the spatial resolution of the presence data.

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 Material

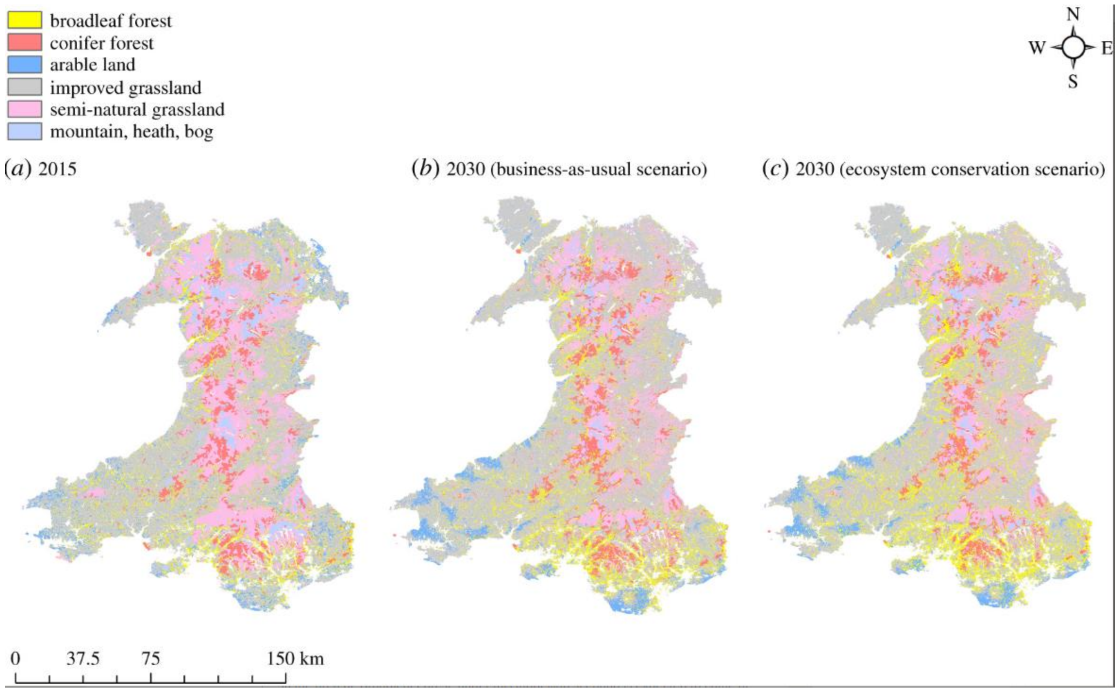

Figure S1. Current (*a*) and projected land use map of Wales, UK for the year 2030 under B-a-U (*b*) and EC (*c*) modelling scenarios. [38]

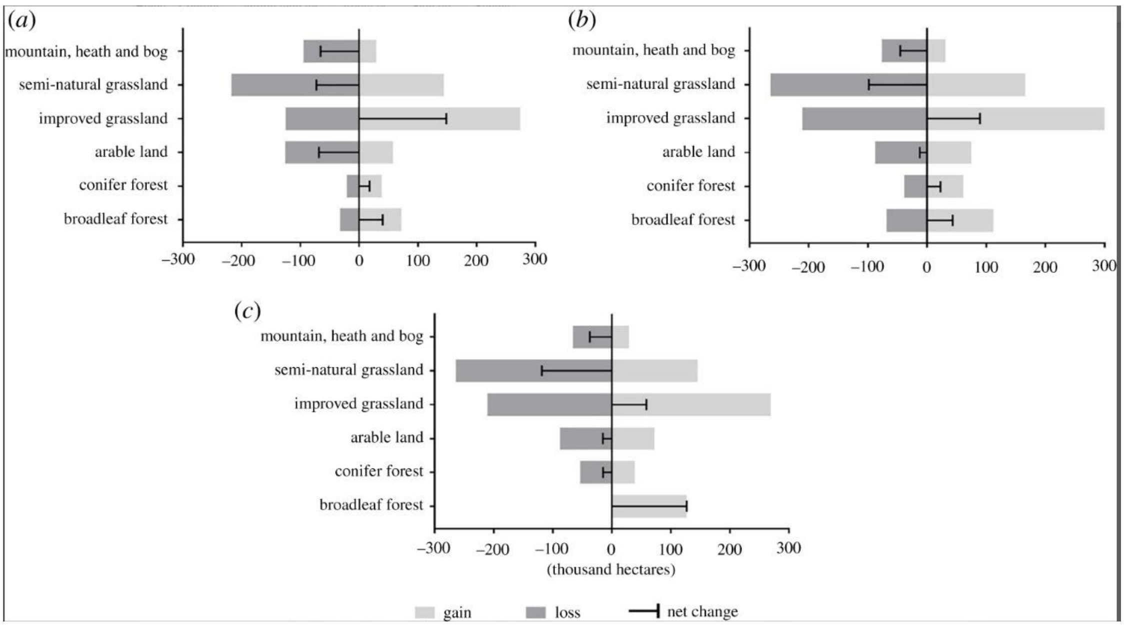

Figure S2. In Wales, UK, gains, losses and net changes between different LULC classes (hectares) during (*a*) 2007–2015, (*b*) 2015–2030 (B-a-U scenario) and (*c*) 2015–2030 (EC scenario) [38]

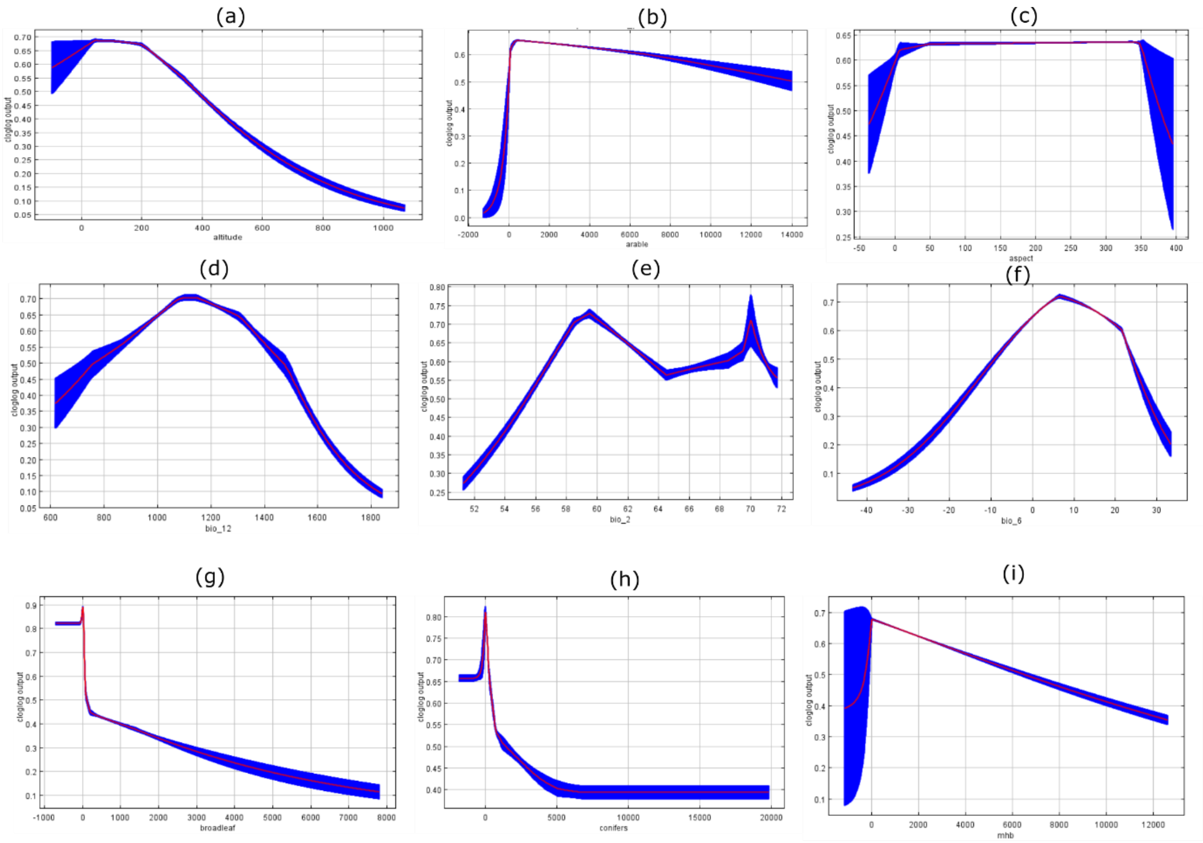

Figure S3. Response curves of environmental variables in the MaxEnt-based *R. ponticum* distribution model. a) altitude, b) distance to arable land, c) aspect, d) bio_12, e) bio_2, f) bio_6, g) distance to broadleaf forest, h) distance to conifer forest, i) distance to mountain, heath & bog.

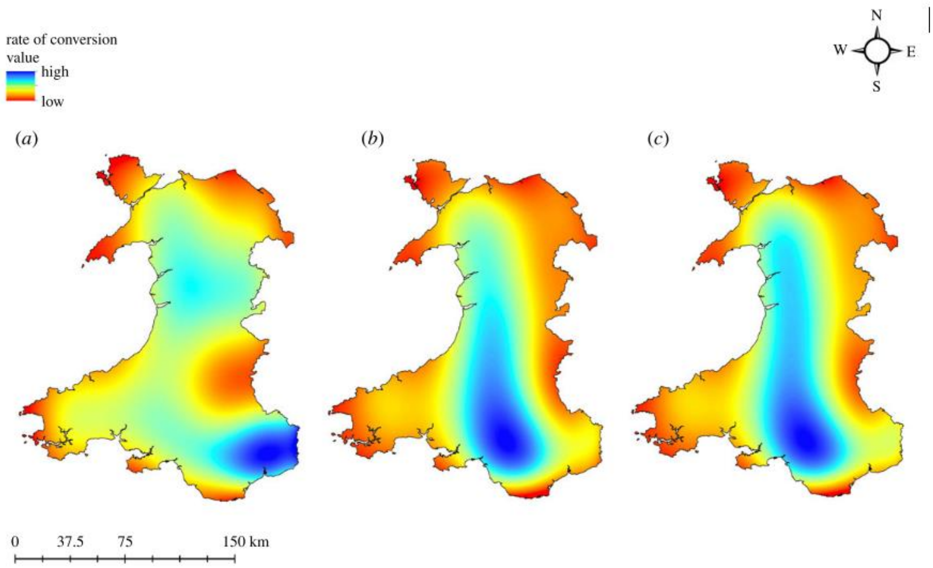

Figure S4. Heat map of large-scale trends of conifer to broadleaf forest conversion in Wales, UK during 2007–2015 (a), 2015–2030 B-a-U scenario (b) and 2015–2030 EC scenario (c). [38]

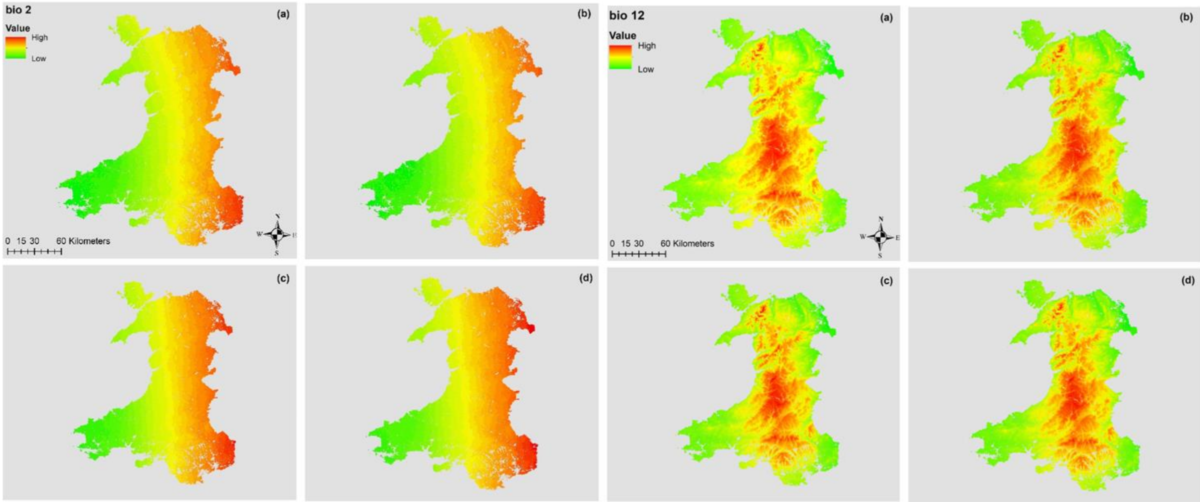

Figure S5. Spatial maps of bio 2 (mean diurnal range) and bio 12 (mean annual precipitation) under future climate change scenarios, a) GISS-E2-R x RCP 2.6, b) GISS-E2-R x RCP 8.5, c) MIROC5 x RCP 2.6, d) MIROC5 x RCP 8.5.

Table S1. 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
Bio 6 (◦C)	-3.8 – 2.7	-1.9 – 4.4	-2.2 – 4.2	-2.5 – 4.0	-2.2 – 4.2

Table S2. 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**	**Overall Forest Cover**
Current	159951	160259	320210
B-a-U	203317	152780	356097
E-C	300367	114906	415273

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