

Land use and climate change interaction triggers contrasting trajectories of biological invasion

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1 Land Use and Climate Change Interaction Triggers Contrasting 2 Trajectories of Biological Invasion

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7

8 Abstract

9 Global change drivers such as land use and climate changes are known to interact in their effects on
10 biodiversity. The impact of these drivers on global biodiversity is increasingly evident in many forms
11 including the spread of invasive species. Climate and land use changes affect introduction, colonization
12 and spread of invasive species by affecting niche availability and dispersal potential. We tested the
13 combined effects of land use and climate changes on the current and future habitat suitability of
14 *Rhododendron ponticum* in Wales using a MaxEnt-based ecological niche model. We used two policy-
15 driven land use change projections for Wales, in combination with two General Circulation Models and
16 two Representative Concentration Pathways to derive eight different land use and climate change
17 scenarios. In seven out of eight scenarios, the habitat suitability for *R. ponticum* is likely to reduce by
18 2030. However, in the eighth scenario representing an extreme where land use change and greenhouse
19 gas emissions both accelerate, the interaction of land use and climate change forces an increase of
20 habitat suitability of *R. ponticum*. The study highlights the importance of considering the combined
21 effect of land use and climate change and including regional policy-based land use change projections
22 to test the potential of an invasive species to expand or retreat in future

23

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

25

26 **1. Introduction**

27 Global environmental change triggered by human activity represents an unprecedented threat to
28 ecosystem function [1]. We know that the stability and functioning of all ecosystems on Earth is
29 underpinned by biodiversity, represented by communities of species inhabiting individual ecosystems
30 [2]. Each ecosystem function is dependent on a community with a specific composition, a change of
31 species assemblage potentially leads to change of function [3]. Invasive species, defined as organisms
32 that cause ecological or economic harm in a new environment where they are not native, contribute to
33 global environmental change due to their increasing presence in all types of ecosystems [4]. Biological
34 invasions increasingly threaten global biodiversity, economy, and even human health [5]. The success
35 of invasive species is predominantly due to their ability to spread to new territories and due to the
36 availability of unoccupied niches in the new area [6]. Niche availability may be altered by climate
37 change and land-use change, both phenomena disturb existing ecosystem structure and create novel
38 environments in the process [7]. Invasive species thus embody an example of a positive feedback; their
39 invasiveness is aided by climate and land use change, while they themselves represent a factor of
40 environmental change [8].

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

52 At the same time, Land use and Land Cover (LULC) changes are critical to the introduction,
53 establishment, and proliferation of invasives [17][18][19]. Changes in LULC create dispersal corridors
54 and accelerate ecosystem disturbance (e.g., fragmentation), favouring the establishment of invasives
55 [17][20]. LULC changes such as forest clearing for agriculture or pastureland, urban expansion, or field
56 abandonment produce conditions suitable for biological invasions [20]. Interestingly, while LULC
57 changes may create favourable conditions for some invasive species, they may inhibit the invasive
58 potential of others [21][22]. Understanding the impact of LULC changes on niche availability is pivotal
59 to forecasting invasion and to managing landscapes to reduce the spread of invasive species [18].

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

69 Currently, one of the most efficient tools to predict the future spread of invasive species in a given area
70 is the use of ecological niche models (ENMs) [29]. ENMs correlate the presence of invasive species to
71 environmental conditions and identify areas vulnerable to invasion, based on projected future
72 conditions. Thus, it is critically important to feed ENMs with all variables that determine the spread of
73 invasives and that reflect the impacts of anthropogenic activities over time [4]. Most existing ENM-
74 based projections are based solely on climate variables and climate change scenarios [30][31][32]. Fewer
75 studies use land cover for mapping the current distribution, but exclude this variable from future
76 projections, making an assumption that either the species' future distribution is not sensitive to LULC
77 changes, or the landscape composition remains constant in future [33]. However, it is no surprise that

78 in a world dominated by humans, landscape patterns and ecosystem composition are rapidly changing,
79 altering ecological ranges of species. Predictive models based on climatic data only may not represent
80 the most plausible scenarios of species' future distribution [24]. There is a need to develop ENMs that
81 combine climate change scenarios with policy-driven LULC projections and predict the distribution of
82 ecologically important species using both of these synergistic factors [23].

83 In this study, we model the current and future distribution of an invasive species, *Rhododendron*
84 *ponticum* (L.), in Wales using both climate and LULC projections for 2030. *R. ponticum* is an invasive
85 plant species that was introduced to the British Isles as an ornamental plant from mainland Europe in
86 the eighteenth century. It is a perennial, evergreen shrub that generally invades woodlands [34],
87 although it is known to colonize other types of habitats too [29]. The species has caused economic and
88 ecological losses by affecting soil health, inhibiting the regeneration of native flora and posing risk to
89 pollinators [35][36]. The novel contribution of this study is the use of current and future LULC maps at
90 high spatial resolution (25 m), based on contrasting policies of forest management and land-use practice
91 in Wales. Our previous work has shown that, a) land cover is the critical determinant of the distribution
92 of *R. ponticum* [29], b) the distribution of *R. ponticum* can be best modelled at high spatial resolution (25
93 m) [37], and c) combinations of current policies of forest expansion and restoration of ecologically
94 important habitats in Wales may lead to diverging patchwork of land use types in Wales by 2030 [38].
95 Thus, we aim to investigate the combined effect of climate change and LULC projections on future
96 distribution of this invasive species in Wales. This study makes a theoretical contribution to the debate
97 on combining climate change and LULC changes to predict species distribution and, at the same time,
98 our observations are directly applicable to managing future invasion patterns of *R. ponticum* in Wales.

99 2. Methodology

100 2.2. Study Area and Species Records

101 Wales, a country in the UK, has an area of approximately 21000 km² and a human population of over 3
102 million [39]. The country is characterized by a wide variety of landscapes, reflecting both its rugged
103 topography and a long history of agricultural settlement and industrialization. A significant proportion

104 of land (approx. 6000 km²) is at an altitude above 300 m and considered mountainous. Welsh landscape
105 contains a range of typical habitats; woodlands, semi-natural grasslands, arable agriculture, heathland,
106 fens, bogs, coastal ecosystems including sand dunes and salt marshes, and a diverse range of upland
107 and montane habitats [29][40].

108 We obtained distributional records for *R. ponticum* in Wales from the Global Biodiversity Information
109 Facility (www.gbif.org/) by using the dismo R package [41]. We retrieved 8,764 presence records of *R.*
110 *ponticum*, which we screened using recommended protocols [42]. Spatial uncertainty of all occurrence
111 records was addressed by removing all duplicate or non-geo-referenced occurrence points. Occurrence
112 records were spatially rarefied by eliminating all but one point within 1 km² of the study area to reduce
113 clustering [37]. This resulted in a dataset of 1,280 presence records which were used in our modelling
114 exercise.

115 **2.3. Predictor Variables**

116 We chose a set of 24 predictor variables based on a review of the literature [43][44][45][46], expert
117 knowledge of the species and of the Welsh landscape, and the results of our earlier study on habitat
118 suitability for *R. ponticum* [29]. We considered 19 bioclimatic variables (www.worldclim.org), 4
119 topographic variables (altitude, slope, hillshade and aspect, <https://lta.cr.usgs.gov/SRTM1Arc>) and
120 land cover (consisted of 6 classes namely, 'broadleaf forest', 'conifer forest', 'arable land', 'improved
121 grassland', 'semi-natural grassland', 'mountain, heath & bog') [38]. For the ease of interpretation, land
122 cover was converted into 6 continuous variables by calculating Euclidian distances of each land cover
123 class to each pixel in the study area.

124 The default spatial resolution of variables was, bioclimatic: ~ 1km, topographic variables: 25 m, and
125 land cover: 25 m. All variables were resampled to 25 m spatial resolution since our earlier investigation
126 on habitat suitability modelling of *R. ponticum* confirmed that the species could be most accurately
127 modelled at this scale [37]. Furthermore, in an earlier investigation we demonstrated that it is useful to
128 conserve the high resolution of land cover and topography when the species being modelled is more
129 sensitive to these variables as compared to bioclimatic variables [42]. We removed highly correlated

130 variables to select the variable layers for use in final model runs by applying a Pearson correlation
131 coefficient cut-off of $r \leq 0.70$ [47]. This step reduced the impact of multicollinearity and improved model
132 conformity with statistical assumptions [48]. After omitting highly correlated variables, we were left
133 with mean diurnal temperature range (bio 2), annual precipitation (bio 12), minimum temperature of
134 the coldest month (bio 6), distance to broadleaf forests, distance to conifer forests, distance to arable
135 land, distance to mountain, heath & bog, altitude and aspect. All raster variables were projected using
136 'British National Grid' projected coordinate system.

137 **2.4. Future Climate Change Scenarios**

138 We used climate change scenarios for the year 2030 based on the IPCC 5th assessment report to model
139 the effect of climate change on future distribution of *R. ponticum*. In an earlier investigation of the
140 distribution of *R. ponticum* in Wales [29], we had tested future climate projections of six of the most
141 recent Global Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, MIROC5, HadGEM2-ES,
142 and MPI-ESM-LR. Three of these projections predicted a minor deviation from the current species
143 distribution, whereas the other three GCMs depicted strong effects on the future distribution of this
144 species. To account for this dichotomy, in the current study we use GISS-E2-R and MIROC5 to represent
145 the high and low ends of the environmental conditions spectrum that may affect the distribution of *R.*
146 *ponticum* in future. Furthermore, under each of the two GCMs, we consider two Representative
147 Concentration Pathways (RCPs) - RCP 2.6 & RCP 8.6 to represent the best and the worst-case scenario
148 of future GHG concentration [49].

149 **2.5. Future Land Use & Land Cover Change Scenarios**

150 We used two *Land Use and Land Cover* (LULC) change projections for Wales for the year 2030 [38]. The
151 projections were derived using a Multi-Layer-Perceptron and Markov Chain ensemble algorithms. The
152 projections based on contrasting policies of forest expansion and land management practice in Wales
153 (see [38] for details). Both projections are informed by past LULC transitions (2007 – 2015). First, past
154 LULC changes were explained by a suite of explanatory variables and then the trajectory of past LULC
155 change was projected into the future using the Markov Chain and Multi-layer perceptron (MC-MLP)

156 ensemble algorithms. The two future LULC scenarios, namely “**Business-as-Usual scenario**” and
157 “**Ecosystem Conservation scenario**” (Supplementary data, Figure 1) were motivated by the following
158 storylines:

- 159 • The business-as-usual scenario (B-a-U) is the default scenario, which represents a linear
160 projection of past trends (2007-2015) to 2030. This scenario assumes that the past trend and
161 intensity of LULC change (e.g., new forest plantations, conversion of existing coniferous forests
162 to broadleaf forests or the degradation of heath and bog) would continue until 2030.
- 163 • The ecosystem conservation scenario (E-C) is based on existing and proposed policies of the
164 Welsh government and Natural Resources Wales on planting new woodlands, increasing the
165 rate of conversion of coniferous forests to broadleaf forests, and improved conservation of
166 heath and bog (see [38] for details). In the E-C scenario, the probability of Conifer-to-Broadleaf
167 Forest conversion and the rate of conservation of heath and bog both increase by 50% as
168 compared to the current rate. The scenario further assumes no deforestation of broadleaf forest
169 until 2030. A detailed analysis of predicted LULC under both projections is presented in
170 supplementary data (Figure 2).

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

174

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180 **Table 1.** Reference list of eight Land Use Land Cover & Climate (LULCC) Change scenarios for Wales
 181 in 2030, based on combinations of two Land Use & Land Cover (LULC) change scenarios, two Global
 182 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

183

184 2.6. Ecological Niche Modelling Algorithm

185 We used MaxEnt, a maximum-entropy based machine learning (presence/background) algorithm to
 186 model the current and future distribution of *R. ponticum* (L.). MaxEnt predicts the distribution of a
 187 species on the basis of a given set of predictor variables and presence-only occurrence data [50]. We
 188 selected MAXENT primarily because it allows for the use of both continuous and categorical
 189 predictor variables [51], can handle complex interactions between predictor and response variables
 190 [52], and performs better than discriminative models while using presence-only records [51]. We used
 191 a reasonably large sample size [53] and applied the recommended screening and verification of
 192 occurrence records [37].

193 In MaxEnt, model complexity is primarily controlled by two factors; feature classes and regularization
 194 parameters [54]. Feature classes - Linear (L), Quadratic (Q), Hinge (H), Product (P), and Threshold (T)
 195 - transform predictor variables, whereas regularization multipliers penalize for overparameterization
 196 (for details, see [29]). MaxEnt-based models are prone to over-fitting due to their reliance on default

197 options describing feature classes and regularization parameters [55][54]. Thus, an optimization of
198 MaxEnt setting is recommended to avoid over-simplified or overly complex models [29]. To tune up
199 the model, we used ENMeval [55] to create all possible combinations of selected parameters. We
200 produced a total of 48 models using six combination of these feature classes (L, H, LQ, LQH, LQHP,
201 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
202 corrected Akaike Information Criterion (AICc) to choose the best combination of feature class and
203 regularization parameters.

204 We then ran MAXENT (version 3.4.1) with the default convergence threshold of 10^{-6} and with 5,000
205 iterations to allow the model a reasonable scope for convergence, thus reducing the risk of over-
206 predicting or under-predicting the model relationships. The selected model used the “Linear,”
207 “Quadratic” “Product,” and “Hinge” feature types and the regularization parameter of 2, as indicated
208 by the lowest AICc value. We processed 25 model replications by bootstrap resampling, randomly
209 allocating 80% of the occurrence records to calibration and 20% to validation. Habitat suitability maps
210 under current and future LULCC change scenarios represent the average of the 25 replicate models.
211 MAXENT produces continuous suitability index in its output; 10 percentile training presence threshold
212 was employed to convert this index into binary form (suitable or unsuitable habitat) [57]. We used
213 Cloglog output format.

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

216 **2.7. Model Evaluation**

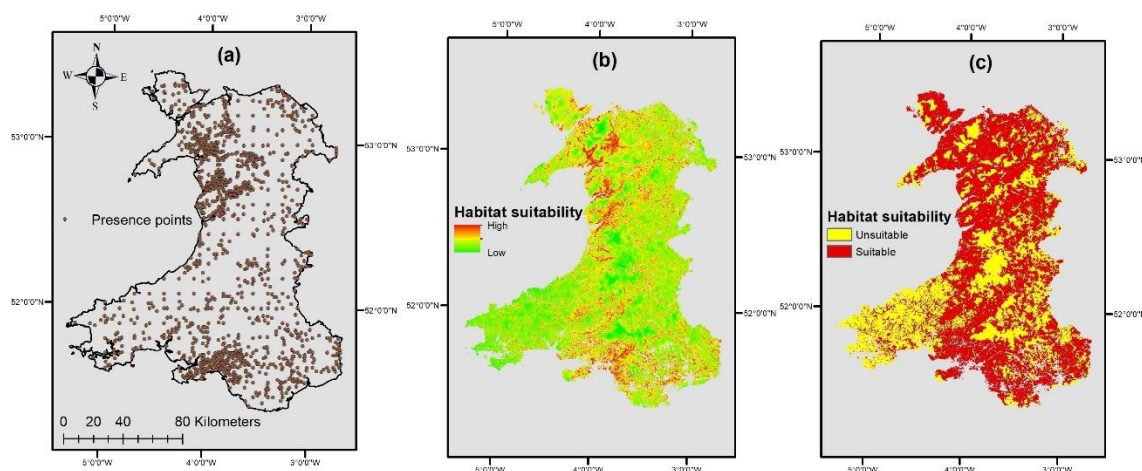
217 We used the Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) to test the
218 performance of the model against presence observations [52]. An AUC value of 0.5 shows that the
219 model does not predict any better than random chance, whereas a value of 1 indicates a perfect
220 performance of the model [59]. Percentage of contribution and permutation importance contribution
221 were used to assess the relative significance of predictor variables. In addition to AUC, we used
222 Continuous Boyce Index (CBI) as an additional assessment tool. The Boyce index requires presence data

223 only and measures by how much model predictions differ from a random distribution of observed
 224 presence across the prediction gradient (for details, see [42]). The continuous values of the Boyce index
 225 vary between -1 and +1. Positive values indicate a model where predictions are consistent with the
 226 distribution of actual presence data, values close to zero mean that the model is no different from a
 227 random model and negative values indicate counter predictions (e.g., predicting no occurrence in areas
 228 where actual presence is recorded) [60][61]. In addition, we calculated a set of null models [62] by
 229 generating 100 random datasets, each equalling the actual number of presence points. We then
 230 calculated a Maxent model for each dataset and used a Kruskal-Wallis test to compare the training AUC
 231 values of the species models with null models.

232 3. Results

233 3.1. Ecological niche model accuracy

234 The Maxent-based model with the lowest AICc showed encouraging predictive capacity: $AUC_{train} =$
 235 79.8, $AUC_{test} = 77.21$, and $CBI = 0.81$. These results suggest that the predictor variables used during
 236 model calibration predicted the presence of *R. ponticum* in Wales with decent accuracy. Moreover, our
 237 model performed significantly better than null models (Kruskal-Wallis with p-values < 0.001).
 238 Continuous and binary habitat suitability maps of the current distribution of *R. ponticum* in Wales are
 239 presented in Figure 1.



240

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

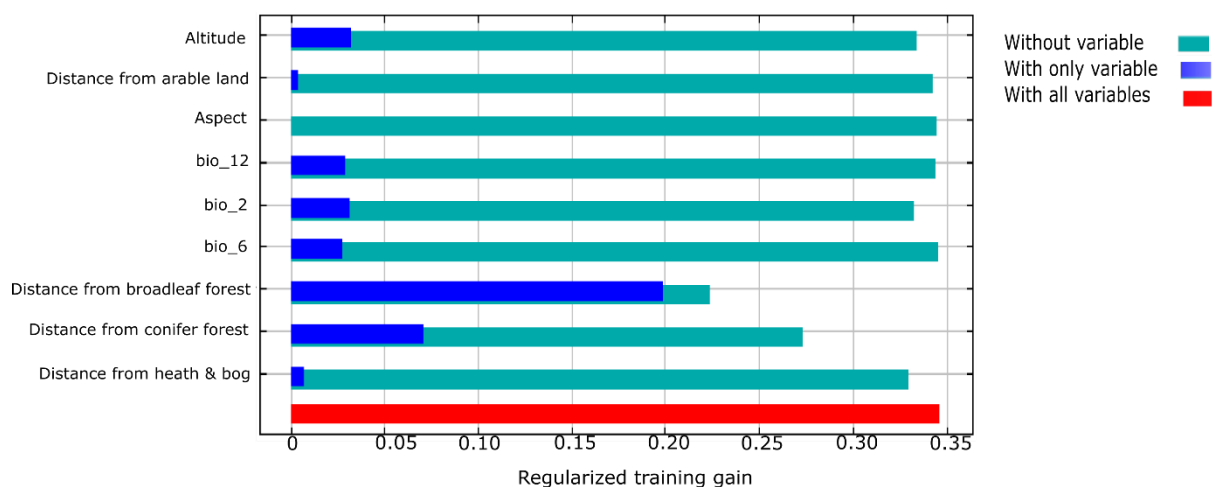
243 3.2. Key environment variables

244 We used percentage contribution, permutation importance, and jack-knife test to assess the relative
 245 importance of environmental variables used to model the distribution of *R. ponticum* in Wales. As
 246 shown in Table & Figure 2, land cover (distance from broadleaf and conifer forests) has the highest
 247 contribution and permutation importance in predicting the distribution of *R. ponticum*.

248 **Table 2.** Percentage contribution and permutation importance of each variable for predicting the
 249 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

250



251

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

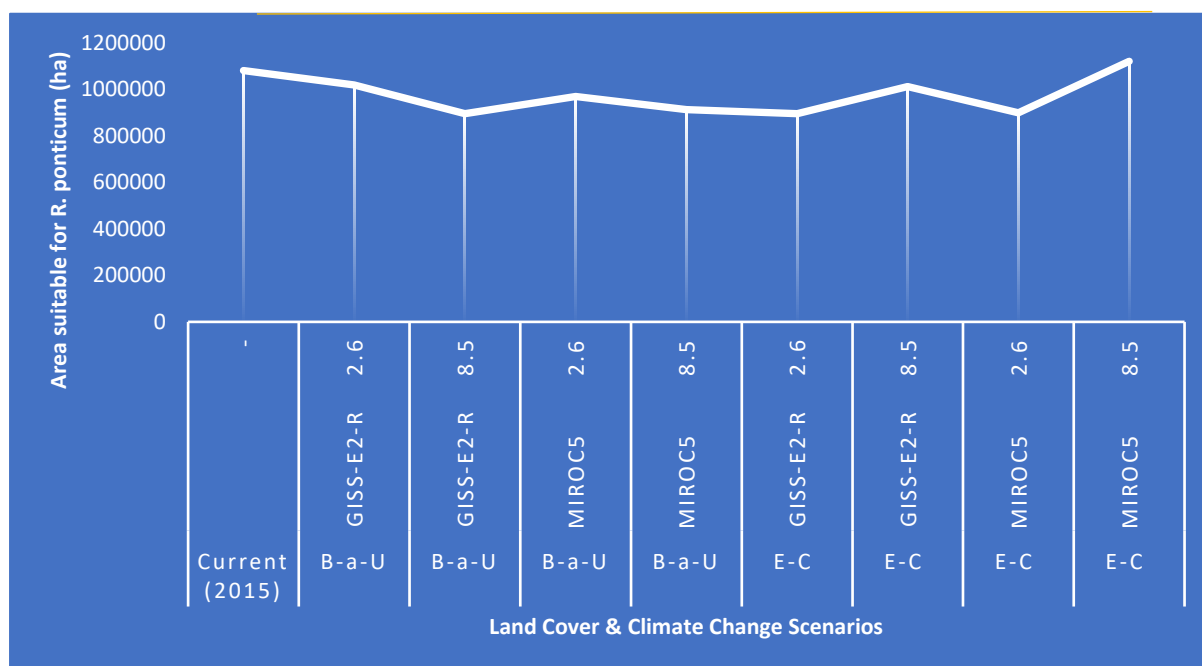
257

258 Close inspection of individual response curves (Supplementary Data, Figure 3) shows logistic
 259 predictions by a specific variable, when the rest of the predictors are artificially kept at their average
 260 values. The response curve for land cover shows that *R. ponticum* favours broadleaf and conifer forests.
 261 Furthermore, the presence of *R. ponticum* is negatively associated with altitude. The response curves of
 262 bio 2 bio 6 show that its presence is lowest at extreme values of these variables.

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

264 Our models show that nearly 52 % or 1081582 ha is currently suitable for *R. ponticum* invasion, out of
 265 the total land area of 2,073,500 ha. Looking ahead on the basis of different LULCC change scenarios,
 266 the extent of habitat suitable for *R. ponticum* in Wales park is likely to contract under most of the LULCC
 267 change scenarios considered in this study (Figure 3).

268



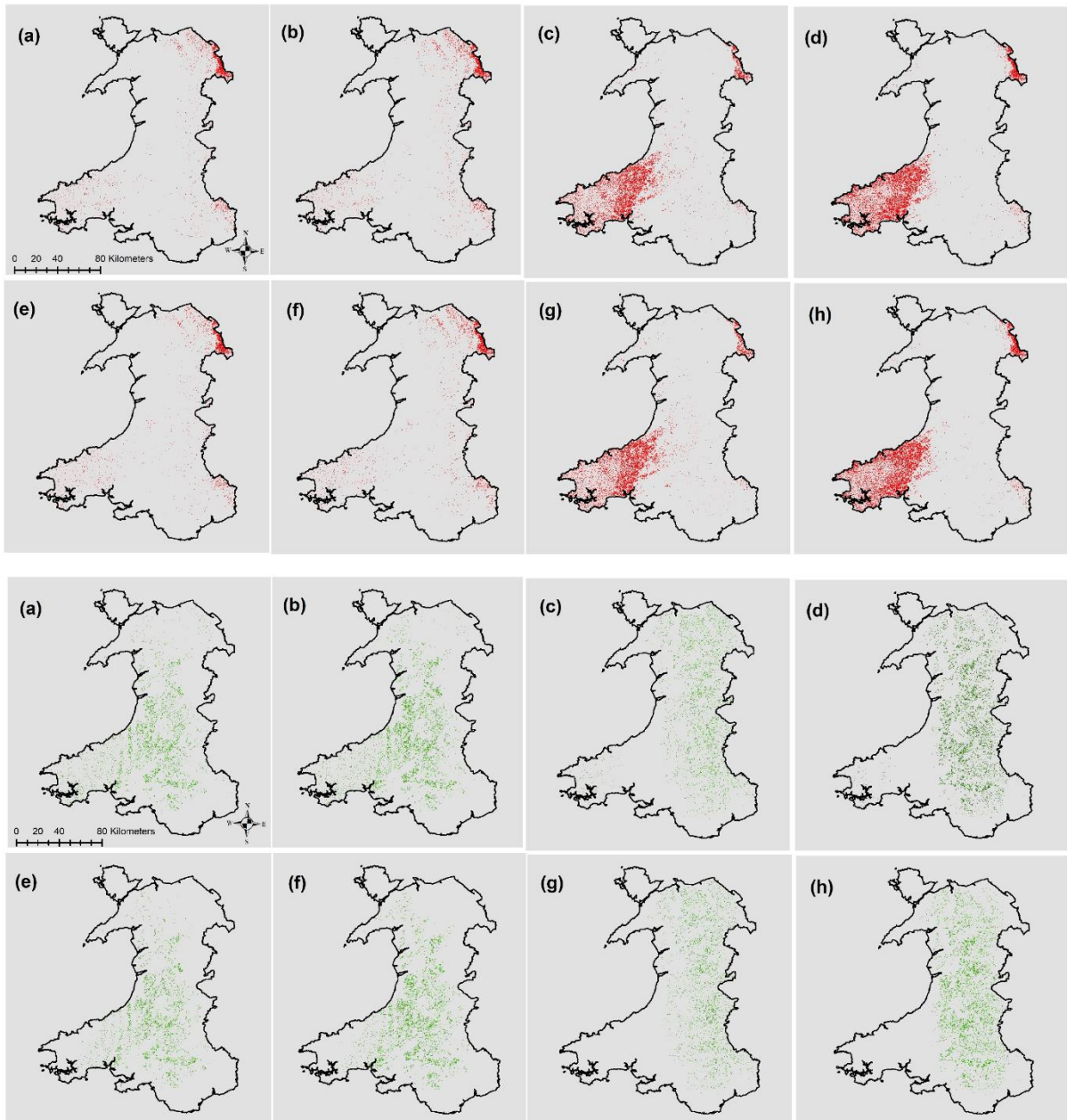
269

270 **Figure 3.** Area suitable for *R. ponticum* in Wales under eight LULCC change scenarios predicted for
 271 2030. Recent Past refers to the baseline land cover and climatic conditions (2015), Scenario 1: GISS-E2-
 272 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,
 273 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
 274 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.

275

276 In all scenarios based on GCMs GISS-E2-R and GCM MIROC5 (Table 1), habitat suitability of *R.*
277 *ponticum* is likely to decrease in future. The lowest habitat suitability is predicted by scenario 2 (B-a-U
278 x GISS-E2-R x RCP 8.5), whereas the only instance of net expansion of habitat suitability is scenario 8
279 (E-C x MICROC5 x RCP 8.5).

280 In all scenarios, including GCM GISS-E2-R (scenarios 1-2 & 5-6), new areas in the north-eastern and
281 north-western edges of Wales are likely to become suitable for *R. ponticum* (Figure 4, a-b & e-f, red
282 pixels) and existing suitable areas of *R. ponticum* are likely to become unsuitable in the central and
283 southern parts of Wales (Figure 4, a-b & e-f, green pixels). In other scenarios, including GCM MIROC5
284 (3-4 & 7-8), new suitability spots are likely to emerge in the south-western coastal areas of Wales (Figure
285 4) whereas reduced suitability is likely along the eastern and northern parts of Wales (Figure 4).



286

287 **Figure 4.** Maps showing areas in Wales which are likely to become suitable (shown in red) and
 288 unsuitable (shown in green) for *R. ponticum* by 2030 under future LULCC changes scenarios. a-h
 289 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
 290 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-
 291 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:
 292 MIROC5 x RCP 2.6 x E-C, (h) Scenario 8: MIROC5 x RCP 8.5 x E-C.

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297 4. Discussion

298 Accurate predictions of invasive species distribution and invasion trends are critical to understanding
299 the impacts of global environmental change on terrestrial ecosystems and hence, pivotal to the
300 development of global environmental change adaptation policy [63]. Such predictions are even more
301 relevant in the contemporary world where the anthropogenic changes are likely to drive the sixth mass
302 extinction event on Earth [64]. A considerable number of studies have looked at biological invasion,
303 most however considering climate and LULC change - two key factors of global change - in isolation
304 [65][66][67][68]. When considered together, the effect of climate and LULC change on ecosystems may
305 be synergistic [69], leading to an under or overestimation of the effects of anthropogenic change on
306 global ecosystems and biodiversity by the majority of the ecological models [70]. To the best of our
307 knowledge, ours is one of the few investigations testing the combined effects of climate and LULC
308 change and is the first attempt to model the distribution of an invasive species in Wales under these
309 future scenarios.

310 4.1. Significance of predictor variables

311 Our results suggest that landscape features exert more influence than climate over the distribution of
312 *R. ponticum* in Wales. Land cover is the most important variable determining its distribution, as it is
313 often the critical variable limiting the distribution of a plant species [71]. LULC changes are closely
314 associated with human population size and activity; invasive species are likely to take advantage of
315 transportation networks and environments simplified by humans [72]. *R. ponticum* can invade a wide
316 range of land cover classes, including forests, upland heaths and grasslands [73]. In Britain, forests
317 represent the land cover class most susceptible to *R. ponticum* invasion [73]. In an earlier investigation
318 of the distribution of *R. ponticum* in Snowdonia National Park, Wales, we found that this invasive
319 species is most often found in "Mosaic Tree & Shrub" & "Needle Leaved Forest" [29]. This current
320 study supports the earlier report by showing the preference of *R. ponticum* for conifer forests. A strong
321 presence of *R. ponticum* in woodlands can be attributed to many reasons; environment suitable for seed

322 germination [45], forest floor litter that supports *R. ponticum* growth [74] and shelter of woods that
323 provides the necessary “cover” to spread without being eradicated [29].

324 Land cover is followed by altitude and mean diurnal temperature range (bio 2) in terms of variable
325 importance in the MaxEnt-based model in this study. The response curve (Supplementary Data, Figure
326 3) shows that the likelihood of *R. ponticum* presence is negatively correlated with altitude. Altitude may
327 not have a direct effect on plant growth, but it is often considered a strong proxy for other variables
328 important to species distribution. For example, exposure to sunlight, hydrology, soil physical and
329 chemical properties, and wind speed may vary with increasing altitude, which in turn may be critical
330 for the colonization by *R. ponticum* [75]. Earlier research has confirmed a strong relationship between
331 mean diurnal temperature range (‘bio 2’ in the current study) and invasive plant species distribution
332 [76]. Mean diurnal temperature range may affect biological invasion in many ways. For example,
333 diurnal fluctuations in temperature increase seed germination and positively affect photosynthetic
334 activity, especially in colder parts of the world [76]. Response curve (Supplementary Data, Figure 3)
335 indicates that *R. ponticum* favours areas with higher values of ‘bio 2’, which is in agreement with earlier
336 reports [76]. Furthermore, mean diurnal temperature range in Iberian Peninsula (the native range of *R.*
337 *ponticum*) is °C 5.2 – 13.0 compared to the °C 5.4 – 7.0 (Supplementary data, Table S1) in Wales which
338 indicates that an increase in mean diurnal temperature range in Wales under future climate change
339 scenarios is likely to improve habitat suitability for *R. ponticum* in Wales.

340 **4.2. Effect of Climate and LULC Change Scenarios on Suitability of *R. ponticum* in Wales**

341 Our analysis shows that the area suitable for *R. ponticum* is likely to contract in future. In our case, 7 out
342 of the 8 LULCC change scenarios considered in this study indicate smaller suitable area than that at
343 present. One of the main reasons for this could be the decline of conifer forest cover from the current
344 scenario under both B-a-U and E-C in future (Supplementary data, Table S1). As shown by the response
345 curves (Supplementary Data, Figure 3), *R. ponticum* is most likely to occur in conifer forests. *R. ponticum*
346 favours acidic soils, coniferous forests may thus offer ideal growing conditions for this invasive species
347 [77]. Existing UK Forestry Standard Guidelines on Biodiversity [78] and the UK Biodiversity Action

348 Plan [38] both encourage large-scale conversion of coniferous forests to native broadleaf forests. This
349 may benefit native species as native broadleaf woodland species would improve soil conditions for
350 local flora and fauna, increase food availability and nesting opportunities for birds, reduce insect pests
351 prevalence and enhance the overall aesthetics of the landscape [79][80][38]. Our model suggests that,
352 alongside overall contraction, there is a possibility of an expansion in the *R. ponticum* habitat suitability
353 in the southern-western and north-eastern parts of Wales. This could be attributed to increased forest
354 cover in the south, which is likely to provide the required habitat, cover, and corridor for establishment
355 and spread of *R. ponticum*. In the north, appearance of new suitability hotspots could be due to expected
356 change in the mean diurnal temperature range which may suit *R. ponticum* (Supplementary Data, Table
357 S1 & Figure S5). Evidence suggests that invasive species generally have higher energy demand for
358 intense physiological activities; mean diurnal temperature range may affect species distribution.

359 The increase in future habitat suitability predicted by the GCM MIROC5 x RCP 8.5 x E-C scenario is
360 very interesting. The E-C LULC change scenario depicts a future where overall forest cover will increase
361 from the current 320,210 ha to 415,273 ha (Supplementary data, Table S2). At the same time, RCP 8.5
362 indicates the highest projected GHG concentration pathway under which the mean diurnal
363 temperature range will increase the most along the eastern foothills of Wales. It is possible that *R.*
364 *ponticum* might take advantage of rapidly increasing forest cover and even though future forests are
365 likely to be broadleaved and not conifers, their increasing extent will create an expanding niche for this
366 invasive species. This observation underlines the importance of incorporating regional policy-driven
367 LULC projections into invasive ecological niche models. Extreme climate change and current plans for
368 forest management may thus conspire to improve the future prospects of *R. ponticum* in Wales.

369 4.3. Regional policy-driven LULC change scenarios deserve more attention

370 There is a strong consensus that models combining climate and LULC predictions are very good tools
371 to predict species' distribution, usually far more accurate than climate-only models [81][82]. At fine
372 spatial scales, land-use is often the factor driving the distribution and dispersal of invasive species [4].
373 The interplay of climate and LULC changes may limit the spread of invasives in some cases, while

374 promoting invasion in others [83][29][84][85]. To date, most invasive ecological niche models have
375 assumed homogenous and unchanging landscapes, mainly focussing on climate as the critical dynamic
376 variable [86][66]. The attention has recently shifted towards considering landscape as a heterogenous
377 variable that can affect the rate and trend of biological invasions [87]. This approach needs to be
378 improved further, for that landscapes are not only heterogeneous but also subject to significant human
379 pressure. Ecological niche models cannot rely only on B-a-U projections to predict future species
380 distributions, the trajectory and intensity of LULC change in the future is not likely to copy the past.
381 The trajectory of change may vary, depending upon the socio-political and socio-economic factors of
382 the region under study [88]. Researchers have considered global or continental LULC change scenarios
383 to predict at local scale [81], we however argue that capturing the impact of local land management
384 plans and policies is essential to develop realistic scenarios. One of the used of the scenarios presented
385 in our study is to relate the spread of *R. ponticum* or other invasive species to possible changes in both
386 future landscapes and climate. A possible outcome of this type of modelling exercise is the design and
387 targeting of land management policies to ecosystem conservation [89].

388 **4.4. Implications for Landscape Management**

389 Management of invasive species requires screening potential invasives through a process of risk
390 assessment, which determines the likelihood that an invasive species would enter and inhabit a
391 recipient area [81]. Most studies used in this type of screening of invasive species suggest either an
392 increase [90] or a decrease in invasiveness [29]. We show that, for a single species in a well-defined area,
393 expected LULC and climate changes may result in both an overall decrease or an increase in future
394 habitat suitability. If the purpose of the modelling exercise is to anticipate future trends of species
395 distribution at fine spatial resolution, we suggest that (a) multiple regional change drivers should be
396 considered, (b) future LULC change scenarios based on regional socio-economic and socio-political
397 policies must be included, and (c) multiple combinations of climate and LULC change scenarios should
398 be run to have confidence in predictions of future distribution of the species in question. We illustrate
399 the use of this modelling framework against the backdrop of an invasive species spread, however its

400 use to model distribution of all types of species can be easily envisaged. Alongside theoretical
401 implications, our study has important traction for practical decisions on land management in Wales.
402 We show that while the Welsh government aims to increase forest cover and cites biodiversity
403 conservation as one of the reasons to do so, it is important to factor in and anticipate the spread of *R.*
404 *ponticum* or other invasive species associated with woodlands. Specifically, a strategy combating the
405 expansion of *R. ponticum* in the north-eastern and south-western regions should be considered.

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

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

418 **Conclusion**

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

426 with a range of climate change scenarios. This approach may capture the heterogeneity of landscape
427 and its changes that is exploited by *R. ponticum* and other invasive species.

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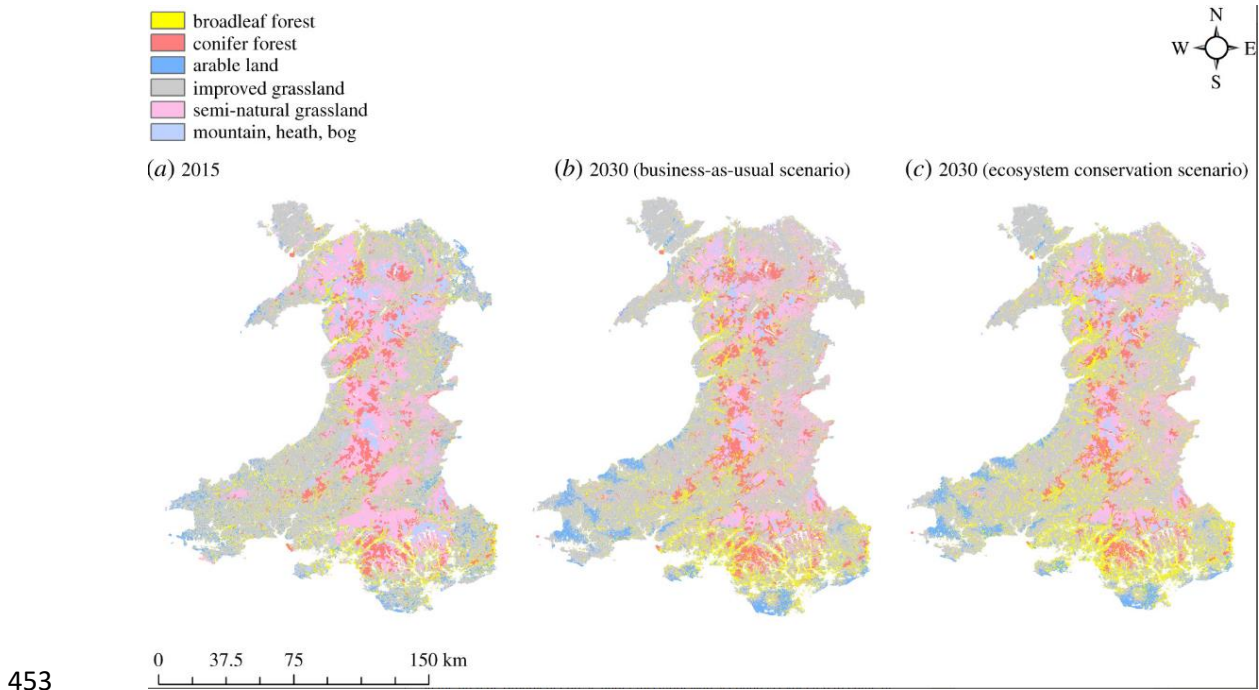
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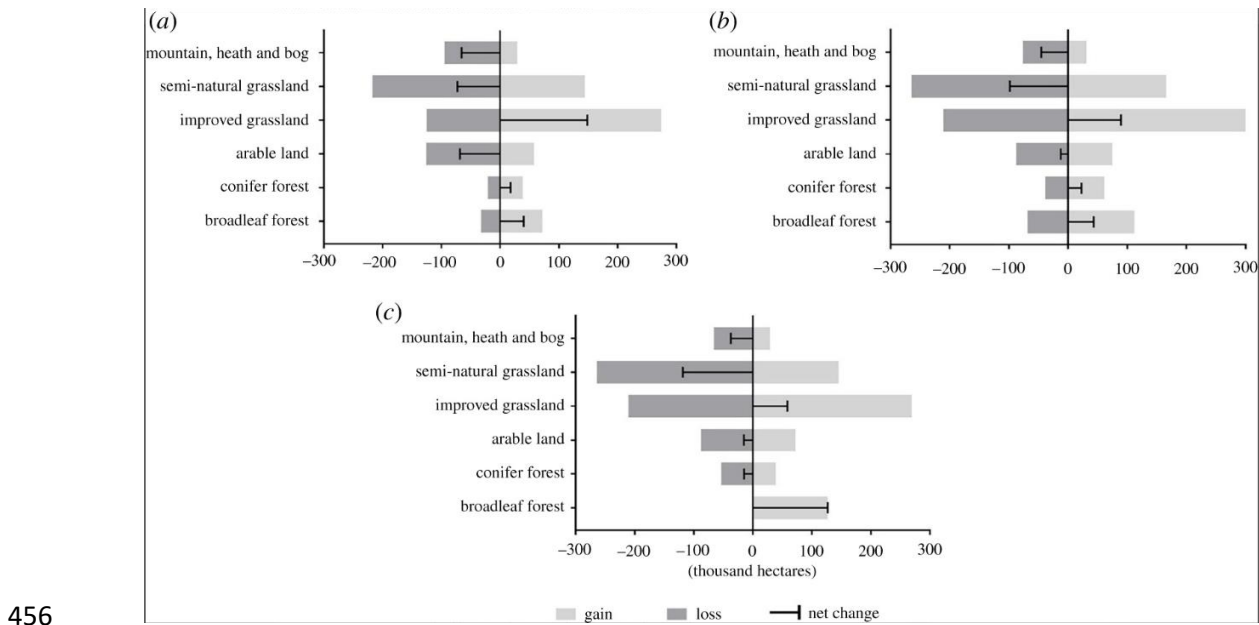
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452 **Supplementary Material**



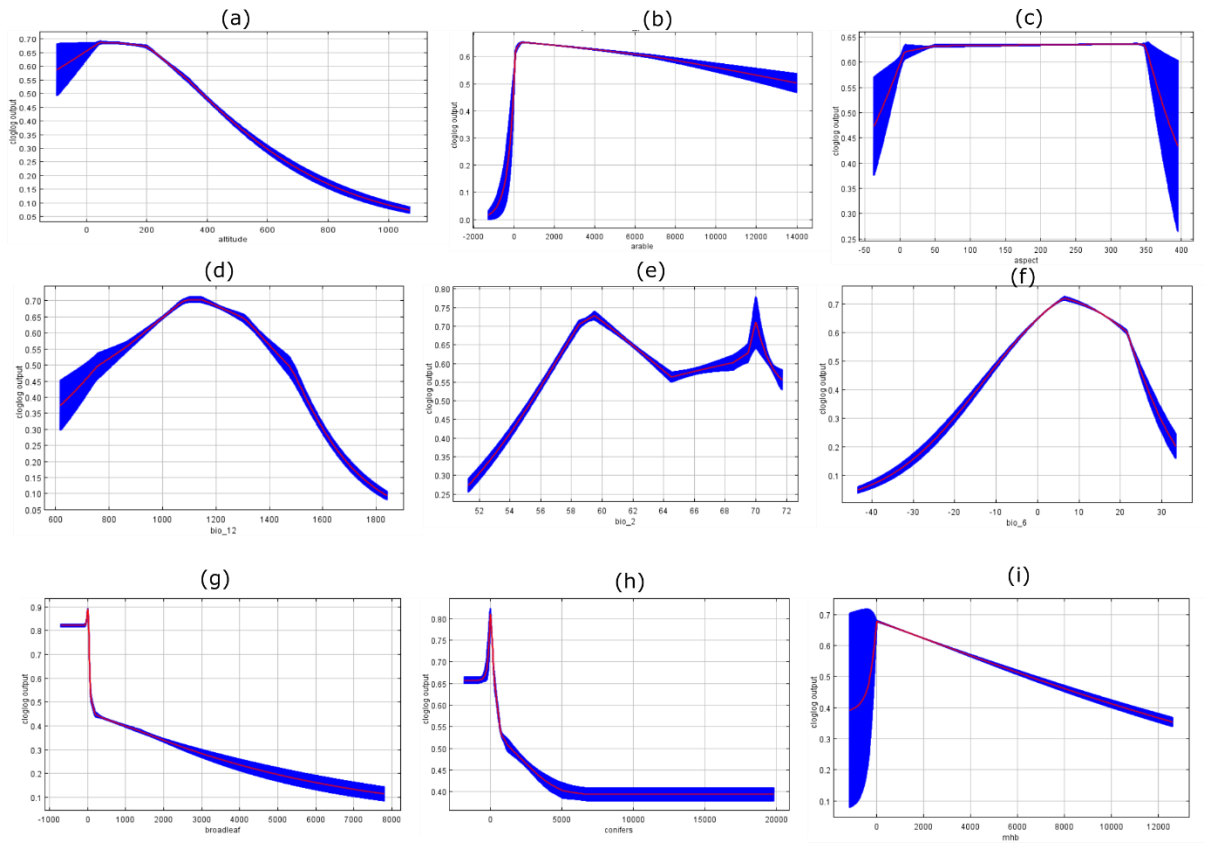
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454 **Figure S1.** Current (a) and projected land use map of Wales, UK for the year 2030 under B-a-U (b) and
 455 EC (c) modelling scenarios. [38]



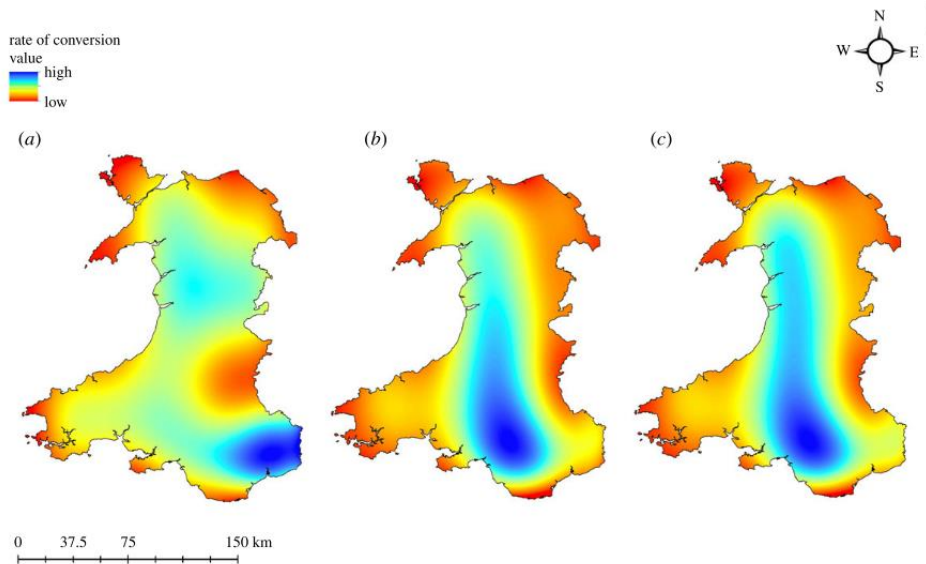
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457 **Figure S2.** In Wales, UK, gains, losses and net changes between different LULC classes (hectares)
 458 during (a) 2007–2015, (b) 2015–2030 (B-a-U scenario) and (c) 2015–2030 (EC scenario) [38]



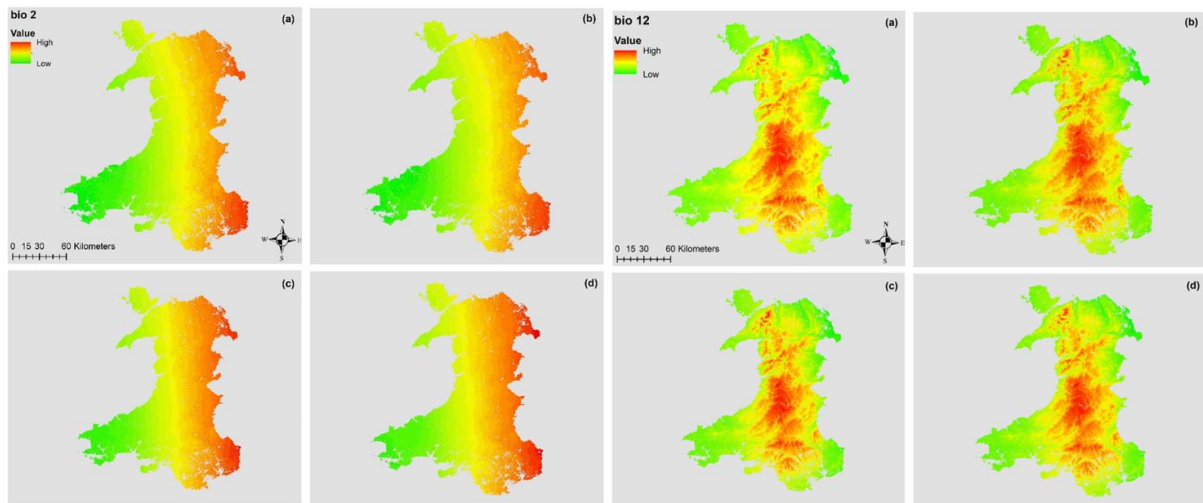
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460 **Figure S3.** Response curves of environmental variables in the MaxEnt-based *R. ponticum* distribution
 461 model. a) altitude, b) distance to arable land, c) aspect, d) bio_12, e) bio_2, f) bio_6, g) distance to
 462 broadleaf forest, h) distance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



463

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



466

467 **Figure S5.** Spatial maps of bio 2 (mean diurnal range) and bio 12 (mean annual precipitation) under
 468 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,
 469 d) MIROC5 x RCP 8.5.

470

471 **Table S1.** Ranges of Bio 2 (mean diurnal range) and Bio 12 (mean annual precipitation) at present and
 472 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

473

474 **Table S2.** Area under broadleaf, conifer and overall forest in Wales at present and under future
 475 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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