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Combining global climate and regional landscape models to improve prediction of invasion risk

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16

17   **(A) Abstract**

18

19   **Aim**

20   It is widely acknowledged that species distributions result from a variety of biotic and abiotic

21   factors operating at different spatial scales. Here, we have aimed to: i) determine the extent to

22   which global climate niche models can be improved by the addition of fine-scale regional

23   data; ii) examine climatic and environmental factors influencing the range of 15 invasive

24   aquatic plant species; and iii) provide a case study for the use of such models in invasion

25   management on an island.

26   **Location**

27   Global, with a case study of species invasions in Ireland.

28   **Methods**

29   Climate niche models of global extent (including climate only) and regional environmental

30   niche models (with additional factors such as human influence, land use and soil

31   characteristics) were generated using MaxEnt for 15 invasive aquatic plants. The

32   performance of these models within the invaded range of the study species in Ireland was

33   assessed, and potential hotspots of invasion suitability were determined. Models were

34   projected forward up to 2080 based on two climate scenarios.

35   **Results**

36   While climate variables are important in defining the global range of species, factors related

37   to land use and nutrient level were of greater importance in regional projections. Global

38   climatic models were significantly improved at the island scale by the addition of fine-scale

39   environmental variables (Area Under the Curve values increased by 0.18 and True Skill

40   Statistic by 0.36), and projected areas decreased from an average of 86% to 36% of the

41   island.

42   **Conclusion**

43   Refining climate niche models with regional data on land use, human influence and landscape

44   may have a substantial impact on predictive capacity, providing greater value for

45   prioritisation of conservation management at sub-regional or local scales.

46

(A) Introduction

Projections of the future range of invasive species based on climate niche models have become increasingly prevalent (Thuiller *et al.,* 2005; Jiménez-Valverde *et al.,* 2011). Niche models are a type of species distribution model that employs correlative techniques to estimate the environmental niche of species based on species distribution data and maps of environmental variables. This estimated species niche is then used to infer species occurrence or habitat suitability. In invasion ecology, niche models are most commonly used to predict 'risk' of invasion based on suitability rather than species occurrence per se. Niche models have identified likely source regions of 'high risk' invaders (e.g. Thuiller *et al.,* 2005), as well as 'hotspots' where multiple invasions are most likely to occur (Ibáñez *et al.*, 2009; O'Donnell *et al.*, 2012) and, conversely, areas where invasive species may decline, creating potential for restoration of native communities (e.g. Bradley *et al.,* 2009).

Species distributions result from a variety of biotic and abiotic factors operating at different spatial scales (Gaston, 2003). In invasion biology, this is often conceptualised as a set of abiotic filters (Theohairdes & Dukes, 2007; Milbau *et al.*, 2009). Hence, while climate limits species distributions at global scales, the prediction of invasion risk on regional scales is likely to be improved by information on factors such as land use, soil or water nutrient concentrations, pH and human influence. The relative importance of climate versus other environmental variables in niche modelling has been investigated for various invasive species within regions or continents (e.g. Thuiller *et al.*, 2006; Nielsen *et al.*, 2008; Ibanéz *et al.,* 2009; Capinha & Anastácio, 2011; Jarnevich *et al.*, 2011; Compton *et al.,* 2012). Further studies have shown the importance of topography, habitat, microclimate and water availability in determining species distributions at smaller spatial scales (e.g. Bossenbroek *et al.*, 2004; Evangelista *et al.*, 2006; Gillingham *et al.*, 2012). However, the optimal method for selecting predictor variables and their appropriate spatial scales in niche models remains

73 uncertain (Austin & Kimberley, 2011), and is likely to depend on the organism being

74 modelled (Araújo & Guisan, 2006).

75   The appropriate spatial extent of a study region depends largely on the aims of the study

76 and the nature of the study species (Elith & Leathwick, 2009). Climate niche models with a

77 global extent are most likely to be useful for modelling species with broad climatic niches

78 and high dispersal capacity such as invasive species. Niche models that include climate data

79 from only either the native or the invaded range of species tend to underestimate potential

80 niche space (Beaumont *et al.,* 2009; Jiménez-Valverde *et al*., 2011). For this reason, several

81 recent authors have used global distribution data to create niche models of invasion risk based

82 on global climate. However, these models rarely incorporate fine-scale data, for example, on

83 local nutrient availability, pH or soil characteristics. This is probably due to the lack of

84 reliable data on such characteristics globally.

85   Another challenge in constructing global niche models may be the considerable

86 uncertainty regarding the precision of species distribution records in global datasets, hence

87 larger grid cells may be more appropriate for building global models. Conversely, national

88 and regional species databases usually have high precision. Here we demonstrate how it may

89 be useful to combine the outputs of global climate niche models with regional niche models

90 in order to create integrated models which make better use of all available datasets.

91   We examined the global climatic factors influencing the distribution of 15 invasive

92 freshwater plants considered 'high risk' in Europe. Aquatic plants are primary components of

93 freshwater ecosystems and invasive species have the capacity to fundamentally alter

94 ecosystem functioning. However, to date climate niche models of freshwater ecosystems

95 have focused mainly on animals (e.g. Liu *et al.,* 2011; Reshetnikov & Ficetola, 2011) and few

96 studies have used climate niche models to examine the global distributions of invasive

97 aquatic plants.

98   We provide a simple method for the amalgamation of global climate niche models with

99   regional data on land use, human influence, soil and water characteristics for the invaded

100   range, and show how this significantly changes predictive capacity at the regional scale.

101   Specifically, we aimed to i) determine the extent to which global climate niche models can be

102   improved by the addition of fine-scale regional data, ii) examine the factors governing the

103   range of key invasive aquatic plant species, and iii) provide a case study for the use of such

104   models in invasion management on an island.

105

106 **(A) Methods**

107

108 **(B) Species selection**

109 We modelled the distributions of eight non-native aquatic plants which are currently

110 established invasives in Ireland (*Azolla filiculoides* Lam.*, Crassula helmsii* (Kirk) Cockayne*,*

111 *Elodea canadensis* Michx.*, Elodea nuttallii* H. St. John*, Lagarosiphon major* (Ridl.) Moss*,*

112 *Lemna minuta* (Kunth)*, Myriophyllum aquaticum* (Vell.) Verdc and *Nymphoides peltata*

113 (S.G. Gmel.) Kuntze). These species represent a range of introduction dates from 1836 to

114 1993. In addition we modelled seven potentially high-risk species which are either not

115 currently present in Ireland (*Cabomba caroliniana* A. Gray*, Eichhornia crassipes* (Mart.)

116 Solms*,* and *Salvinia molesta* D.S. Mitch) or present at less than 5 locations in Ireland (*Egeria*

117 *densa* Planch.*, Hydrilla verticillata* (L.f.) Royle*, Hydrocotyle ranunculoides* L.f.*, Ludwigia*

118 *grandiflora* (Michx) Greuter & Burdet). These were chosen based on the European and

119 Mediterranean Plant Protection Organisation (EPPO) lists of high risk species

120 (http://www.eppo.int/invasive_plants/ias_plants.htm). *H. verticillata* is a cryptogenic species

121 in Europe and its origin and status in Ireland are unclear. The native status of the species in

122 Ireland has been questioned due to its isolated distribution, distance from its native range,

123 sub-optimal growth conditions and the occurrence of female plants only (Minchin, 2007).

124 The decision to include this species reflects this uncertainty.

125

126 **(B) Niche models**

127 Firstly, niche models fitted with global climate data (Climate Niche Models (CNMs)) were

128 constructed for all species based on global distribution data. Secondly, for all 8 species which

129 are established in the study region (Ireland), niche models fitted with regional land cover

130 data, human influence, soil characteristics and climate suitability outputs from global CNMs

131   were constructed using species distributions within Ireland (hereafter regional Environmental

132   Niche Models (ENMs)). The projected output raster from the global CNM, representing the

133   climatic suitability of each cell for the target species, was included as an explanatory variable

134   in regional ENMs.

135   This two-stage integrated modelling approach was adopted for a number of reasons.

136   Firstly, it was not appropriate to build a climate suitability model based solely on Ireland or

137   Europe as the potential climatic range of each species was likely to be larger than either

138   region. Niche models that incorporate global climate data and global species distributions are

139   likely to be important when projecting species ranges into future climates which are novel to

140   the study region, but similar to current climates elsewhere. Secondly, reliable fine-scale

141   regional data were sometimes available only for Ireland (e.g. water nutrient content) or

142   Europe (e.g. CORINE land cover maps) and were, therefore, best suited to regional scale

143   modelling. Thirdly, uncertainty regarding the precision of records obtained from global

144   databases made them unsuitable for regional model building. Our two-stage approach

145   allowed for the incorporation of global climatic data into regional ENMs. Models were built

146   using MaxEnt 3.3.3k (Phillips *et al.,* 2010).

147

148   **(B) Global Climate Niche Models (CNMs)**

149   Data on the recorded distribution of each species were downloaded from the Global

150   Biodiversity Information Facility data portal (www.gbif.org). Records with no location

151   coordinates were excluded from the dataset; >97% of included records had a precision of

152   greater than 0.1 decimal degrees. Records prior to 1950 were excluded to match the

153   timeframe for the 'current' climate data (1950-2000). Species had between 122 and 4,474

154   records (mean = 1,395). Records from both native and invaded ranges were used to avoid

155   underestimation of climatic niche space. All species included had invaded ranges outside the

156 island of Ireland, and all species present in Ireland were also invasive in other climatically

157 similar regions (e.g. the UK). Plant records from Ireland were not included in the global

158 CNMs as these records would be used in training and testing of subsequent regional models.

159 Ireland is small and has a narrow range of climatic conditions which were not novel when

160 compared with global training data. This assumption was validated after model fitting by

161 examining the multivariate environmental similarity surface (MESS) output from MaxEnt

162 (following Elith *et al.*, 2010).

163   Standard climatic variables were downloaded from WorldClim at a 2.5º cell resolution

164 (http://www.worldclim.org/bioclim). A total of 8 variables were used, namely annual mean

165 temperature (Bio1), temperature seasonality (Bio4), maximum temperature of warmest month

166 (Bio5), minimum temperature of coldest month (Bio6), annual precipitation (Bio12),

167 precipitation seasonality (Bio15), mean precipitation of wettest quarter (Bio16) and

168 precipitation of driest quarter (Bio17). These variables were selected based on their relevance

169 to the ecology of freshwater plants. All other WorldClim variables were excluded in order to

170 reduce multi-collinearity and subsequent model over-fitting (Jiménez-Valverde *et al.,* 2011).

171 Terrestrial climate variables will not exactly reflect the conditions of freshwater systems;

172 however, terrestrial climate data have been shown to be an effective proxy for shallow waters

173 (e.g. Reshetnikov & Ficetola, 2011).

174   Forecast projections for future climatic scenarios were from the International Panel on

175 Climate Change (IPCC) 4th assessment report (IPCC, 2007), in particular, the Special Report

176 Emissions Scenarios (SRES) 'A2' ("high energy requirements and emissions") and 'B2'

177 ("low energy requirements and emissions"). Spatial climate projections were the CSIRO

178 MK2 global climate model for each scenario for the 2020s (2010 to 2039), 2050s (2050 to

179 2069) and 2080s (2070 to 2099) and were downloaded from http://www.ccafs-

180 climate.org/data/.

181   Plant records were split into a 75% model 'training set' and a 25% model 'test set'.

182   Duplicate records were excluded. A combination of linear, quadratic and product features

183   was used for estimating the response of each species to each predictor variable. Extrapolation

184   was not used so climate suitability was not projected where conditions were outside the range

185   of the training data (i.e. background and presence data).

186   Presence-only modelling techniques are particularly susceptible to recorder-bias (Phillips

187   *et al.,* 2009; Yackulic *et al.*, 2013), due to the fact that they rely on random background data

188   points rather than recorded absences. Sample bias can be minimised in MaxEnt by restricting

189   the selection of background points to represent the environmental conditions that were

190   sampled (Elith *et al.,* 2011). Here, we used GBIF records of two major aquatic plant families

191   (Hydrocharitaceae and Menyanthaceae) to account for the distribution of recording effort of

192   aquatic botanists. These plant families have a cosmopolitan distribution, and contain only

193   aquatic and semi-aquatic species. Background points ($n = 10,000$) were chosen exclusively

194   from locations in which these aquatic plant families or the invasive species studied were

195   recorded, rather than assuming uniform recording effort.

196

197   **(B) Regional Environmental Niche Models (ENMs)**

198   Data on species distributions in Ireland were collated from local government agencies, data

199   providers and botanical societies (see Appendix S1 in Supporting Information). Regional

200   ENMs were built using Irish data only and within the spatial extent of the island (for those 8

201   species already established in Ireland). Records with a resolution of >100 m were excluded in

202   order to match the cell size of the environmental data. As with the global dataset, duplicates

203   and records pre-1950 were excluded. Species had between 13 and 1,646 records (mean =

204   262) (data from within Ireland only).

205   Environmental variables were chosen based on ecological relevance to study species, with

206   both "direct" and "indirect" associations with the distributions of study species (Austin,

207   2007). Variables included were human impact i.e. propagule transport and disturbance

208   facilitating establishment (Buchan & Padilla, 2000; Aznar *et al.,* 2003; Leung, 2006; Capers

209   *et al.*, 2009); land use, including forestry (Buchan & Padilla, 2000) and agriculture (Heegaard

210   *et al.,* 2001) which affect aquatic species indirectly due to their impact on surface water run-

211   off and water chemistry; and physicochemical parameters directly influencing plant growth

212   including pH, nutrient availability, substratum types and amount of standing freshwater

213   (Heegaard *et al.,* 2001; Capers *et al.,* 2009; Alahuhta *et al.,* 2011).

214   Landscape composition was derived from CORINE Land Cover maps (EEA, 2002).

215   Specifically, the coverage of arable land, broad-leaved woodland, coniferous plantations,

216   pasture, urban and standing freshwater was quantified at seven candidate spatial scales (0.5

217   km, 1.5 km, 2.5 km, 4.5 km, 6.5 km, 10.5 km and 20.5 km) and attributed to the central 0.5

218   km grid cell around which they had been extracted. These spatial scales were chosen to

219   represent the scales on which land use and human influence could plausibly influence the

220   establishment of aquatic plants. The total length of riparian corridor and an index of human

221   influence, representing a proxy for human-mediated vectors of dispersal, were also quantified

222   at the same scales. The Human Influence Index was a composite of population density, access

223   infrastructure (major roads, railways, navigable rivers and coastline) and night-time light

224   emissions downloaded from the Socio-Economic Data and Applications Centre (Wildlife

225   Conservation Society & Center for International Earth Science Information Network, 2005).

226   Nutrient concentrations were obtained from the Environmental Protection Agency of

227   Ireland (EPA) and the Northern Ireland Environment Agency (NIEA), expressed as

228   'orthophosphate' (mg/l) measured at river monitoring sites. Data for missing areas were

229   interpolated between empirical data points using the Kriging function in the Spatial Analyst

230   toolbar for ArcGIS 10.1 (ESRI, California, USA). Soil pH was taken as a proxy of water pH

231   and downloaded from http://eusoils.jrc.ec.europa.eu. Soil type (texture) was expressed as a

232   categorical variable representing levels of mineral coarseness (Gardi *et al.,* 2008).

233   Orthophosphate, soil pH and soil texture were expressed at the 0.5 km scale. The projected

234   output raster from the global CNM for each species, representing the climatic suitability of

235   each cell for the target species, was also incorporated into the regional ENMs.

236   As with global records, Irish records were biased due to sampling effort. However, the

237   nature of this bias differed from that of the GBIF records. Aquatic plants have been

238   systematically recorded throughout Ireland in the vast majority of lakes and rivers (as part of

239   European Water Framework Directive monitoring). Hence, it was not necessary to use the

240   recording of other major aquatic plant species as a proxy for aquatic plant recording.

241   However, it was evident that the volume of recording per unit area for Northern Ireland was

242   substantially greater than that in the Republic of Ireland. To account for the

243   disproportionately high density of records in Northern Ireland, a 'bias' layer was constructed

244   with values of 1 for the Republic of Ireland and 10 for Northern Ireland based on relative

245   prevalence of records of the most commonly recorded species (*Elodea canadensis*). This bias

246   layer was included in MaxEnt models (following Elith *et al.,* 2011). Models of invasive

247   species may also be biased when background data are included from outside the area where

248   the target species has had the opportunity to colonise (Elith *et al.*, 2010; Jiménez-Valverde *et*

249   *al.*, 2011). Therefore, background points (*n*=10,000) were randomly selected within the

250   'invaded range' of each species (based on the minimum convex polygons (MCP) that

251   included all records).

252   Prior to final model construction, separate models were constructed for each land use

253   variable and the Human Influence Index to ascertain the optimal spatial scale for each

254   variable for each species. One variable (e.g. area of arable land) was fitted at all seven

255 candidate spatial scales. The optimal spatial scale for each variable was chosen based on the

256 maximum Area Under the Curve (AUC) value when only one spatial scale was included

257 (based on Jackknife AUC results for test data; see Appendix S2). Response features were

258 limited to linear and quadratic excluding product features as we were not interested in

259 interactions between scales within variables.

260 The final regional ENMs used linear, quadratic and product features. A 10-fold replicated

261 cross-validation routine was used for all species. The averaged model across replicates was

262 used for analysis of variable permutation importance and estimated suitable range. As with

263 global CNMs, all models were projected up to 2080 under A2 and B2 scenarios. All non-

264 climate variables were held constant in future scenarios.

265

266 **(B) Statistical analyses**

267 The projected 'estimated suitable range' was calculated for each species, model and scenario

268 based on the percentage of grid cells with an occurrence probability of greater than the 10th

269 percentile training presence threshold (providing a conservative estimate allowing records in

270 suboptimal habitats). Changes in the estimated suitable range were expressed as the increase

271 or decrease compared to the total land area of Ireland, rather than percentage increase

272 compared with the current range (e.g. an expansion of estimated suitable range from 20% to

273 40% of the island was expressed as an increase of 20%, not 100%).

274 For species currently invasive in Ireland (n=8) differences in the estimated suitable range

275 between species, scenarios and years were examined using a General Linear Model (GLM).

276 Species, model type (i.e. global CNM or regional ENM) and scenario were fitted as fixed

277 factors, year as an ordinal factor and all two-way interactions were included. GLM residuals

278 were checked to ensure they conformed to normality.

279   Similarly, for species currently invasive in Ireland the performance of both model types

280   (global CNMs and regional ENMs) was evaluated using AUC values (as a threshold

281   independent metric), sensitivity (proportion of presences which are predicted correctly),

282   specificity (proportion of absences which are predicted correctly) and True Skill Statistic or

283   TSS (using the 10th percentile training presence as the threshold value). TSS is equal to

284   sensitivity plus specificity minus one and is a prevalence independent model evaluation

285   metric (Allouche *et al.*, 2006). Therefore, TSS is the only metric in this study which can be

286   compared between species. TSS ranges from -1 to +1, where 1 indicates perfect agreement

287   and values of less than 0 indicate models which perform worse than random. We include

288   sensitivity and specificity separately from AUC and TSS to clarify the relative importance of

289   omission and commission errors in model performance (Jiménez-Valverde *et al*., 2008; Lobo

290   *et al.*, 2008).

291   While specificity conveys important information about commission errors, it should be

292   interpreted with caution in studies such as this one, where species are not at equilibrium with

293   the environment. In particular, in the case of invasive species misleading commission errors

294   are likely to arise in areas which are potentially suitable for species, but which the species

295   have not yet colonised. Hence, low specificity (i.e. high commission error) may arise when

296   models are actually accurately predicting areas of suitability which have not yet been

297   colonised. This is most likely in the early stages of invasion (Václavík & Meentemeyer,

298   2012). This will affect AUC values, specificity and TSS which all include commission error.

299   Here, we have minimised this source of error by selecting pseudo-absences from within a

300   minimum convex polygon containing currently invaded sites.

301   These evaluation statistics were calculated for global and regional models using the same

302   testing of sub-sets of Irish data and background points within the invaded range in Ireland.

303   The presence records (test datasets) and numbers of background points were the same as

304   those used in the 10-fold cross-validation of regional ENMs (such that no model was tested

305   against the same data set that was used to build the model). In our analyses, we focus on

306   differences in evaluation metrics between global CNMs and regional ENMs within species

307   where evaluation metrics were calculated on same datasets (hence equal prevalence).Model

308   performance of global CNMs and regional ENMs was then compared using a Generalised

309   Linear Model (GLM), with model type and species as fixed factors. A gamma error

310   distribution with a log link function was used to account for non-normality of the response

311   variables.

312   The importance of each predictor variable in global CNMs and regional ENMs was

313   described using the permutation importance (%). For regional ENMs the permutation

314   importance values were grouped into 'Land use and nutrient concentration' (arable farming,

315   broad-leaved woodland, coniferous plantations, farming type and water nutrient

316   concentration), 'Human Influence Index', 'Natural landscapes' (riparian length, soil pH, soil

317   type and amount of standing freshwater) and 'Climate' (output from global CNMs).

318   The estimated suitability of projections for multiple species was calculated for each grid

319   cell by summing the number of species for which the projected suitability was greater than

320   the 10th percentile training presence threshold under the high emissions scenario. Suitability

321   for multiple invasive species was mapped and coloured to identify putative hot- and coldspots

322   of invasion. Mapping and spatial analysis were conducted in ArcGIS 10. Model evaluation

323   statistics, GLM and GLMM analyses were conducted in R 2.14.1, using the add-on packages

324   "PresenceAbsence" (Freeman & Moisen, 2008) and "glmmADMB" (Fournier *et al*., 2012).

325   Graphs were generated in Sigma Plot 10 (Systat, 2010).

326

327   **(A) Results**

328

329   **(B) Comparison between global CNMs and regional ENMs**

330

331   Regional ENMs had significantly higher AUC, TSS and specificity values than global CNMs,

332   whilst the opposite was true for sensitivity values (Table 1). Species which showed an

333   increase in estimated suitable range over time in global CNMs also increased in regional

334   ENMs, similarly species which showed a decrease in estimated suitable range over time in

335   global CNMs also decreased in regional ENMs. Estimates of suitable range were

336   significantly larger in global CNMs than in regional ENMs (Table 1 and Fig. 1).

337

338   **(B) Factors influencing invasive aquatic plant distributions**

339

340   The permutation importance of variables varied considerably between species for both global

341   climatic and regional landscape variables. In the global CNMs, annual mean temperature

342   (Bio1) and minimum temperature of coldest month (Bio6) were the most important variables

343   (Fig. 2 and Appendix S3). In regional ENMs, land use and nutrient concentration variables

344   had the greatest overall permutation importance. Climate was generally least important in

345   regional ENMs (Fig. 3 and Appendix S4). However, climate was the single most important

346   variable associated with the range of *Azolla filiculoides* (permutation importance = 32%),

347   although for other species it was less informative (permutation importance 0-7%).

348

349 **(B) Case study: Invasion risk in Ireland**

350 The estimated suitable range for each invasive species in Ireland varied between species ($F =$

351 59.31, $p < 0.001$). Changes in the estimated suitable range differed between species, with

352 some species showing range expansions under projected climate scenarios and some

353 declining ($F = 5.97$, $p < 0.001$; Fig. 1 and Appendix S5). There was an increase in the

354 estimated suitable range for aquatic invasive plants under both climate scenarios between

355 current conditions and projections up to 2080 ($F = 3.54$; $p = 0.018$). Typically, such changes

356 were greater under scenario A2 or high emissions than B2 or low emissions.

357   Global CNMs projected that under the high emissions scenario the estimated suitable

358 range would increase moderately for three species already well-established in Ireland (*A.*

359 *filiculoides* +7%, *Lemna minuta* +7% and *Myriophyllum aquaticum* +12%). The ranges of a

360 further three species recorded from only one or two sites in Ireland were projected to increase

361 dramatically under the same scenario (*Egeria densa* +91%, *Hydrilla verticillata* +40% and

362 *Ludwigia grandiflora* +33%). In contrast, the ranges of two well-established species (*Elodea*

363 *canadensis* -9%, and *E. nuttallii* -32%), were projected to decrease under this scenario.

364 Concurrently, there was projected to be little change in three well-established species

365 (*Crassula helmsii*, *Lemna major* and *Nymphoides peltata*). Current and future climates were

366 projected to be unsuitable for three 'high risk' invaders (*Cabomba caroliniana*, *Eichhornia*

367 *crassipes* and *Salvinia molesta*) and indicated that the climate may remain unsuitable for

368 these species until at least 2080. *Hydrocotyle ranunculoides* is present at only a few sites but

369 projections indicated that climate is currently, and will remain, very suitable.

370   Regional ENMs projected that the estimated suitable range under high emissions would

371 increase for two of the three species which were also projected to increase using the global

372 CNM models (*A. filiculoides* +22% and *M. aquaticum* +44%). In addition, the range

373 decreased for one well-established species (*E. canadensis* -31%) for which declines were

374   projected by global CNMs. Concurrently, regional ENMs projected little change in the

375   remaining five species (*C. helmsii*, *E. nuttallii*, *L. major*, *L. minuta* and *N. peltata*; Fig. 1)*.

376

377   **(B) Temporal changes in hot- and coldspots of invasion**

378   Projected hotspots of invasion suitability exist currently around major cities and river systems

379   (Fig. 4). Future projections based on regional ENMs under the high emissions scenario

380   indicated that the major temporal change will be the increasing suitability of currently

381   unsuitable locations (Fig. 4 a-d). Approximately 6% of cells were projected to be unsuitable

382   for any of the 15 invasive species under current conditions, however, this decreased to <1%

383   by 2080. There was also a decrease in the number of cells projected to have just one species

384   (from *ca*. 20% to *ca*. 15% by 2080). Predicted changes appear to make areas currently

385   suboptimal (principally upland and northern areas) increasingly suitable over time. To a

386   lesser extent, it was projected that the number of cells with 3-4 species may increase by 2080.

387   Changes in hot- and coldspots of invasion were mainly due to the projected expansion of *A.*

388   *filiculoides* and *M. aquaticum* concomitant with a decline in *E. canadensis.* Projections only

389   took account of current invasive species and did not include potential invaders.

390

(A) Discussion

Our results illustrate how global climate niche models can be integrated with regional environmental niche models to improve the precision of invasive species risk by accounting for landscape factors which limit species establishment at local scales. Model AUC values increased by 0.18 and TSS values by 0.36. The estimated suitable range of invasive aquatic plants in Ireland was reduced by 50% of the total land area when global CNMs were combined with regional ENMs accounting for land use, nutrient concentration, natural landscape and human influence. However, global CNMs did show higher sensitivity (average difference = 0.18) than regional ENMs. Conversely, the specificity of global CNMs was lower than regional ENMs (average difference = 0.54). The ability of models to correctly predict presence is of particular concern for invasive species, as failure to identify invaded locations can cause problems for management and eradication. However, for management purposes 'estimated suitability maps' with higher sensitivity could easily be achieved using regional ENMs by changing the presence-absence threshold to achieve the desired sensitivity level or using the minimum training presence threshold rather than the 10th percentile training presence threshold. These options would increase the estimated suitable area and decrease model specificity, reducing the risk of under-prediction but increasing the cost of survey and intervention.

True evaluations of model performance are difficult during the invasion process as species are not at equilibrium, and false-presences may be misleading if they represent areas that have yet to be colonised (Peterson *et al.*, 2008). In addition, models based on data from invaded ranges may underestimate suitable range of species, due to the fact that suitable areas which have not yet been colonised are treated as pseudo-absences in model building. This effect has been shown to be most evident in the early stages of invasion (Václavík & Meentemeyer, 2012). Species in this study represent a range of invasion stages, with the

416   earliest species introduced in 1836 and the most recent in 1993. If stage of invasion were a

417   key factor causing the difference between estimated suitable ranges by global CNMs and

418   regional ENMs we would expect to see a smaller difference between range estimates of

419   species which had been introduced earlier than for those introduced more recently. No such

420   pattern was evident in this study and the two earliest introductions (*Elodea canadensis* and

421   *Nymphoides peltata*, both introduced in 1836) differed in range estimates between global

422   CNMs and regional ENMs by 58% and 33% respectively.

423   Alternatively, presences may occur in areas of marginal habitat quality where species

424   would be unable to reproduce, reach high abundance or survive in the long term. This may

425   lead to an overestimation of the potential impact of invasive species (Bradley, 2013).

426   Future projections have increased uncertainty due to the unpredictability of species

427   responses to novel combinations of landscape and climate, and uncertainties associated with

428   meteorological forecasting. Hence, uncertainties increase with distance into the future.

429   Moreover, as there are no test datasets available for future time periods it is difficult to

430   evaluate the accuracy of future projections (Elith & Leathwick, 2009). We recommend that

431   our models are re-evaluated and revised throughout the lifetime of their projections, for

432   example by using iterative survey methods (e.g. Stohlgren & Schnase, 2006) or by

433   incorporating novel data from physiological studies (Kearney & Porter, 2009).

434   Climate was the least important factor associated with the regional distribution of seven

435   out of eight aquatic invasive species in Ireland. This may be due to the low climatic variation

436   at regional scales characteristic of temperate maritime islands such as Ireland. The global

437   ranges of the majority of species examined were most strongly associated with climatic

438   tolerances set by mean annual temperature and minimum temperature of coldest month. It is

439   possible that a stronger association with climatic variables would emerge if variables specific

440   to freshwater habitats were used (e.g. max, min and mean water surface temperatures).

441   However, we are not aware of any such global databases.

442   Climate acts as an initial coarse filter which allows for the establishment of invasive

443   species regionally, and is a useful tool for assessing risk for species not currently present.

444   Here, global CNMs allowed us to distinguish between species for which climate suitability

445   was likely to increase considerably by 2080 (*E. densa, H. verticillata* and *L. grandiflora*) and

446   those for which there was a low risk of widespread establishment (*C. caroliniana, E.*

447   *crassipes* and *S. molesta*). Hence, global CNMs can be used to prioritise species for

448   preventative action such as legislation on sale and importation. However, in the case of these

449   latter three species, it remains possible that they will establish in Ireland as a result of

450   phenotypic adaptation to colder climates or through the introduction or evolution of novel

451   genotypes (Clements & Ditommaso, 2011; Shaw & Etterson, 2012).

452   At the regional scale, land use, nutrient concentration and natural landscape were the most

453   important factors associated with species ranges. However, the response of individual species

454   varied considerably. Similar species-specific responses to landscape have been noted

455   previously for many invasive terrestrial plants (e.g. Ibáñez *et al.*, 2009; Syphard & Franklin,

456   2009).

457   Human Influence Index was positively associated with the presence of all species except

458   *L. major*. Association with human activity has been reported before for invasive species and

459   aquatic plants (e.g. Buchan & Padilla, 2000; Mack *et al*., 2000; Aznar *et al*., 2003; Thuiller *et*

460   *al.*, 2005; Capers *et al*., 2009) and probably reflects an increase in propagule pressure and

461   disturbance facilitating establishment. Risk projections could be improved by including

462   further data on known vectors e.g. boating and angling (Leung *et al.*, 2006)

463   Present ranges are likely to be restricted by invasion histories. In Ireland, all study species

464   occupied only a small fraction of the range that was projected to be at risk and substantial

465   expansion is expected over the next century, even in the absence of climate change.

466   Notably, the range of a high-latitude species (*E. canadensis*) was projected to contract

467   throughout the 21st century. Retreat in range and vigour of some species may provide

468   opportunities for the restoration of native plant communities (Bradley *et al.,* 2009). Ireland is

469   predicted to become generally more suitable for colonisation, resulting in fewer coldspots in

470   upland and northern parts of the island, which is of particular concern for upland oligotrophic

471   lakes as they currently represent an important refuge for rare native aquatic species

472   (Heegaard *et al.,* 2001).

473   Despite the potential limitations of ecological niche modelling and the uncertainties

474   inherent in future projections, the amalgamation of global CNMs and regional ENMs

475   provides a useful framework for the estimation of invasion risk. In the case of invasive

476   aquatic plants, this approach improved model performance in terms of AUC, TSS and

477   specificity and greatly reduced estimates of suitable ranges. Hence, integrated models may

478   provide more precise information about invasion risk at sub-regional scales and provide

479   useful information for species management and the prioritisation of resources.

480

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693

694 **(A) Biosketch**

695

696 Research group: *Quercus* is Northern Ireland's Centre for Biodiversity and Conservation

697 Science, which uses species distribution modelling as a tool for identifying areas of high

698 conservation value (www.quercus.ac.uk).

699

700 Author contributions: All authors contributed to the conceptualisation and development of

701 this work. Data collation and analysis was conducted by R.K. Advice on analysis was

702 provided by A.C. and N.R. The manuscript was drafted by R.K. and edited by K.L., C.A.M.

703 and N.R.

704

705   **Table 1.** Model evaluation metrics and percentage estimated suitable area for

706   global Climate Niche Models (CMNs) and regional Environmental Niche Models

707   (ENMs) of 8 invasive freshwater plants in Ireland. Generalised linear model

708   results show differences between global CNMs and regional ENMs for each

709   model evaluation metric.

710

Metric	Mean values (standard error.)		GLM result	
	Global CMNs	Regional ENMs	Wald	p
AUC	0.64 (0.01)	0.82 (0.01)	117.12	<0.001
Sensitivity	0.96 (<0.01)	0.78 (0.30)	9.97	0.002
Specificity	0.07 (<0.01)	0.61 (0.02)	725.75	<0.001
TSS	0.03 (<0.01)	0.39 (0.03)	180.12	<0.001
% estimated suitable area	86.5 (3.0)	35.5 (3.0)	1060.56	<0.001

711

712

713 **Figure legends**

714

715 **Fig. 1** Suitable climate range from global climate niche models (A2 = brown line, B2 = red

716 line) and suitable environmental niche (from regional environmental niche models including

717 local landscape data) (A2 scenario = dark blue line, B2 scenario = light blue line) for current

718 conditions, 2020, 2050 and 2080).

719

720 **Fig. 2** Permutation importance of predictor variables in global climate niche models for 15

721 invasive species. Boxplot shows 10th, 25th, 50th, 75th, 90th percentiles. Dotted lines indicate

722 mean values.

723

724 **Fig. 3** Permutation importance of predictor variables in environmental niche models for 8

725 invasive species grouped into descriptive categories. Boxplot shows 10th, 25th, 50th, 75th,

726 90th percentiles. Dotted lines indicate mean values.

727

728 **Fig. 4** Temporal changes in 'hot- and coldspots' of invasions under **a)** current conditions, **b)**

729 2020, **c)** 2050 and **d)** 2080. Future projections are shown for the A2 or high CO_2 scenario.

730 Colours indicate the number of invasive species. Histograms show the distributions of

731 invasive species richness.

732

733   Fig 1.

734

735

736   Fig. 2

737

738   Fig. 3

739

740

741   Fig. 4

a) Current   b) 2020   c) 2050   d) 2080

Km² x 10³

Invasive species richness
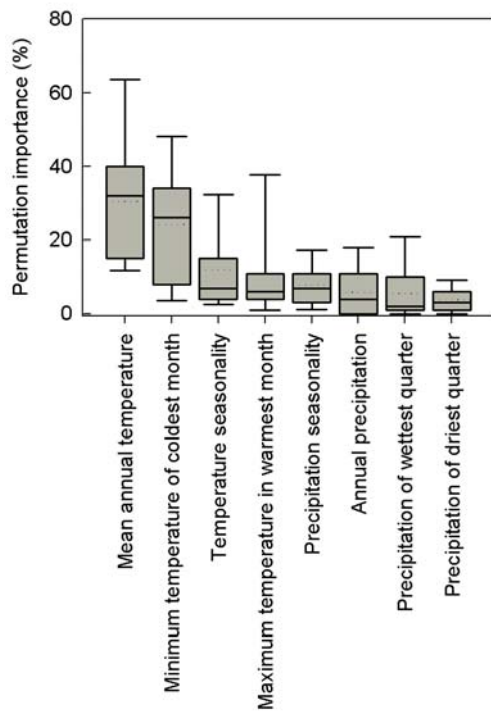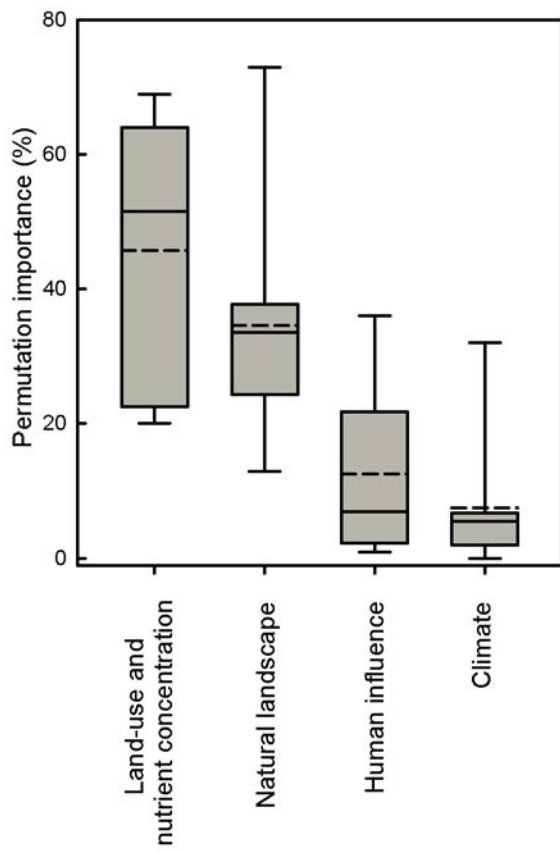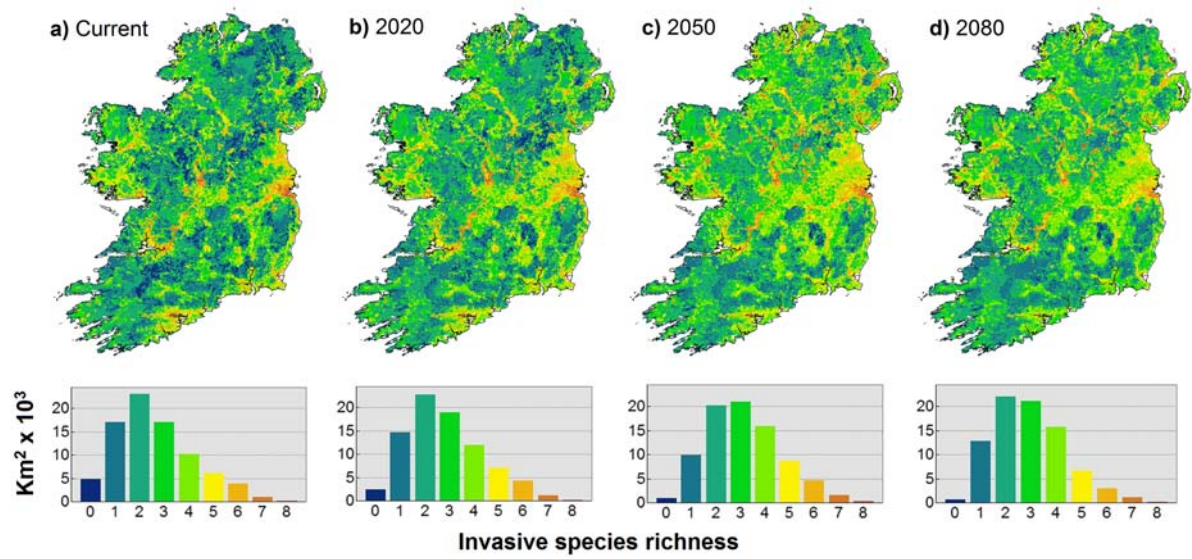
742

Supplementary Information – supplied as separate word document

Appendix S1   Data agencies by whom data on species distributions in the Republic of
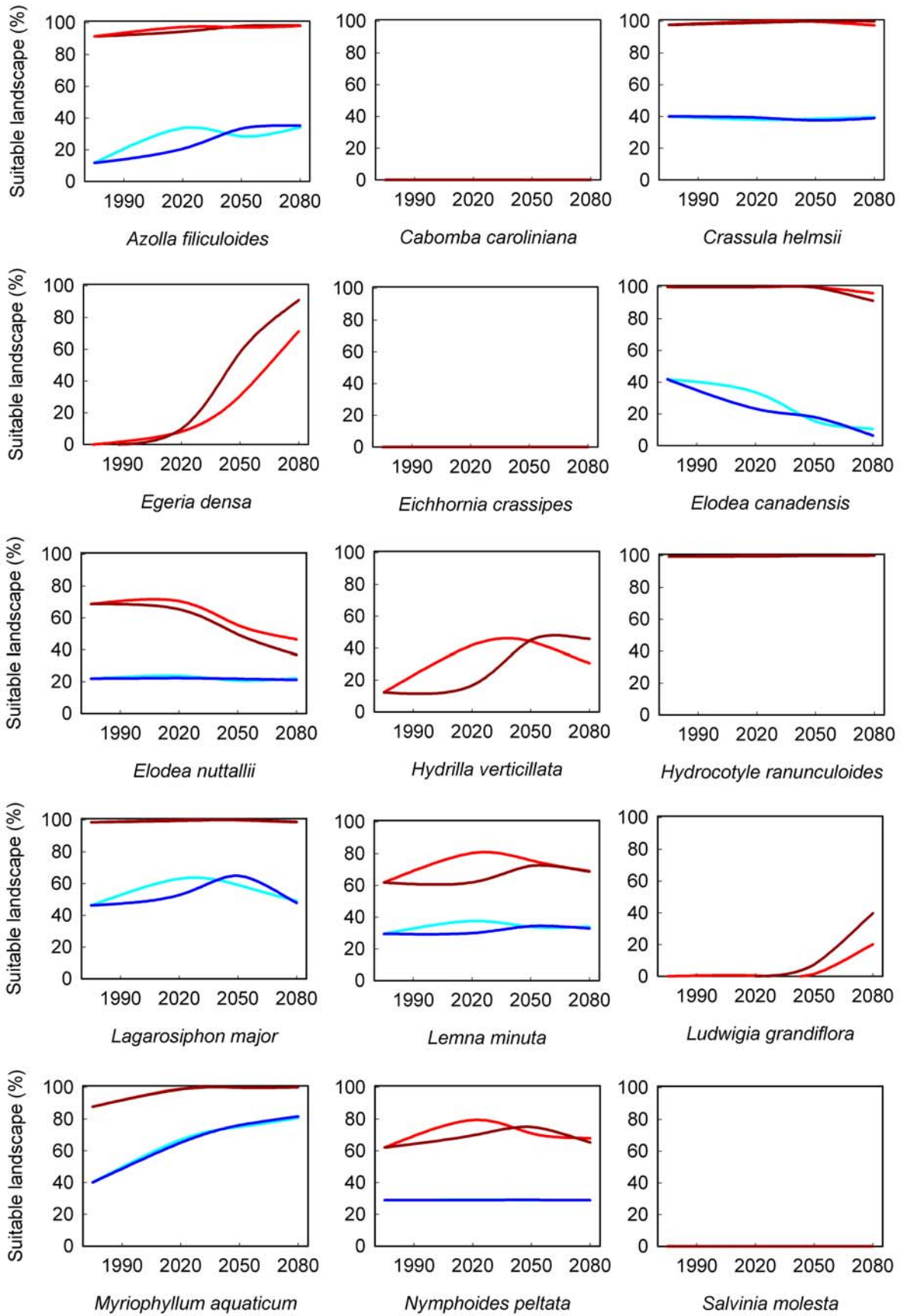
Ireland and Northern Ireland was contributed.

Appendix S2   Optimal spatial scales of land use and human influence variables, showing

Jacknife AUC value of the model with only that variable at that spatial scale.

Appendix S3   Permutation importance of climatic variables in global climate niche models.

Appendix S4   Permutation importance of climate, landscape, human influence index and

natural landscapes in Irish species distribution models for 8 invasive aquatic

plants already established in Ireland.

Appendix S5   Projected 'estimated suitable range' of each species within Ireland based on

regional environmental niche models.

Appendix S6   Projected 'estimated suitable range' of each species within Ireland based on

global climate niche models.

Appendix S1

Data agencies by whom data on species distributions in the Republic of Ireland and Northern Ireland was contributed.

- Botanical Society of the British Isles (BSBI)

- Centre for Environmental Data and Recording (CEDaR)

- Invasive Species Ireland (ISI)

- National Biodiversity Data Centre (NBDC)

- National Biodiversity Network (NBN)

- Northern Ireland Environment Agency (NIEA)

Appendix S2

Optimal spatial scales of land use and human influence variables; showing Jacknife AUC value of the model with only that variable at that spatial scale.

Species	Variable	Spatial scale (km^2)	Jacknife AUC
Azolla filiculoides	Arable land	10.5	0.550
	Broad leaved woodland	10.5	0.633
	Coniferous woodland	6.5	0.740
	Human impact	4.5	0.727
	Pastural farming	1.5	0.634
	Riparian length	20.5	0.647
	Standing freshwater	1.5	0.682
Crassula helmsii	Arable land	1.5	0.614
	Broad leaved woodland	1.5	0.517
	Coniferous woodland	6.5	0.679
	Human impact	20.5	0.552
	Pastural farming	1.5	0.737
	Riparian length	0.5	0.569
	Standing freshwater	4.5	0.562
Elodea canadensis	Arable land	10.5	0.623
	Broad leaved woodland	20.5	0.663
	Coniferous woodland	10.5	0.571
	Human impact	20.5	0.581
	Pastural farming	4.5	0.558
	Riparian length	1.5	0.714
	Standing freshwater	2.5	0.707
Elodea nuttallii	Arable land	10.5	0.649
	Broad leaved woodland	10.5	0.625
	Coniferous woodland	6.5	0.656
	Human impact	0.5	0.846
	Pastural farming	0.5	0.664
	Riparian length	0.5	0.787
	Standing freshwater	1.5	0.803
Lagarosiphon major	Arable land	0.5	0.557
	Broad leaved woodland	10.5	0.624
	Coniferous woodland	4.5	0.627
	Human impact	20.5	0.624
	Pastural farming	1.5	0.778
	Riparian length	1.5	0.867
	Standing freshwater	1.5	0.819
Lemna minuta	Arable land	10.5	0.527
	Broad leaved woodland	10.5	0.687
	Coniferous woodland	6.5	0.589
	Human impact	4.5	0.692
	Pastural farming	6.5	0.645
	Riparian length	1.5	0.660
	Standing freshwater	4.5	0.673
M. aquaticum	Arable land	4.5	0.636
	Broad leaved woodland	10.5	0.661
	Coniferous woodland	4.5	0.632
	Human impact	1.5	0.770
	Pastural farming	10.5	0.713
	Riparian length	20.5	0.701
	Standing freshwater	20.5	0.560
Nymphoides peltata	Arable land	20.5	0.679
	Broad leaved woodland	10.5	0.703
	Coniferous woodland	20.5	0.624
	Human impact	10.5	0.813
	Pastural farming	1.5	0.711
	Riparian length	0.5	0.707
	Standing freshwater	4.5	0.656

Appendix S3

Permutation importance of climatic variables in global climate niche models.

Species	N	Mean annual temperature	Temperature seasonality	Maximum temperature (in hottest month)	Minimum temperature (in coldest month)	Annual precipitation	Precipation seasonality	Maximum precipitation (in wettest month)	Minimum precipitation (in driest month)
A. filiculoides	2,035	15	4	1	56	7	11	0	6
C. caroliniana	260	40	5	10	15	0	10	14	6
C. helmsii	879	21	27	8	14	18	2	5	6
E. densa	570	16	7	57	7	1	4	1	8
E. crassipes	1,261	34	7	19	3	3	21	3	11
E. canadensis	4474	58	4	2	26	6	4	1	0
E. nuttallii	3,070	13	13	11	32	11	0	20	0
H. verticillata	1,935	33	11	4	4	15	11	22	0
H. ranunculoides	449	14	39	1	27	0	15	1	3
L: major	572	10	28	5	24	18	4	10	1
L. minuta	1,839	32	3	4	43	0	12	0	6
L. grandiflora	508	18	6	25	34	4	11	1	2
M. aquaticum	1,139	46	8	7	30	4	2	1	3
N. peltata	1,810	34	15	6	40	0	3	2	1
S. molesta	122	72	2	5	8	0	7	2	4
Mean	**1,395**	**30**	**12**	**11**	**24**	**6**	**8**	**6**	**4**

Appendix S4

Permutation importance of climate, landscape, human influence index and natural landscapes in Irish species distribution models for 8 invasive aquatic plants already established in Ireland.

Species	Climate	Land use and eutrophication					Human influence	Natural landscape			
	Predicted probability from global models	Arable	Broad-leaved woodland	Coniferous plantations	Pastoral farming	Eutrophication Orthophosphate	Human Influence Index	Riparian length	Standing freshwater	Soil Type	Soil pH
A. filiculoides	32	3	2	11	7	4	6	10	20	4	0
C. helmsii	2	24	0	12	11	22	6	4	7	12	1
E. canadensis	7	0	12	3	4	1	1	53	20	0	0
E. nuttallii	5	4	6	3	8	0	36	14	23	0	1
L. major	6	13	1	10	20	17	1	12	4	12	5
L. minuta	2	14	10	25	3	1	8	16	8	13	0
M. aquaticum	6	6	5	29	7	3	21	7	4	12	2
N. peltata	0	22	17	4	1	21	22	5	2	5	1
Mean	**8**	**11**	**7**	**12**	**8**	**9**	**13**	**15**	**11**	**7**	**1**

Appendix S5

Predicted 'suitable range' within Ireland based on regional environmental niche models.

Species	N	Current recorded range (No. of 500m cells (%))	Current suitable range (%)	B2 'low emmissions' Difference in suitable range			A2 'high emmissions' Difference in suitable range		
				2020	2050	2080	2020	2050	2080
A. filiculoides	110	116 (0.03)	12	+9	+22	+23	+22	+17	+22
C. helmsii	13	20 (0.01)	40	-1	-3	-1	-2	-2	0
E. canadensis	1,646	1659 (0.50)	42	-19	-24	-35	-8	-26	-31
E. nuttallii	104	112 (0.03)	22	+0	0	-1	+2	-1	0
L. major	77	84 (0.03)	46	+7	+19	+2	+17	+13	+3
L. minuta	98	116 (0.03)	29	+0	+5	+3	+8	+4	+4
M. aquaticum	18	28 (<0.01)	40	+25	+36	+42	+27	+35	+41
N. peltata	29	31 (<0.01)	29	0	0	0	0	0	0
Mean	262	271 (0.08)	**32**	**+3**	**+7**	**+4**	**+8**	**+5**	**+5**