

White-faced darter distribution is associated with coniferous forests in Great Britain

MATTHEW GEARY and ACHAZ VON HARDENBERG Conservation Biology Research Group, Department of Biological Sciences, University of Chester, Chester, UK

Abstract. 1. Understanding of dragonfly distributions is often geographically comprehensive but less so in ecological terms.

2. White-faced darter (*Leucorhinnia dubia*) is a lowland peatbog specialist dragonfly which has experienced population declines in Great Britain. White-faced darter is thought to rely on peat-rich pool complexes within woodland, but this has not yet been empirically tested.

3. We used dragonfly recording data collected by volunteers of the British Dragonfly Society from 2005 to 2018 to model habitat preference for white-faced darter using species distribution models across Great Britain and, with a more detailed landcover data set, specifically in the North of Scotland.

4. Across the whole of Great Britain, our models used the proportion of coniferous forest within 1 km as the most important predictor of habitat suitability but were not able to predict all current populations in England.

5. In the North of Scotland, our models were more successful and suggest that habitats characterised by native coniferous forest and areas with high potential evapotranspiration represent the most suitable habitat for white-faced darter.

6. We recommend that future white-faced darter monitoring should be expanded to include areas currently poorly surveyed but with high suitability in the North of Scotland.

7. Our results also suggest that white-faced darter management should concentrate on maintaining Sphagnum rich-pool complexes and the maintenance and restoration of native forests in which these pool complexes occur.

Key words. Conservation, distribution, dragonfly, habitat, SDM.

Introduction

Dragonflies and damselflies (Odonata) are relatively 'charismatic' invertebrate species and have received some considerable attention in the scientific literature (Córdoba-Aguilar, 2008; Kalkman *et al.*, 2018; Teermat *et al.*, 2019). Nevertheless, conservation research on Odonata is still in its relative infancy (Clausnitzer *et al.*, 2009; Bried & Samways, 2015) and even in countries where conservation is seen as a social priority, such as the United Kingdom, there is relatively little conservation action specifically focused on this taxon despite 25% of UK dragonfly and damselfly species being included in the Odonata

Red Data List for Great Britain (Beynon *et al.*, 2008). The seven obstacles for invertebrate conservation suggested by Cardoso *et al.* (2011), and in particular the lack of basic research on habitat requirements and distribution, certainly apply to Odonata conservation at both global and regional scales (Clausnitzer *et al.*, 2009). Indeed, priorities highlighted on the UK red list for Odonata for several species (Beynon *et al.*, 2008) include the urgent need to increase monitoring efforts, to establish species distributions and habitat requirements and understand the factors affecting population change, particularly for those species with a current distribution restricted to remote areas.

As for other invertebrates, the multi-stage life-cycle of Odonata species leaves them vulnerable to multiple threats at different life stages (Córdoba-Aguilar, 2008): The aquatic larval stage is vulnerable to aquatic pollution (Monteiro-Júnior *et al.*, 2014), introduced plant species (Samways & Taylor, 2004), predation by introduced fish (Schilling *et al.*, 2009) and land-use changes

Correspondence: Matthew Geary, Conservation Biology Research Group, Department of Biological Sciences, University of Chester, Chester, CH1 4BJ, UK. E-mail: m.geary@chester.ac.uk

Editor: Christopher Hassall; Associate Editor: Göran Sahlén

(Clausnitzer *et al.*, 2012) and adult stages are particularly vulnerable to land-use changes and habitat fragmentation (Saunders *et al.*, 1991; Drinan *et al.*, 2013). Scale is also an important factor in assessing threats to individual populations. Globally, peatland dragonflies tend to be of lower conservation priority (Clausnitzer *et al.*, 2009); however, peatland habitats can be locally threatened and are considered as priority habitats for conservation in the United Kingdom (Whitfield *et al.*, 2011). In these areas, peatland specialist species may thus potentially be of conservation concern (Elo *et al.*, 2015).

White-faced darter (*Leucorrhinia dubia*) is a lowland bog specialist dragonfly species (Smallshire & Swash, 2004; Clausnitzer *et al.*, 2009, Cham *et al.*, 2014). Great Britain represents the western extent of their range and they are found as far East as Japan. In Western Europe, their range extends from the Pyrenees north to Scandinavia. They are locally common across the continent and so are classified as Least Concern on the European Red List for Odonata although further research into their range and population trends are recommended (Clausnitzer, 2009; Kalkman *et al.*, 2010). In Great Britain, their distribution is heavily biased towards the Scottish highlands (Cham *et al.*, 2014) and their range is probably contracting (Hickling *et al.*, 2005). There are several populations further south, in England, which have been the focus of conservation attention, including reintroduction programmes (Meredith, 2017). In Scotland, the distribution of white-faced darter stretches from Argyll (56°13'51"N 5°20'37"W) in the South to Ross-shire (57°51'08"N 5°33'54"W) in the North although the bulk of the population is found in the North on both sides of the Great Glen Fault. In the East, they are found in parts of the Cairngorms and Grampians and they can be found on the West coast although they do not reach as far as the Inner Hebrides. The Scottish populations are thought to be declining but currently receive little conservation intervention (Cham *et al.*, 2014). The species is well monitored in some areas, but their patchy distribution across a large landscape means that the species is thought to be under-recorded (Cham *et al.*, 2014). As with many dragonfly species, white-faced darter has not been the subject of quantitative studies regarding habitat associations except at the very local scale (Davies *et al.*, 2018). White-faced darter is generally found in acidic pool complexes associated with pine or birch woodland (Boudot & Kalkman, 2015). In Great Britain, these pools are generally free from fish (Beadle *et al.*, 2015) and subsequently British white-faced darter has shorter larval spines than Scandinavian populations (Johansson *et al.*, 2017). White-faced darter has a particularly strong association with sphagnum moss, which appears to be an essential requirement for the habitats inhabited by their larval stage (Henrikson, 1993; Meredith, 2017).

Species distribution models (SDMs) are a useful tool for the planning of future monitoring programmes (Bourke *et al.*, 2012) and for identifying priority areas for conservation action (Nazeri *et al.*, 2012). SDMs are also useful for estimating the distribution of poorly known species (Wilting *et al.*, 2010), or those which are difficult to survey effectively (Nazeri *et al.*, 2012) as well as for species which are well known locally but poorly known over wider areas (Sutton & Puschendorf, 2018). A patchy,

heterogeneous distribution of monitoring effort and species records can lead to biases in the estimated distribution of species (Millar *et al.*, 2018). This can be a particularly serious problem for understudied taxa where expertise may be localised or restricted to only a few specialists (Robinson *et al.*, 2018).

Where species are monitored sporadically, only through incidental sightings or are extremely rare, we might only have access to presence records for a species. Similarly, where taxa are monitored using volunteer recording schemes there is a trade-off between the complexity of survey methodologies and the ease with which volunteers can complete records in the field which can result in data with reduced information content (Tweddle *et al.*, 2012). More complex surveys, which result in information-rich data, require more experienced/trained recorders potentially limiting the geographic coverage of the survey. On the other hand, simpler more widespread surveys can introduce issues with data quality due to identification mistakes by inexperienced observers or patchy records (Donnelly *et al.*, 2014). Information-limited data restrict the choice of methods available to investigate species distributions (Elith *et al.*, 2006) and can make it hard to project models onto unknown or under-recorded areas (Owens *et al.*, 2013). This is particularly problematic because, although species presence can be established relatively error-free, there are likely to be few or low-quality records of species absence (if any).

Modelling methods to predict species distributions using data where absences are unavailable or uncertain requires the use of background or pseudo-absence data to differentiate suitable from unsuitable habitat (Elith *et al.*, 2006). One of the most widely used algorithms used to achieve this, MaxEnt (Phillips *et al.*, 2006; Phillips & Dudík, 2008), is a machine-learning implementation of a point process regression, which uses LASSO penalties to prevent overfitting (Renner & Warton, 2013). MaxEnt has been shown to outperform several other presence-only species distribution modelling methods (Huerta & Peterson, 2008; Elith & Graham, 2009) and is widely used in conservation research.

Here, we use MaxEnt models to investigate the habitat requirements of white-faced darter (*Leucorrhinia dubia*) and map its potential distribution in the whole of Great Britain with a particular focus on its main range in the North of Scotland using records collected by members of the British Dragonfly Society as presence points along with environmental data reflecting tree cover, climate and the presence of bogs. Understanding drivers of white-faced darter presence across large scales can contribute to conservation of this species by informing landscape management and will help to target future surveys for the species.

Methods

Species data

White-faced darter presence records between 2005 and 2018 were obtained from the British Dragonfly Society through the United Kingdom's National Biodiversity Network. These data have been collected as incidental, presence-only, records rather

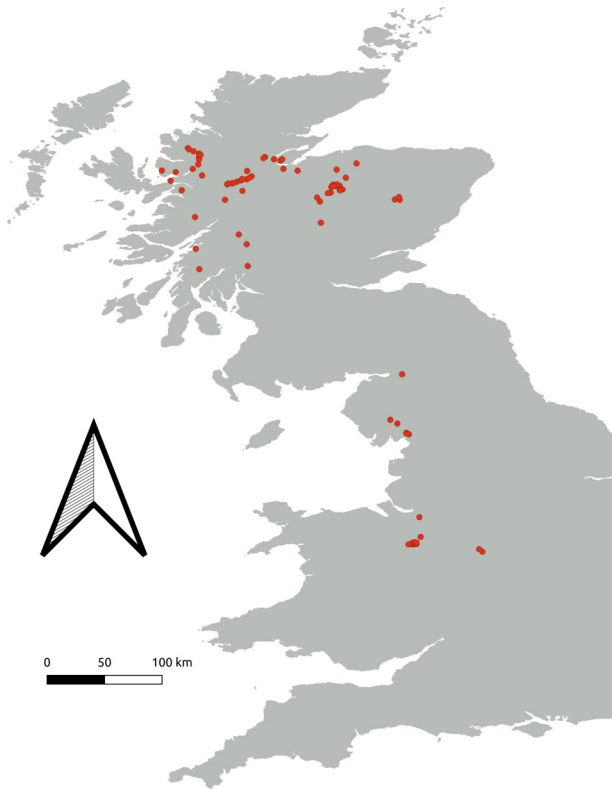


Figure 1. Location of presence records for white-faced darter (in red; $n = 77$) in Great Britain. [Color figure can be viewed at wileyonlinelibrary.com]

than in a standardised stratified recording scheme and records about flying adults, larvae and exuviae are available in the data set. Incidental records such as these are likely to be spatially biased due to unequal distribution of recording effort. This has the potential to create biased distribution models. Our original data set consisted of 980 individual records; 540 of these were in England and Wales along with 440 in Scotland. The records were heavily biased to a series of well-visited sites with 220 of the records from England and Wales coming from just two sites. We used spatial filtering to combine records within 1.5 km of each other to reduce potential issues related to spatially biased sampling (Fourcade *et al.*, 2014). Species records were thinned using the 'spThin' package (Aiello-Lammens *et al.*, 2015) in R

(R Core Team, 2019) resulting in 77 presence records across the whole of Great Britain of which 61 were in the North of Scotland (Figure 1).

Environmental variables

Great Britain model. Land cover data to parameterise our species distribution models was obtained from the CEH LCM2015 landcover data set (Rowland *et al.*, 2017). The variables chosen were based on those described in the United Kingdom (Cham *et al.*, 2014) and European (Boudot & Kalkman, 2015) dragonfly atlases which specify wet, boggy areas within a woodland complex. We calculated the proportion of coniferous woodland, deciduous woodland, standing water and bogs within 1 km of each 100 m \times 100 m square in Great Britain using the 'focal' function in the 'raster' package (Hijmans & van Etten, 2012) in R. Additionally, we used data from the Centre for Ecology and Hydrology (CHES) data set (Robinson *et al.*, 2016) to represent potential evapotranspiration (PET), indicating the 'wetness' of the habitat, and BIOCLIM layers from WorldClim. The BIOCLIM layers were highly correlated with each other so we chose four variables which were ecologically relevant [Annual Mean Temperature (BIO1), Annual temperature range (BIO7), Annual precipitation (BIO12) and Precipitation Seasonality (BIO15)] and highly correlated with a number of the other variables but not each other ($r_s > 0.7$ with 5, 7, 9 and 10 variables, respectively) at our presence locations. We then reduced this to two BIOCLIM variables (Annual Temperature and Annual temperature range) as the two precipitation variables were both highly correlated ($r_s > 0.77$) with the PET layer at our presence points. In this case, we retained the PET layer due to its more accurate resolution. These three layers were resampled to match the resolution of our landcover data using the 'raster' package in R.

North of Scotland model. Environmental variables used to predict the distribution of white-faced darter were downloaded from the European Nature Information System (EUNIS) landcover classification for Scotland. This data set is more detailed than the CEH LCM2015 data set and allows us to investigate the influence of more detailed habitat types such as bog woodland and native pine forest. We used established EUNIS classes (Davies *et al.*, 2004) to produce variables representing Scots pine (*Pinus sylvestris*) forest, coniferous forest (including native pine

Table 1. Comparison of all MaxEnt models with $\Delta AICc < 2$ predicting white-faced darter distribution in the Scottish highlands. Models were tested with linear, quadratic and product responses to predictors along with combinations of these and regularisation values between 0 and 3 at 0.5 increments. Please see Electronic Supplementary Material for the results of all candidate models.

Features	Regularisation multiplier	Training AUC	Testing AUC	AICc	$\Delta AICc$
Linear and quadratic	1	0.89	0.81	6242.71	0
Linear and quadratic	1.5	0.89	0.8	6243.23	0.52
Linear and quadratic	2	0.89	0.81	6243.45	0.74
Linear and quadratic	2.5	0.89	0.81	6243.67	0.97
Linear and quadratic	3	0.89	0.81	6243.9	1.19

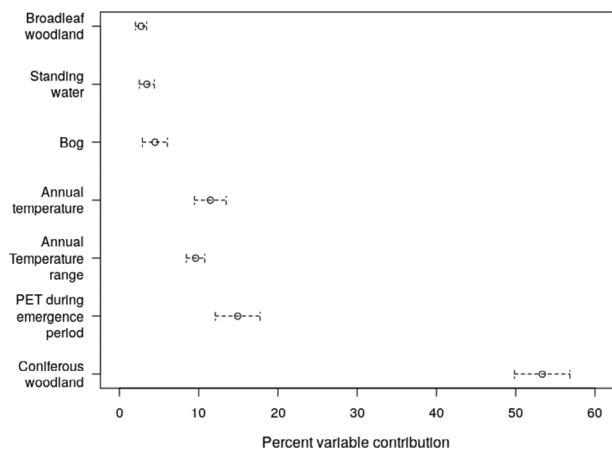


Figure 2. Percentage importance for each variable, calculated from the contribution of each variable to regularised gain, used to predict white-faced darter presence across Great Britain \pm Standard Error (dotted lines).

forest and plantation forestry), moorland, bogs, bog woodland and standing water. Other potential variables such as mixed woodland or ancient woodland measures (e.g. from the National Forest Inventory Scotland) were not used in our analyses due to issues with collinearity. Instead, we retained only the variables, which we can hypothesise to have an ecological connection with white-faced darter presence based on what is known in the available literature (Dormann *et al.*, 2012). We converted our environmental variables to the proportion of each variable within a 1 km buffer around each pixel at a 10 m resolution from the original categorical landcover maps using the ‘raster’ package (Hijmans & van Etten, 2012) in R. These values were then aggregated to maps at a resolution of 250 m \times 250 m retaining the mean value. PET, annual mean temperature and annual temperature range were used in the same way as for the Great Britain model.

Species distribution models. Distribution models were fitted using MaxEnt version 3.3.3 k through the ‘dismo’

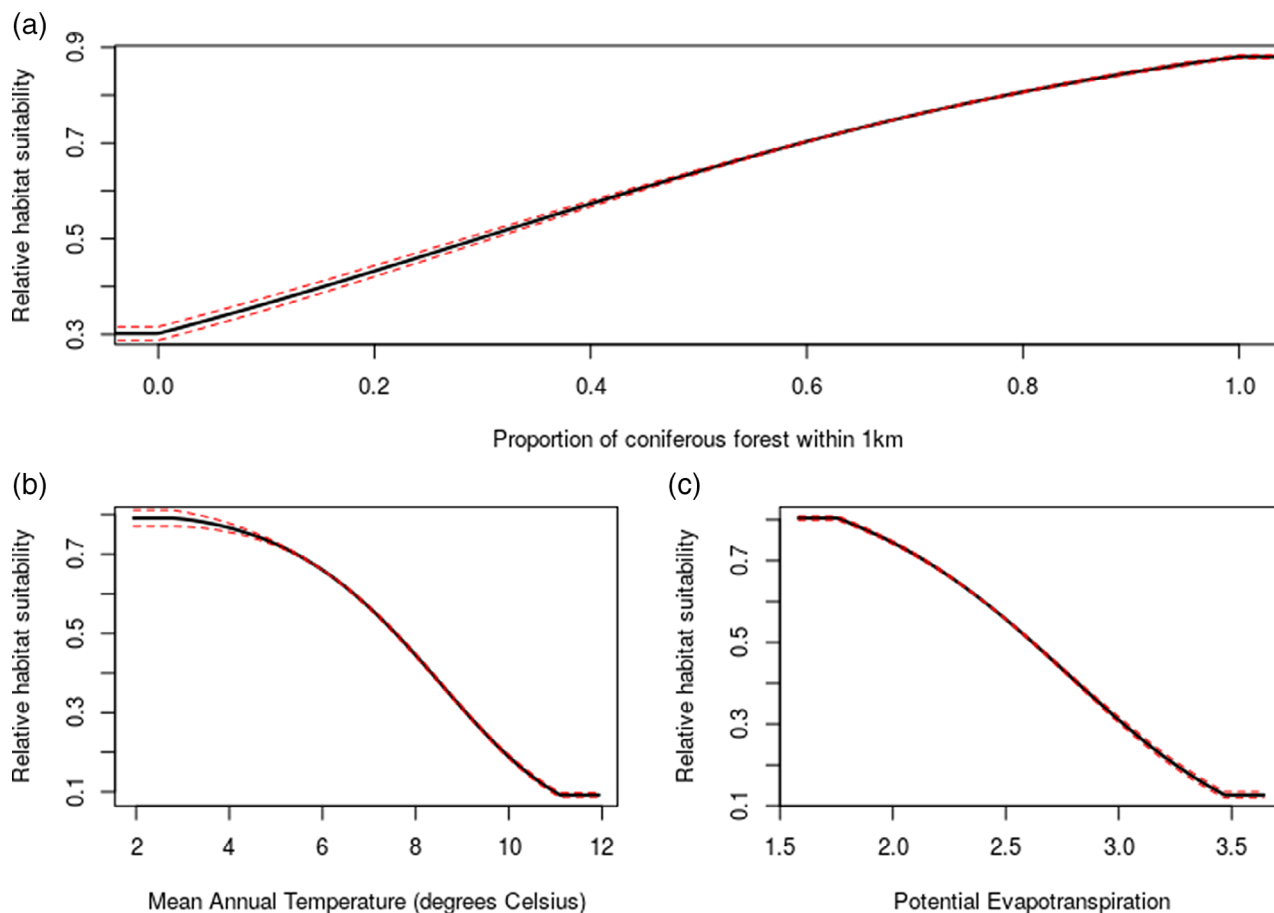


Figure 3. Response curves for each of the three most important predictors, calculated from regularised gain, in Maxent models predicting white-faced darter presence for the whole of Great Britain. For (a) coniferous forest and (b) mean annual temperature and (c) Potential evapotranspiration during the emergence period is represented in mm/day. Y-axes represent the relative suitability for white-faced darter from models using each variable in isolation. Mean response from 10 cross-validated replicate models in shown in black with 95% confidence intervals in red. [Color figure can be viewed at wileyonlinelibrary.com]

(Hijmans *et al.*, 2017) package in R. MaxEnt has been shown to perform consistently well in cases in where few occurrence points are available (Hernandez *et al.*, 2006) and has been shown to maintain consistency of performance across sampling scenarios (Grimmett *et al.*, 2020). We used the variance inflation factor through the ‘vif’ function in the R package ‘usdm’ (Naimi *et al.*, 2014) to check for collinearity between predictor variables and in all cases these were less than the correlation threshold of 0.7. We used the ‘ENMEval’ R package (Muscarella *et al.*, 2014) to find the ‘best’ combination of potential relationships with variables and the optimum regularisation parameter for Maxent models based on Northern Scotland. Using only Northern Scotland, the spatially smaller model, reduced the necessary computational time for model optimisation. We tested linear, quadratic and product features along with combinations of these. We used regularisation values between 0 and 2.5 at 0.5 increments. The optimum model was assessed by comparing AICc across models (Warren & Seifert, 2011). Models with

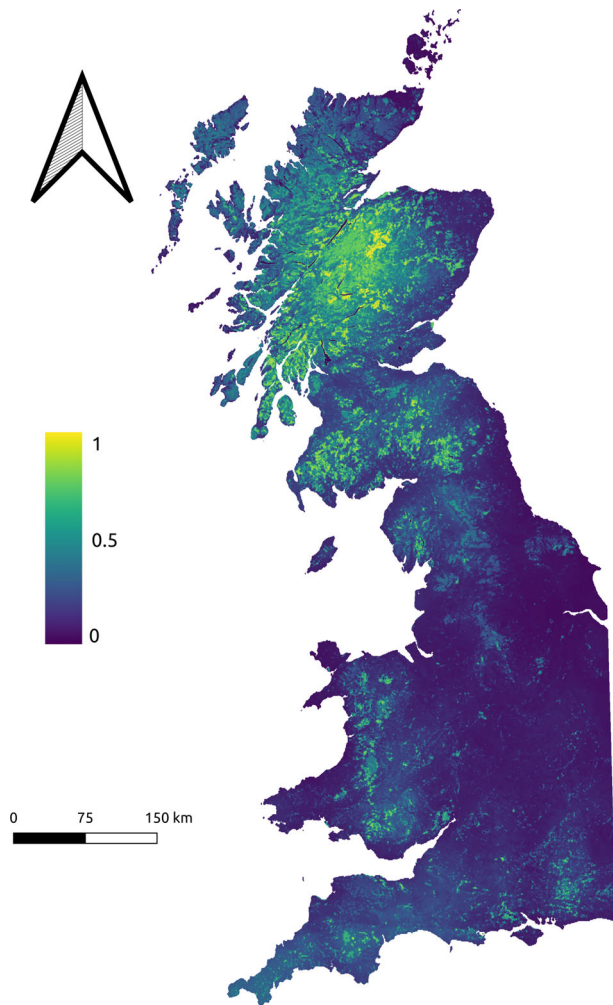


Figure 4. Predicted relative habitat suitability for white-faced darter across Great Britain obtained from a MaxEnt Species Distribution model. [Color figure can be viewed at wileyonlinelibrary.com]

© 2020 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society., *Insect Conservation and Diversity*, doi: 10.1111/icad.12438

$\Delta\text{AICc} < 2$ were considered equivalent (Burnham & Anderson, 1998). Once selected, we fitted the ‘best’ model using 10-cross-validated replicates (Merow *et al.*, 2013) for both Great Britain and the North of Scotland. Models were evaluated based on ecological realism (Zurell *et al.*, 2020) and using the area under the receiver operating characteristic curve (AUC; Fielding & Bell, 1997) as well as the True Skill Statistic (Allouche *et al.*, 2006). We used Moran’s I statistic to check for autocorrelation in the residuals (Dormann *et al.*, 2007; Václavík *et al.*, 2012).

Results

Model

Model selection indicated that the ‘best’ combination of parameters for our model was to use only linear and quadratic features with a beta multiplier of one (Table 1 and Electronic Supplementary Material).

The model for the whole of Great Britain has reasonable predictive power (AUC = 0.78; TSS = 0.47). The most important variable in this model was the proportion of coniferous forest within 1 km (53.4% variable contribution; Figure 2) followed by potential evapotranspiration (14.9%), mean annual temperature (11.5%) and annual temperature range (9.6%). The proportion of bogs, standing water and broadleaved woodland all had importance values of less than 5%. Relative habitat suitability for white-faced darter increased with increasing proportions of coniferous woodland (Fig. 3a) and with decreasing mean annual temperature (Fig. 3b) and decreasing potential evapotranspiration (Fig. 3c). The model showed significant spatial autocorrelation in model residuals (Moran’s I = 0.69, $P = 0.0001$).

Projecting this model onto environmental layers for Great Britain (Fig. 4) shows a predicted distribution which largely represents uplands in Great Britain. The areas of highest predicted

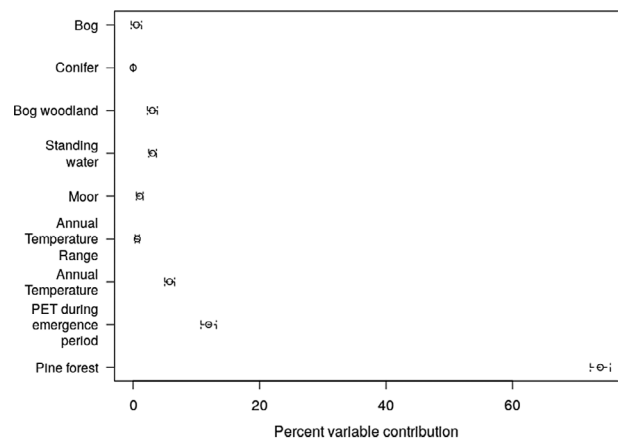


Figure 5. Percentage importance for each variable, calculated from the contribution of each variable to regularised gain, used to predict white-faced darter presence across the North of Scotland \pm Standard Error (dotted lines).

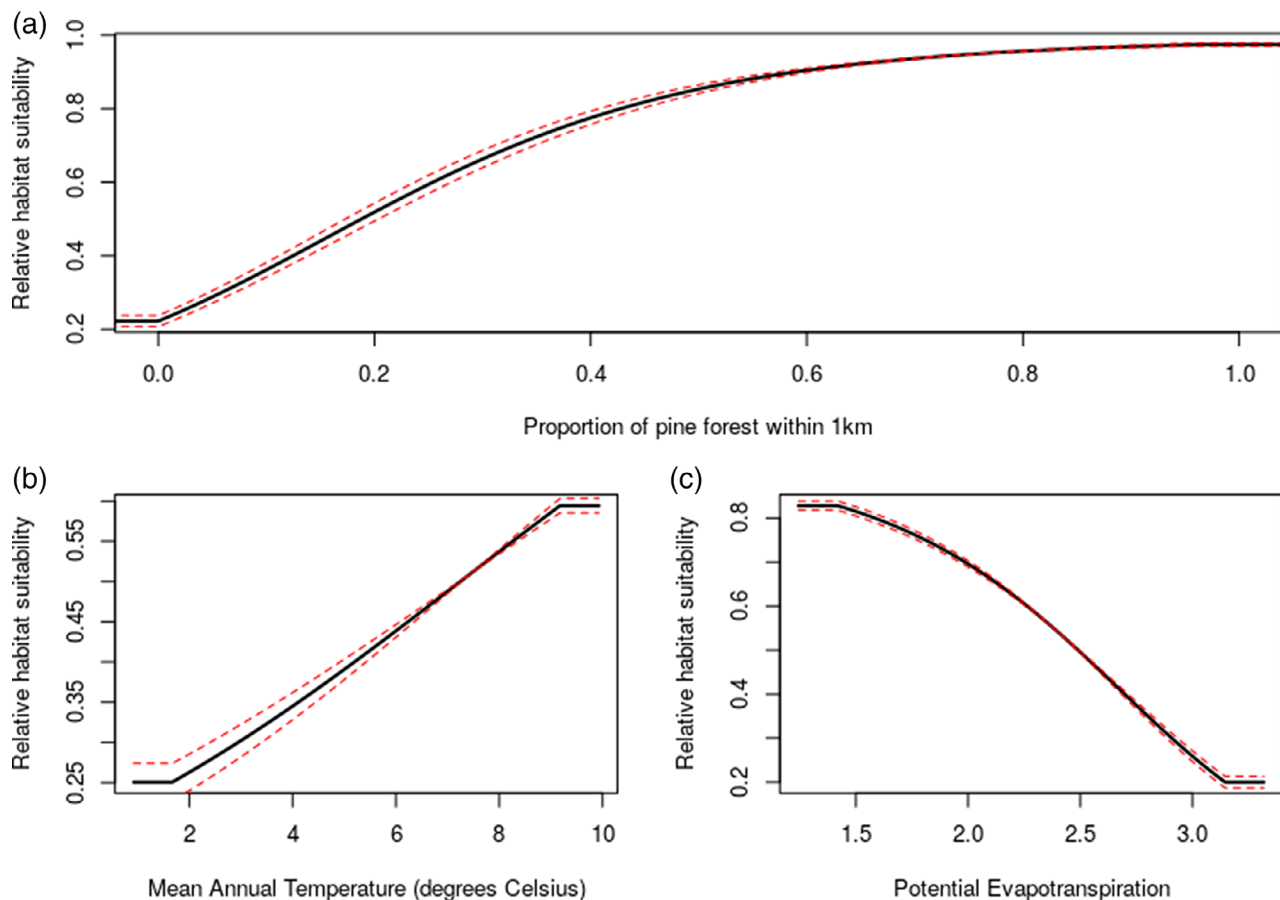


Figure 6. Response curves for each of the three most important predictors, calculated from regularised gain, in Maxent models predicting white-faced darter presence for the North of Scotland. For (a) pine forest and (b) mean annual temperature and (c) Potential evapotranspiration during the emergence period is represented in mm/day. Y-axes represent the relative suitability for white-faced darter from models using each variable in isolation. Mean response from 10 cross-validated replicate models is shown in black with 95% confidence intervals in red. [Color figure can be viewed at wileyonlinelibrary.com]

suitability correspond to important strongholds in the Scottish Highlands such as Abernethy forest but also predict a number of areas with no records for this species in Scotland, Wales and the South of England. The model is unable to predict important sites such as Fenn's and Whixall Moss on the border between England and Wales but successfully predicts sites in Cumbria and the white-faced darter reintroduction site in Delamere Forest, Cheshire.

The North of Scotland model shows a good fit to the data (AUC = 0.80, TSS = 0.49). The most important variable in the model (73.9% variable contribution) is the percentage of pine forest (Fig. 5) within 1 km. Other variables are considerably less important with the potential evapotranspiration (11.9%) and mean annual temperature (5.8%) having slightly higher contributions than annual temperature range, percentage of bog woodland, percentage of bogs, percentage of conifer and percentage of moorland within 1 km which all have percentage contributions of less than 5%. Model residuals show significant spatial autocorrelation (Moran's $I = 0.05$, $P = 0.0005$). Response curves indicate that increasing proportions of pine forest within 1 km

result in higher relative suitability for white-faced darter (Fig. 6a). The relative suitability is increases when the mean annual temperature is higher (Fig. 6b) and the potential evapotranspiration is lower (Fig. 6c).

Projecting the model onto the environmental data layer for the whole of Scotland produces maps which accurately predict many current strongholds for white-faced darter (Fig. 7). In particular, our model successfully predicts the presence of white-faced darter in Abernethy forest and Glen Affric. Yet, our model fails to predict a well-known population of white-faced darter at Monadh Mor on the Black Isle.

Discussion

Our models suggest that the strongest drivers of white-faced darter distribution are increasing proportions of coniferous forest, specifically pine forest in the North of Scotland, along with low potential evapotranspiration. These results provide quantitative support for the current descriptions of white-faced darter

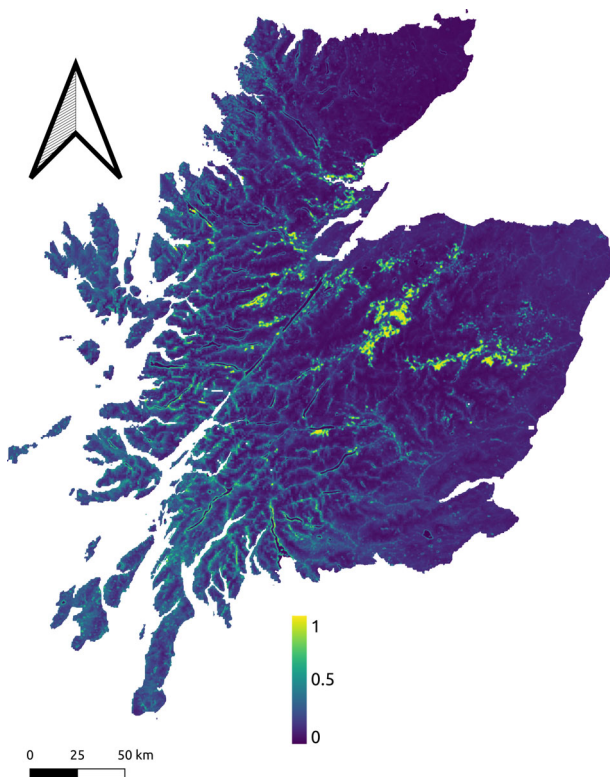


Figure 7. Predicted relative habitat suitability for white-faced darter across the North of Scotland obtained from a Maxent species distribution model. [Color figure can be viewed at wileyonlinelibrary.com]

habitat (Cham *et al.*, 2014) and also agree with local-scale descriptions of habitat associations (Meredith, 2017). Nevertheless, our models differ in the relationship between habitat suitability and annual mean temperature. In the model for the whole of Great Britain, white-faced darter are associated with higher temperature, however, in the North of Scotland model the opposite is true. As white-faced darter is found at both more northerly and southerly latitudes in mainland Europe, it is likely that these relationships are broader than our models are able to identify.

Both of our distribution maps predict strongly in several core areas for white-faced darter such as Abernethy forest and Glen Affric. Yet, in other areas, our predictions are less successful and the inability to predict all known locations along with the potential for records of mobile adults to be in areas of unsuitable habitat when recorded (Raebel *et al.*, 2010) are two plausible reasons for significant spatial autocorrelation in our model residuals. In fact, we miss some locations entirely as we are unable to successfully predict Fenn's and Whixall Moss on the English and Welsh border using our Great Britain model and fail to predict the population found at Monadh Mor on the Black Isle using our North of Scotland model. These sites may represent unusual cases for the species, several sites in Southern Britain do not have the level of tree cover associated with white-faced darter habitat further North and are heavily managed landscapes. Our models also only highlight coniferous forest as important and

do not include the birch forests suggested by several sources (Cham *et al.*, 2014). We see this as a limitation of our model and the data available for analysis, due to the correlation between the distribution of pine forest and other forest types at a landscape scale, rather than an indication that birch forests are not important. More successfully, our models predict high suitability for white-faced darter presence in areas in which the species was not found until very recently, locations not included in our data (Batty, 2017, 2018).

Our models currently predict a high suitability for several areas where white-faced darter has not been recorded yet. In England and Wales, the majority of these locations are likely to be distant from source populations and therefore unlikely to be occupied but may contain some suitable habitat. Although it is unlikely that white-faced darter is under-recorded in the South of Britain, this is possible in the North of Scotland which has lower recorder-effort and so some 'suitable' sites here may contain currently unrecorded populations of white-faced darter. There are a number of areas such as the Grampians, which may offer suitable habitat along with specific locations such as Glen Moriston and areas around Tain in Easter Ross and Banchor in Nairn. Our results suggest that these areas would be good targets for expanding monitoring efforts on this species. Remote areas are often difficult to obtain data for when relying on volunteer recorders. One approach to this in UK bird surveys is to encourage volunteers from elsewhere in the country to adopt remote squares (Gillings *et al.*, 2019). This method may be particularly applicable to dragonfly recorders who are fewer in number than those who contribute bird records. Two larger areas of habitat are predicted by our model based around Abernethy forest and Glen Affric. These two sites are well-known locations for the species and our models suggest they may be important sites for the white-faced darter conservation. Large areas of contiguous habitat are likely to hold larger populations. White-faced darter should continue to be considered in management plans for these two sites with the maintenance of bog pool systems within woodland as a conservation focus.

Current management recommendations for white-faced darter suggest maintaining lowland peat pool complexes within woodland using scrub control and maintaining water quality (Cham *et al.*, 2014). Our results confirm that these current recommendations should be maintained and prioritised. The most important variable along with woodland cover in both of our models was potential evapotranspiration. This suggests that white-faced darter is likely to be impacted by drainage as part of woodland management and this should be avoided where this species is present. This also adds support to management operations put in place as part of the white-faced darter reintroduction project in Delamere forest, England where areas are being re-wetted to provide more suitable habitat for the reintroduced population (Meredith, 2017).

Our models, particularly the model for the North of Scotland, suggest that suitable white-faced darter habitat is patchy within the landscape and that populations may be fragmented at some distance from each other. Within sites, white-faced darter favours pool complexes and may use different areas in different years (Kharitonov & Popova, 2011). These two features of white-faced darter populations suggest that connectivity at

multiple scales may be important in terms of population persistence. White-faced darter has the potential to travel relatively long distances (Johansson *et al.*, 2017), but it is particularly reliant on sphagnum filled pools within their preferred habitat (Henrikson, 1993). The ability to move across a landscape matrix can be influenced by structural features in the landscape such as forest cover and type (Chin & Taylor, 2009). It would be extremely valuable for informing conservation efforts for white-faced darter in the United Kingdom, to assess how populations are connected at both large and small distances and how habitat and landscape features might influence this connectivity. Although some tracking studies have been performed on Odonata (e.g. Wikelski *et al.*, 2006) the numbers of animals which would be possible to involve is likely to be very low. Equally, mark-recapture studies, although they have been successfully used to estimate white-faced darter local population sizes (Dolný *et al.*, 2018), generally have low recapture rates in Odonata (Cordero-Rivera & Stoks, 2008) making them unsuitable for studies on population connectivity. Genetic methods are therefore likely to hold the most value in investigating this issue (Keller *et al.*, 2010; Dolný *et al.*, 2018).

Our models currently only use presence records to investigate distribution. However, records of species presence not only depend on the distribution of that species but also on the detectability of the species (Lahoz-Monfort *et al.*, 2014). Presence-only methods like MaxEnt cannot disentangle the detection probability (i.e. the probability a species is detected if present) from the probability a site is occupied, generally underestimating the true occupancy and thus potentially providing biased predictions of the distribution (Lahoz Monfort *et al.*, 2014) or population status (Bried *et al.*, 2012). We are confident that the impact of imperfect detection is limited in our model because these presence records are part of a wider dataset of dragonfly records where the presence of other species indicates at least some searching effort by dragonfly enthusiasts. However, in future, we recommend that data are collected in a way which facilitates the incorporation of detectability into models of dragonfly distributions. This would involve making repeated visits to sites (MacKenzie *et al.*, 2002) and indicating when a complete list of all species present has been provided to the national recording scheme (Isaac & Pocock, 2015).

Despite the inherent limitations of relatively information-poor data, presence-only modelling can still be an extremely valuable tool in mapping and understanding the distribution of important species allowing to use and obtain conservation relevant information from incidental records, often collected in the past, and for which repeated visits are not available (Elith *et al.*, 2006). This kind of data, often collected over extended periods of time (years if not decades) and over extended ranges, incidentally by volunteers like those of the British Dragonfly Society, can provide large-scale information on temporal and spatial changes in species distribution happened in the past which would not be possible to obtain with methods taking into account imperfect detection, simply because we cannot go back in time to collect the necessary data with these approaches. Here, we have demonstrated that at broad scales, the distribution of suitable habitat for white-faced darter is dependent on wet areas in coniferous woodland and that pine forest, in particular, is an important habitat in

Scotland. Our specific predictions can be useful to land-managers who are looking to develop landscapes for this species and also to conservation organisations designing surveys for this species. In future, it would be beneficial to investigate the drivers of white-faced darter distribution at finer scales as well as population connectivity across landscapes. Our research supports, with quantitative evidence, the importance of protecting wet habitats within coniferous woodlands in order to manage landscapes for this species.

Acknowledgements

All dragonfly presence records were provided by the British Dragonfly Society (BDS) and collected by volunteers. The authors would like to express our thanks to the BDS for helping us to access these data and providing scientific support as well as to all of the volunteers who contributed records. The EUNIS Scotland land cover data set contains SNH information licenced under the Open Government Licence v3.0.

Authors Contribution

M.G. originally formulated the idea, M.G. and Av.H. developed methodology, analysed the data and wrote the manuscript.

Data availability statement

The white-faced darter presence data used in the current study are available from the British Dragonfly Society on reasonable request or through the UK's National Biodiversity Network.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Electronic Supplementary Material. Comparison of all MaxEnt models predicting white-faced darter distribution in the Scottish highlands. Models were tested with linear, quadratic and product responses to predictors along with combinations of these and regularisation values between 0 and 3 at 0.5 increments.

References

- Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, **38**, 541–545.
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.

- Batty, P. (2017) Scotland VC72-112. *Darter Magazine - British Dragonfly Society*, **34**, 26–27.
- Batty, P. (2018) Highlands of Scotland. *Darter Magazine - British Dragonfly Society* **35**, pp. p. 30–31.
- Beadle, J.M., Brown, L.E. & Holden, J. (2015) Biodiversity and ecosystem functioning in natural bog pools and those created by rewetting schemes. *WIREs Water*, **2**, 65–84. <https://doi.org/10.1002/wat2.1063>.
- Beynon, T., Cham, S., Johnson, I., Dodds, R.M., Mill, P., Moore, N., Murray, C., Parr, A., Peacock, B., Perrin, V. (2008) *The Odonata Red Data List for Great Britain*.
- Boudot, J.-P. & Kalkman, V.J. (2015) *Atlas of the European Dragonflies and Damselflies*. KNNV Publishing.
- Bourke, J., Busse, K. & Böhme, W. (2012) Searching for a lost frog (*Rhinoderma rufum*): identification of the most promising areas for future surveys and possible reasons of its enigmatic decline. *North-Western Journal of Zoology*, **8**.
- Bried, J.T., D'Amico, F. & Samways, M.J. (2012) A critique of the dragonfly delusion hypothesis: why sampling exuviae does not avoid bias. *Insect Conservation and Diversity*, **5**(5), 398–402.
- Bried, J.T. & Samways, M.J. (2015) A review of odonatology in freshwater applied ecology and conservation science. *Freshwater Science*, **34**(3), 1023–1031.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag.
- Cardoso, P., Erwin, T.L., Borges, P.A. & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144**, 2647–2655.
- Cham, S.A., Nelson, B., Parr, A., Prentice, S., Smallshire, D. & Taylor, P. (2014) *Atlas of Dragonflies in Britain and Ireland*. Field Studies Council.
- Chin, K.S. & Taylor, P.D. (2009) Interactive effects of distance and matrix on the movements of a peatland dragonfly. *Ecography*, **32**, 715–722.
- Clausnitzer, V. (2009) *Leucorrhinia dubia*. The IUCN Red List of Threatened Species 2009: e.T158683A5250370. <https://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T158683A5250370.en>. Downloaded on 08 July 2020.
- Clausnitzer, V., Dijkstra, K.-D.B., Koch, R., Boudot, J.-P., Darwall, W. R., Kipping, J., Samraoui, B., Samways, M.J., Simaika, J.P. & Suhling, F. (2012) Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. *Frontiers in Ecology and the Environment*, **10**, 129–134.
- Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E.M., Bedjanić, M., Darwall, W.R.T., Dijkstra, K.-D.B., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, D., Schütte, K., Suhling, F., Villanueva, R.J., von Ellenrieder, N. & Wilson, K. (2009) Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation*, **142**, 1864–1869. <https://doi.org/10.1016/j.biocon.2009.03.028>.
- Cordero-Rivera, A. & Stoks, R. (2008) Mark-recapture studies and demography. *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*, pp. p. 7–20. OUP Oxford, Oxford, UK.
- Córdoba-Aguilar, A. (2008) *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. OUP Oxford, Oxford, UK.
- Davies, C.E., Moss, D. & Hill, M.O. (2004) EUNIS habitat classification revised 2004. Report to: European Environment Agency-European Topic Centre on Nature Protection and. *Biodiversity*, 127–143.
- Davies, R., Von Hardenberg, A. & Geary, M. (2018) Recapture rates and habitat associations of White-faced Darter *Leucorrhinia dubia* on Fenn's and Whixall Moss, Shropshire, UK. *Journal of the British Dragonfly Society*, **34**, 89–101.
- Dolný, A., Šigutová, H., Ožana, S. & Choleva, L. (2018) How difficult is it to reintroduce a dragonfly? Fifteen years monitoring *Leucorrhinia dubia* at the receiving site. *Biological Conservation*, **218**, 110–117.
- Donnelly, A., Crowe, O., Regan, E., Begley, S. & Caffarra, A. (2014) The role of citizen science in monitoring biodiversity in Ireland. *International Journal of Biometeorology*, **58**, 1237–1249.
- Dormann, C.F., Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2012) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Drinan, T.J., Foster, G.N., Nelson, B.H., O'Halloran, J. & Harrison, S.S. C. (2013) Macroinvertebrate assemblages of peatland lakes: Assessment of conservation value with respect to anthropogenic land-cover change. *Biological Conservation*, **158**, 175–187.
- Elith, J. & Graham, C.H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66–77. <https://doi.org/10.1111/j.1600-0587.2008.05505.x>.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R. & Lehmann, A. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Elo, M., Penttinen, J. & Kotiaho, J.S. (2015) The effect of peatland drainage and restoration on Odonata species richness and abundance. *BMC ecology*, **15**, 11.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49. <https://doi.org/10.1017/S0376892997000088>.
- Fourcade, Y., Engler, J.O., Rödder, D. & Secondi, J. (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS One*, **9**, e97122. <https://doi.org/10.1371/journal.pone.0097122>.
- Gillings, S., Balmer, D.E., Caffrey, B.J., Downie, I.S., Gibbons, D.W., Lack, P.C., Reid, J.B., Sharrock, J.T.R., Swann, R.L. & Fuller, R.J. (2019) Breeding and wintering bird distributions in Britain and Ireland from citizen science bird atlases. *Global Ecology and Biogeography*, **28**, 866–874. <https://doi.org/10.1111/geb.12906>.
- Grimmett, L., Whitsed, R. & Horta, A. (2020) Presence-only species distribution models are sensitive to sample prevalence: evaluating models using spatial prediction stability and accuracy metrics. *Ecological Modelling*, **431**, 109–194.
- Henrikson, B.I. (1993) Sphagnum mosses as a microhabitat for invertebrates in acidified lakes and the colour adaptation and substrate preference in *Leucorrhinia dubia* (Odonata, Anisoptera). *Ecography*, **16**(2), 143–153.
- Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**(5), 773–785.
- Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., Hijmans, M.R.J. (2017). dismo: Species Distribution Modeling. R package.
- Hijmans, R.J., van Etten, J. (2012) raster: Geographic analysis and modeling with raster data. R package version 1.9-63.

- Huerta, M.A.O. & Peterson, A.T. (2008) Modeling ecological niches and predicting geographic distributions: a test of six presence-only methods. *Revista Mexicana de Biodiversidad*, **1**, 205–216.
- Isaac, N.J. & Poccock, M.J. (2015) Bias and information in biological records. *Biological Journal of the Linnean Society*, **115**, 522–531.
- Johansson, F., Halvarsson, P., Mikolajewski, D.J. & Höglund, J. (2017) Genetic differentiation in the boreal dragonfly *Leucorrhinia dubia* in the Palearctic region. *Biological Journal of the Linnean Society*, **121** (2), 294–304.
- Kalkman, V.J., Boudot, J.P., Bernard, R., Conze, K.J., De Knijf, G., Dyatlova, E., Ferreira, S., Jović, M., Ott, J., Riservato, E. & Sahlén, G. (2010) *European Red List of Dragonflies*. Publications Office of the European Union, Luxembourg.
- Kalkman, V.J., Boudot, J.P., Bernard, R., De Knijf, G., Suhling, F. & Termaat, T. (2018) Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia*, **811**(1), 269–282.
- Keller, D., Brodbeck, S., Flöss, I., Vonwil, G. & Holderegger, R. (2010) Ecological and genetic measurements of dispersal in a threatened dragonfly. *Biological Conservation*, **143**, 2658–2663.
- Kharitonov, A.Y. & Popova, O.N. (2011) Migrations of dragonflies (Odonata) in the south of the West Siberian plain. *Entomological review*, **91**, 411–419.
- Lahoz-Monfort, J.J., Guillera-Aroita, G. & Wintle, B.A. (2014) Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, **23**, 504–515.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- Meredith, C. (2017) Reintroduction of *Leucorrhinia dubia* (Vander Linden) (White-faced Darter) to Delamere Forest, Cheshire. *Journal of the British Dragonfly Society*, **33**, 50–72.
- Merow, C., Smith, M.J. & Silander, J.A., Jr. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, **36**(10), 1058–1069.
- Millar, E.E., Hazell, E.C. & Melles, S.J. (2018) The 'cottage effect' in citizen science? Spatial bias in aquatic monitoring programs. *International Journal of Geographical Information Science*, 1–21.
- Monteiro-Júnior, C.S., Juen, L. & Hamada, N. (2014) Effects of urbanization on stream habitats and associated adult dragonfly and damselfly communities in central Brazilian Amazonia. *Landscape and Urban Planning*, **127**, 28–40.
- Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J. M., Uriarte, M. & Anderson, R.P. (2014) ENM eval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, **5**, 1198–1205.
- Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K. & Toxopeus, A. G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography*, **37**(2), 191–203.
- Nazeri, M., Jusoff, K., Madani, N., Mahmud, A.R., Bahman, A.R. & Kumar, L. (2012) Predictive modeling and mapping of Malayan Sun Bear (*Helarctos malayanus*) distribution using maximum entropy. *PLoS One*, **7**, e48104.
- Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M. & Myers, C.E. (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, **263**, 10–18.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175. <https://doi.org/10.1111/j.2007.0906-7590.05203.x>.
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raebel, E.M., Merckx, T., Riordan, P., Macdonald, D.W. & Thompson, D.J. (2010) The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. *Journal of Insect Conservation*, **14**(5), 523–533.
- Renner, I.W. & Warton, D.I. (2013) Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*, **69**, 274–281.
- Robinson, E., Blyth, E., Clark, D., Comyn-Platt, E., Finch, J., Rudd, A. (2016) *Climate Hydrology and Ecology Research Support System Meteorology Dataset for Great Britain (1961–2015)[CHESS-met]*.
- Robinson, O.J., Ruiz-Gutierrez, V. & Fink, D. (2018) Correcting for bias in distribution modelling for rare species using citizen science data. *Diversity and Distributions*, **24**, 460–472.
- Rowland, C., Morton, D., Carrasco Tornero, L., McShane, G., O'Neil, A., Wood, C. (2017) Land Cover Map 2015 (1km dominant aggregate class, GB) NERC Environmental Information Data Centre 11 April 2017, <https://doi.org/10.5285/711c8dc1-0f4e-42ad-a703-8b5d19c92247>
- Samways, M.J. & Taylor, S. (2004) Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata): working for water. *South African Journal of Science*, **100**, 78–80.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation biology*, **5**, 18–32.
- Schilling, E.G., Loftin, C.S. & Huryn, A.D. (2009) Effects of introduced fish on macroinvertebrate communities in historically fishless headwater and kettle lakes. *Biological Conservation*, **142**(12), 3030–3038.
- Smallshire, D. & Swash, A. (2004) *Britain's Dragonflies*. Old Basing Wild Guides Ltd.
- Sutton, L.J. & Puschendorf, R. (2018) Climatic niche of the Saker Falcon *Falco cherrug*: predicted new areas to direct population surveys in Central Asia. *Ibis*, **162**, 27–41. <https://doi.org/10.1111/ibi.12700>.
- Termaat, T., van Strien, A.J., van Grunsven, R.H., De Knijf, G., Bjelke, U., Burbach, K., Conze, K.-J., Goffart, P., Hepper, D., Kalkman, V.J., Moot, G., Prins, M.D., Prunier, F., Sparrow, D., van den Top, G.G., Vanappelghem, C., Winterholler, M. & WallisDeVries, M.F. (2019) Distribution trends of European dragonflies under climate change. *Diversity and Distributions*, **25**(6), 936–950.
- Tweddle, J.C., Robinson, L.D., Pocock, M.J.O. & Roy, H.E. (2012) *Guide to Citizen Science: Developing, Implementing and Evaluating Citizen Science to Study Biodiversity and the Environment in the UK*. NERC/Centre for Ecology & Hydrology.
- Václavík, T., Kupfer, J.A. & Meentemeyer, R.K. (2012) Accounting for multi-scale spatial autocorrelation improves performance of invasive species distribution modelling (iSDM). *Journal of Biogeography*, **39**, 42–55.
- Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.
- Whitfield, S., Reed, M., Thomson, K., Christie, M., Stringer, L.C., Quinn, C. H., Anderson, R., Moxey, A. & Hubacek, K. (2011) Managing peatland ecosystem services: current UK policy and future challenges in a changing world. *Scottish Geographical Journal*, **127**, 209–230.
- Wikelski, M., Moskowicz, D., Adelman, J.S., Cochran, J., Wilcove, D. S. & May, M.L. (2006) Simple rules guide dragonfly migration. *Biological Letters*, **2**, 325–329.
- Wilting, A., Cord, A., Hearn, A.J., Hesse, D., Mohamed, A., Traeholdt, C., Cheyne, S.M., Sunarto, S., Jayasilan, M.-A., Ross, J., Shapiro, A.C., Sebastian, A., Dech, S., Breitenmoser, C.,

Sanderson, J., Duckworth, J.W. & Hofer, H. (2010) Modelling the species distribution of flat-headed cats (*Prionailurus planiceps*), an endangered South-East Asian small felid. *PLoS one*, **5**, e9612. <https://doi.org/10.1371/journal.pone.0009612>.

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A. &

Lahoz-Monfort, J.J. (2020) A standard protocol for reporting species distribution models. *Ecography*.

Accepted 22 July 2020

Editor: Christopher Hassall; Associate Editor: Göran Sahlén