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Incorporating movement in species distribution models: how do simulations of dispersal affect the accuracy and uncertainty of projections?

Species distribution models (SDMs) are one of the most important GIScience research areas in biogeography and are the primary means by which the potential effects of climate change on species' distributions and ranges are investigated. Dispersal is an important ecological process for species responding to changing climates, however, SDMs and their subsequent spatial products rarely reflect accessibility to any future suitable environment. Dispersal-related movement can be confounded by factors that vary across landscapes and climates, as well as within and among species, and it has therefore remained difficult to parametrise in SDMs. Here we compared 20 models that have previously been used (or have the potential to be used) to represent dispersal processes in SDM to predict future range shifts in response to climate change. We assessed the different dispersal models in terms of their accuracy at predicting future distributions, as well as the uncertainty associated with their predictions. Atlas data for 50 bird species from 1988–1991 in Great Britain were treated as base distributions (t_1), with the species-environment relationships extrapolated (using three commonly used statistical methods) to 2008–2011 (t_2). Dispersal (in the form of the 20 different models) was simulated from the base distribution (t_1) to 2008-2011 (t_2). The results were then combined and used to identify locations that were both abiotically suitable (obtained from the statistical methods) and accessible (obtained from the dispersal models). The accuracy of these coupled projections was assessed with the 2008–2011 atlas data (the observed t_2 distribution). There was substantial variation in the accuracy of the different dispersal models, and in general, the more restrictive dispersal models (e.g. fixed rate dispersal) resulted in lower accuracy for the metrics which reward correct prediction of presences. Ensemble models of the dispersal methods (generated by combining multiple projection outcomes) were created for each species, and a new Ensemble Agreement Index (EAI), which ranges from 0 (no agreement among models) to 1 (full agreement among models) was developed to quantify uncertainty among the projections. EAI values ranged from 0.634 (some areas of disagreement and

therefore medium uncertainty among dispersal models) to 0.999 (large areas of agreement and low uncertainty among dispersal models). The results of this research highlight the importance of incorporating dispersal and also illustrate that the method with which dispersal is simulated greatly impacts the projected future distribution. This has important implications for studies aimed at predicting the effects of changing environmental conditions on species' distributions.

Keywords: species distribution modelling; uncertainty; dispersal; climate change; birds

Introduction:

Climate change and concomitant urbanization have led to many species shifting to higher latitudes and altitudes across Europe and North America, while many other species have simply gone extinct (Smith *et al.* 1993, Chen *et al.* 2011). In order to mitigate these potentially devastating scenarios for biodiversity, it is imperative to better understand current and future patterns of species' distributions. Species distribution models (SDMs) are a powerful spatial ecological tool for studying the geographic distribution of plants, animals, and other biogeographic phenomena such as vector-borne diseases (Franklin 2009). This modelling framework provides a robust methodology for researchers and practitioners seeking to quantitatively assess the relationship between species' distributions and environmental factors, and they have been used across an array of disciplines in order to test biogeographical hypotheses (Bolker *et al.* 2009), support nature reserve network design (Araújo *et al.* 2004), identify areas of rare species occurrence (Engler *et al.* 2004), assess species invasion risk (Medley 2010), explore the spatial scale of species-environment relationships (Miller and Hanham 2011), and assess the impact of climate change on species (Wiens *et al.* 2011).

An increasingly important application area for SDMs is to study the effects of climate change on species' distributions. The extrapolation of species-environment relationships

across space or time involves several conceptual and methodological issues that introduce uncertainty, such as novel environmental combinations, species interactions, unpredictable feedbacks related to land cover change, as well as the dispersal capacity of the species. The 'BAM' framework (Figure 1) was developed by Soberón and Peterson (2005) and illustrates the individual and joint effects of the three most important factors in determining species' distributions: biotic (B), abiotic (A), and movement (M). Biotic factors represent interactions with other species (i.e. competition, herbivory), abiotic factors represent the physiological tolerances of a species (i.e. temperature, precipitation) and movement factors refer to the processes that lead to an area being accessible to a species within a relevant timeframe (e.g., via dispersal or migration). While the importance of all three factors (abiotic, biotic and movement) is now well recognized, the majority of SDM studies have not incorporated movement, and those that do often rely on overly simplistic conceptualizations of movement (Franklin 2010, Peterson *et al.* 2011).

When movement has been incorporated in SDM research, it has often been to address questions related to range shifts in response to the changing climate or to track the spread of invasive species. Terms such as 'dispersal limitations', 'dispersal capacities', 'migration rates', and 'spread rates' have been used interchangeably by SDM researchers to refer to the cumulative movement of a species or a population across a broad time scale and often across multiple generations (Miller and Holloway 2015). It is this temporally-broad, species-level type of movement which we herein refer to as dispersal and subsequently address.

When dispersal has been implemented in SDM research, it has often taken one of two extreme facile approaches: unlimited dispersal or no dispersal (e.g. Araújo *et al.* 2006, Lawler *et al.* 2006, Araújo and Luoto 2007). Unlimited dispersal can be considered the best case scenario representation of movement under climate change as it assumes that all future suitable habitat is accessible, while no dispersal can be considered the pessimistic worst case

scenario as it assumes that only future suitable habitat that matches currently suitable habitat is accessible. Using both of these approaches together was an improvement on studies that overlooked dispersal (and thus implicitly assumed unlimited dispersal). However, these two approaches overly simplify movement and as a result of their extreme variation, can be used to represent the uncertainty associated with the effects of climate change. In reality, the actual dispersal capacity would most likely be found somewhere in the middle of those two predictions. For example, Engler and Gusian (2009) found a 95% areal difference in the projected distributions of two virtual plant species between their model incorporating dispersal and their model that ignored it. Similarly, in a study of the spread of the non-native common waxbill (*Estrilda astrild*) in the Iberian Peninsula, Sullivan *et al.* (2012) found differences in the accuracy of predictions when a distance weight was incorporated into the SDM compared to one that assumed unlimited dispersal. Likewise, Cunze *et al.* (2013) found differences in the predicted 2080 distributions of European flora between unlimited dispersal and a measure of 'realistic' dispersal, which took into account a combination of discrete dispersal kernels fit for different dispersal vectors (e.g., dispersal by wind, animals, *etc*.).

Recent reviews (Franklin 2010, Miller and Holloway 2015) have identified several ways in which dispersal has been incorporated in SDM studies. Within these conceptualizations of dispersal, there are several different types of methods and subsequent variations of these methods that can be implemented, but to date, they remain untested. With such wide variation in the way that dispersal is represented in these methods, it is likely that resulting predictions will vary markedly. Limited comparisons have been made (see Engler and Guisan 2009, Sullivan *et al.* 2012, Cunze *et al.* 2013), but there is a need for more extensive testing across all implementations of dispersal models.

One of the challenges associated with comparing methods for projecting the effects of climate change on species' distributions has been the lack of appropriate data with which to

validate. The British Trust for Ornithology (BTO) has led the production of breeding bird atlases offering complete coverage of Great Britain at a 10km resolution in three periods spanning 40 years, in 1968–72, 1988–91, and 2008–11. These datasets can be used to test the accuracy of the dispersal models implemented in SDM research, as we can take the earliest known distribution (t_1) and project the species-environment relationships alongside dispersal to the latest time period (t_2), and compare the results with the observed atlas data from the same period (Araújo *et al.* 2005). This will provide researchers with a framework to compare the differences between the dispersal models currently implemented and will subsequently allow discussions about future distributions, extinction rates and dispersal patterns to be made with a better understanding of the accuracy and inherent uncertainty associated with the simulation of dispersal.

Methodology

Data Collection:

Distribution data for 50 breeding species were extracted from bird atlases for 1988-91 (herein 1990) (Gibbons *et al.* 1993) and 2008-2011 (herein 2010) (Balmer *et al.* 2013). Species were chosen based on a positive distribution expansion between 1990 and 2010 and visual inspection of distributions (see Balmer *et al.* 2013), thus reducing any limitation in discussing the accuracy of the dispersal models from using species whose distributions did not change over the course of the time period (and thus would have no variation in dispersal models). Consequently, the species span a range of attributes, such as their ubiquity, migration strategy, and whether they are native or introduced to Great Britain. Twelve birds are classified as migrant breeders, ten are classified as migrant resident breeders, 21 as resident breeders and seven as introduced breeders. The 1990 distribution was chosen instead of the 1968–1972 atlas as the earliest known distribution (t_1) due to the lack of available land cover

data pre-1990. British bird distributions vary among land cover types (Fuller *et al.* 2007), and land cover has changed significantly over the period (Carey *et al.* 2008), so must be incorporated into a dynamic model if we are to ascribe model errors to dispersal rather than a poorly constructed static model. Corresponding climate data for the 12 UK Climate Projection 2009 annual variables (Perry and Hollis 2005a, 2005b, UKCP09 © Crown Copyright 2009) were averaged to match the temporal range of the atlas data, as well as the five years around 2000 (see *Dispersal Modelling*). The climate variables included, temperature ranges, degree days, seasonal heat- and cold-waves, dry days, precipitation intensity and maximum precipitation. Land cover data for 1990 (Fuller *et al.* 1993), 2000 (Fuller *et al.* 2002), and 2007 (Morton *et al.* 2014) was obtained from the Centre for Ecology and Hydrology, with percentage coverage of arable land, coniferous forest, deciduous forest, freshwater, saltwater and urban included. Finally, a 90m Shuttle Radar Topography Mission digital elevation model from the U.S. Geologically Survey was acquired, with the mean and maximum values recorded to a 10km resolution.

Species Distribution Modelling:

Figure 2 is a conceptual diagram which highlights the main steps involved within this SDM framework. The abiotic suitability was determined by three statistical models, and accessibility across the temporal extent from 1990 to 2010 was determined with 20 dispersal models. The statistical models were used to identify abiotically suitable habitat, from which a binary surface of presence or absence was created. The dispersal models were used to identify accessible habitat, from which a binary surface of accessible or inaccessible was generated. Both of these outputs were coupled to identify habitat that was both abiotically suitable and accessible.

Although the 'BAM' framework considers biotic factors as one of the three main drivers of

species' distributions, interactions can vary from species to species, and are also unknown for a large number of organisms. Additionally, these interactions often occur at a spatial scale that is much finer than abiotic and movement factors (e.g. climate and dispersal – Guisan and Thuiller 2005). Habitat factors (which have been included in this research) have been suggested as a proxy for biotic interactions such as food resources (see Wisz et al. 2013), however in order to ease interpretation of the dispersal models (the main focus of this manuscript), explicit biotic interactions were not included in the analysis. For future research, biotic interactions could be incorporated as an environmental layer in the statistical modelling (e.g. presence or absence of a competing species, Guisan and Thuiller 2005).

Statistical Modelling - Abiotic Suitability:

To predict the abiotically suitable habitat, we considered three commonly used statistical methods known for generating accurate results: Generalized Linear Models (GLM), Maximum Entropy (MaxEnt), and Random Forest (RF).We fit the 1990 atlas data to the 1990 climate, habitat and topography data using biomod2 (Thuiller et al. 2013). For each species, stepwise selection of environmental variables based on minimizing the Akaike Information Criterion (AIC) was used to select one final GLM, classification random forest was used to generate a RF model, and one MaxEnt model using default settings (with the exception of 5000 maximum iterations) was created (see Phillips and Dudik 2008). Final models will therefore differ among the 50 species, with the climate, topography and habitat variables each varying in their importance and contribution to the model.

A threshold was used to convert the suitability index into a binary measure of presence or absence. The threshold was determined based on prevalence of presences in the 1990 atlas data for GLM and RF, and the maximum training sensitivity plus specificity threshold was used for MaxEnt. The differences in threshold selection between the models were due to

GLM and RF using presence/absence data in their specification and MaxEnt using presence-only data. Thresholds were selected based on guidelines recommended by similar studies (Liu *et al.* 2005, Hu and Jiang 2011).

Once the final statistical models had been selected, we extrapolated the relationships to the topography, climate conditions, and land cover present in 2010. Each of the three statistical methods deals with extrapolation (predicting in future, and sometimes novel or non-analogue, climate conditions) differently; GLM extrapolates by continuing the fitted trend beyond the last observation, MaxEnt acts consistently and is 'clamped' so it extrapolates in a horizontal line from the fit at the most extreme environmental value in the training data, and random forest extrapolates at a constant value from the last 'known' site (Elith and Graham 2009). These models can be considered as models with unlimited dispersal, and the dispersal models we consider essentially constrain these model predictions according to different conceptualizations of dispersal.

Dispersal Modelling – Movement Suitability:

The predominant conceptualization of dispersal beyond an all or nothing approach in SDM has been to apply a parameterized constraint of dispersal to the species' distribution (Franklin 2010, Miller and Holloway 2015). Within this conceptualization there are four further sub-conceptualizations: fixed rate dispersal, dispersal kernels, landscape-derived metrics and demographic models. We identified a total of 20 dispersal models within the all or nothing, fixed rate dispersal and dispersal kernel conceptualizations (Table 1). The 1990 atlas data was taken as the base distribution for which the 20 dispersal models were simulated from. The decision to simulate dispersal from this observed distribution rather than a distribution generated by an SDM was taken so that discussion could centre on the accuracy and uncertainty of the dispersal models rather than the different distributions that the three

statistical methods would have generated. All dispersal models were implemented using original R functions written by the authors in R 3.1.2 (R Development Core Team 2008), with the exception of the probabilistic dispersal kernel which used the kernel function in the MigClim package (Engler *et al.* 2013). See Supplementary Information for computational details on the dispersal models. The total 20 dispersal models and a reference code (for use in results) are provided in Table 1.

All or Nothing. Unlimited dispersal (UD) represents an overly optimistic scenario, and assumes that all suitable habitat in future geographic space is accessible. No dispersal (XD) is a pessimistic scenario, and assumes that only currently suitable habitat is accessible in future projections. A variant of this, limited dispersal assumes that only contiguous areas of suitable habitat in future geographic space that overlap with the areas of suitable habitat in current geographic space become suitable. This method can be varied by using both rook's (L1) and Queen's (L2) cases of connectivity.

Fixed Rate Dispersal. Fixed rate (FR) involves using a rate of dispersal and applying this as a time-based distance buffer around the current distribution. This has previously been implemented using different measures of dispersal distances. For example, Gallardo *et al.* (2012) used the mean recorded dispersal rate of the killer shrimp (*Dikerogammarus villosus*) in the Rhine River to predict future distributions in the River Great Ouse in the UK, while Hsu *et al.* (2012) used the maximum recorded dispersal distance of tropical plants in East Asia to predict the fixed dispersal rates of forests in Taiwan. Paradis *et al.* (1998) published both the arithmetic and geometric means of natal dispersal distances for 75 birds in the UK from the BTO ringing scheme, and identified that dispersal distance scaled with body size with the ¼ exponent (a common feature of ecological variables, see Peters 1983). As the species between our study and Paradis *et al.* (1998) differed, we ran linear regression between

natal dispersal distances and average body mass of these 75 birds (Robinson 2005) (Supplementary Information 2). Based on the AIC score, the model with birds grouped by breeding status was selected and used to calculate both the arithmetic and geometric means of natal dispersal distance for the birds in our study. The geometric mean restricts the impact of outliers on the mean value, which for dispersal may be representative of infrequent long-distance dispersal events and so could restrict dispersal rates.

Whether this projection is based on a fixed rate for one time step (i.e. from current [t_1] to future [t_2]), or using a number of time steps (i.e. from current [t_1], to an intermediate period [$t_{1.5}$], to future [t_2]) has also been shown to produce different results (Midgley *et al.* 2006). The multiple time step model does not assume homogenous abiotic suitability across the entire temporal extent, and couples the dispersal model with a statistical model at each time step. As this has been known to have a potential impact on the dispersal rates, we included fixed rates for one time step (1990-2010) and two time steps (1990-2000 and 2000-2010), using corresponding climate and habitat data from that time period.

Dispersal Kernels: Dispersal kernels extend these fixed rates of movement by calculating the probability density function (PDF) describing the number of dispersal units as a function of distance from the source, with an advantage being that they can incorporate long-distance dispersal events, something that is thought to play an important role in determining broad-scale processes of population spread (Nathan et al. 2008). Dispersal kernels can be fit with a variety of shapes. This shape is often theoretical as recorded dispersal distances for a large number of species are rare. The shape of this theoretical curve could have important consequences regarding what is considered accessible, with implementations in SDMs to date including a Gaussian distribution, an inverse exponential distribution and a fat-tailed Cauchy distribution (e.g. Conlisk et al. 2012).

The probability density function of a Gaussian distribution can be defined as:

$$f(x, \mu, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (1.0)$$

where μ is the mean, σ is the standard deviation.

The probability density function of an exponential distribution is:

$$f(x) = \frac{1}{\lambda} e^{-\frac{x-\mu}{\lambda}} \qquad x \geq \mu;\ \lambda > 0 \quad (2.0)$$

where λ is the rate parameter, which can be defined as $1/\mu$. With the inverse of this function used for the inverse exponential PDF.

Finally, the probability density function of a Cauchy distribution is:

$$f(x; \mu, y) = \frac{1}{\pi y\left[1+\left(\frac{x-x_0}{y}\right)^2\right]} = \frac{1}{\pi y}\left[\frac{y^2}{(x-x_0)^2+y^2}\right] \quad (3.0)$$

where μ is the location parameter specifying the location of the peak of the distribution, and y is the scale parameter.

There are two current methodologies to implement a dispersal kernel within an SDM framework. The first is to use a discrete dispersal kernel (DK), and estimate a fixed dispersal rate according to the maximum value drawn from the kernel based on a random sample size equal to the net reproductive rate (R_0), multiplied by the temporal period (T) divided by the age at which the species first breeds (A) (Clark *et al.* 2001, Cunze *et al.* 2013). R_0 was set to the maximum population density recorded for a species in an observation (Massimino *et al.* 2015) multiplied by the average clutch size of the species (Baillie *et al.* 2014), T was set to the time period (e.g. 20 years), and A was set to the breeding age for each species (Robinson and Clark 2014) (n.b. if there was no information regarding a specific species in these products, then the maximum values from another species with the same breeding status were

used). The second methodology is to use a probabilistic dispersal kernel (PK) which assigns each grid a conditional probability to be colonized and generates presence based on these values. This method is currently available in the MigClim package (Engler *et al.* 2013).

Model Evaluation:

Model evaluation in SDM has focused on quantifying prediction accuracy as a measure of model performance or validity, such that it is known that the model has produced empirically correct predictions to a degree of accuracy that is acceptable for the models proposed application (Franklin 2009). The primary aim of this study is to assess the accuracy of SDMs projected to 2010 which are fit on 1990 environmental data and then coupled with the dispersal models. As such, the training data consists of every 1990 atlas observation, and the testing data consists of every 2010 atlas observation.

Beforehand though, it was important to evaluate the species-environment relationship fit between the 1990 atlas data and the 1990 environmental data, as without model evaluation, any judgement of the performance of the dispersal models when coupled with the 2010 statistical model cannot be excluded from the possibility of poor model fit in general. Our final SDMs were built with every observation; however, we did explore alternative strategies (e.g. partitioning the data into 80% training and 20% testing, Fielding and Bell 1997) and found that the accuracy was equally high if we used independent test data, or resubstituted test data (data not shown). The species used in this study were deemed to have sufficiently high accuracy scores for data trained and tested on the 1990 observations (e.g. sensitivity of 0.7 or higher).

Similarly, it is important to assess the performance of the 2010 base models, which are also the models of unlimited dispersal. As unlimited dispersal is the most optimistic scenario, any dispersal models coupled with this prediction will either result in the same

number of predicted presences or fewer. If the base model contains only a few presences, then the dispersal models will fail to restrain the projections and the results will suggest that the models have little impact on the results when in fact this would be based on a poorly specified statistical model. Finally, we want to evaluate the performance of the 2010 statistical models coupled with all the of the dispersal models. All three stages can be evaluated using threshold-dependent accuracy metrics, while threshold-independent metrics will also be used to assess the 1990 and 2010 base models.

The conversion of the probability surface into a binary (presence/absence) product allows the model to be evaluated by a two-by-two contingency table which cross-tabulates true and false positives (presences) and true and false negatives (absences) (Franklin 2009). Table 2 identifies the five threshold-dependent metrics used to evaluate our models. Threshold-independent metrics have also been used in recent studies due to the potential uncertainty and subjectivity related to the selection of thresholds (see Liu *et al.* 2005 for a discussion). The receiver operating characteristic (ROC) plot, the most commonly used threshold-independent metric, is a graph of the false-positive error rate on the x-axis plotted against the true positive rate on the y-axis, with the area under the curve (AUC) calculated by summing the area under the ROC curve. However, as the process of coupling the abiotic suitability models with the dispersal models requires the use of a presence/absence product, AUC can only be used to evaluate the original 1990 SDM and the 2010 SDM with unlimited dispersal.

Quantification of uncertainty:

In order to effectively interpret the uncertainty associated with the 20 dispersal models, we developed an Ensemble Agreement Index (EAI) which ranks full agreement across every observation as 1, and no agreement across every observation as 0:

$$EAI = \frac{\left(\frac{E-\min(E)}{\max(E)-\min(E)}\right)}{N} \quad (4.0)$$

where N is the total number of presence observations in the output, and E is defined as:

$$E = \left(\sum \frac{\mathrm{e}}{m}\right) \quad (5.0)$$

where *e* is the ensemble score for one presence observation, defined as the number of coupled statistical and dispersal models that predicted occupancy at a particular location, and *m* is the total number of dispersal models used to generate the ensemble. The use of descriptive statistics can be used with categorical variables in order quantify the shape of the distribution of outcomes and be used as a measure of confidence to assess the index (Hill *et al.* 2005). A measure of kurtosis was calculated alongside the Ensemble Agreement Index, with a leptokurtic distribution suggesting a peaked distribution (or high agreement among dispersal models), and a platykurtic distribution suggesting a flat distribution (or low agreement among dispersal models). A kurtosis value twice the standard error was considered significantly different from a normal distribution, and recorded as such.

Results

Table 3 shows the mean and standard deviation of the accuracy scores for the three statistical methods fit on the 1990 environmental data and projected using the 2010 environmental data, with the assumption of unlimited dispersal across the 50 species. No single statistical method reported consistently higher accuracy metrics when averaged across the 50 species. We found that GLM and RF reported high accuracy scores for the 2010 model for the more widespread species in 1990; however these methods seriously under-predicted the 2010 distributions for many of the species with sparser ranges in 1990 (data not shown). While under-prediction did occur for MaxEnt, it was only an issue for a few species, as is evident by the higher average

sensitivity score (Table 3).

This is further supported by Figure 3, which illustrates the range of sensitivity scores for the 20 dispersal models and the three statistical methods for the 50 species (separated based on UK breeding status). Boxplots are ordered so that XD is no dispersal (or worst case scenario) and UD is unlimited dispersal (or best case scenario), with intermediate conceptualizations of dispersal in between. (n.b. the six iterations of the discrete dispersal kernel are consolidated under DK, as there were no visible differences in sensitivity scores, but that these methods are treated separately for statistical analysis).

The largest variability in sensitivity scores occurs for the MaxEnt models, then to a lesser extent GLM, but there is minimal variation in the RF models. The largest difference in accuracy measures occurs for the MaxEnt models of the introduced breeders. The two most extreme dispersal models (XD and UD) bound the other methods, which vary quite substantially in their sensitivity scores. The two limited dispersal models (L1 and L2) result in higher sensitivity than many of the dispersal models with parameterized constraints. We also observe differences in the overall sensitivity score for the probabilistic dispersal kernels (PK) for birds with different breeding statuses.

No dispersal model recorded the highest accuracy for all 50 species and five accuracy metrics (Figure 4). No dispersal (XD) achieved the most 'successes', obtaining the highest accuracy scores in 113 scenarios. In part this is because XD recorded the highest specificity for all 50 species, with only PK1 recording an equal specificity score for the great skua (*Stercorarius skua*). While XD resulted in the highest number of accuracy metrics, it achieved the fewest highest sensitivity scores. Several dispersal models recorded the highest sensitivity score for all 50 species (UD, PK3, DK1, DK3, DK5, DK6), and this was the most variable accuracy metric among dispersal models.

In addition to differences in accuracy, these methods also resulted in quite variable areal extents of predicted presence. Table 4 shows a pairwise comparison of the performance of the different dispersal models when coupled with MaxEnt, which shows the difference in area (km^2) predicted present among each of the 20 dispersal models averaged across the 50 species. Whether this areal change was also accompanied by a significant change in the true skill statistic (TSS) is also highlighted. TSS was chosen as the accuracy metric, as it rewards both prediction for correctly predicted presences and absences. Paired sampled t-tests were used to identify significant differences in accuracy among the methods ($\alpha < 0.05$). The use of no dispersal (XD) resulted in a decrease in predicted area compared to every other method, as well as a significant decrease in TSS compared to all the other methods, with the difference in area varying between values of 29,708km^2 for FR4 and 36,640km^2 for UD. Unlimited dispersal (UD) differed in TSS when compared to only six methods, including four of the probabilistic dispersal kernels, however, the limited dispersal models (L1 and L2) and one step fixed rate dispersal models (FR1 and FR2) did not differ significantly.

Differences in performance of methods using geometric and arithmetic means were minimal, suggesting that the restriction of the geometric average did not constrain the models as expected. However, the one-step fixed rate methods (FR1 and FR2) resulted in an increase in accuracy compared to the geometric two-step method (FR4), but not the arithmetic two-step method (FR3). There were no significant differences between the different iterations of the discrete dispersal kernels. The two discrete kernels with Cauchy PDFs (DK5 and DK6) and the inverse exponential using arithmetic values (DK3) were the only methods which did not result in any change in predicted area compared to each other or unlimited dispersal (UD) for all 50 species.

Figure 5 shows the ensemble maps for nine species varying in breeding status and model uncertainty. The ensemble scores for the three medium uncertainty species (Figures

4(a-c)) and the three introduced species (Figures 4(d-f)) all identify a core area of low uncertainty (approximate score of 16-20), but then as distance from this core increases, the ensemble score decreases. Likewise, the more fragmented a predicted distribution, the greater variability and uncertainty of accessibility increases.

Table 5 presents the Ensemble Agreement Index (EAI) developed in order to quantify the uncertainty related to the dispersal models for all 50 species. The EAI score ranges from 0 (high uncertainty, low agreement) to 1 (low uncertainty, high agreement). When all 20 dispersal models are incorporated in the EAI, the scores range from 0.740 for the Dartford warbler (a resident breeder) to 0.999 for the Blackcap (a migrant breeder). Several species have EAI scores over 0.990, suggesting a very high number of observations with full agreement. When the six discrete kernel methods were removed, the species with medium to low uncertainty dropped to medium uncertainty (e.g. Dartford warbler and wood duck). However, this did not alter the EAI scores of the low uncertainty species (e.g. blackcap and green woodpecker), showing that this method proves robust in identifying low uncertainty among methods.

The use of kurtosis added confidence to the EAI as it illustrated whether all the observations were in one category or spread across several. Many of the species have leptokurtic distributions and are accompanied by a high EAI (Table 5), suggesting that there is high agreement among all of the methods. Some species (Cetti's warbler, firecrest) have a relatively low EAI score, but leptokurtic dispersion. This suggests that many of the methods do in fact agree, but the distribution of observations is most likely grouped into two peaks, one containing the expansive methods of dispersal, and another containing the more restrictive methods. Platykurtic dispersion suggests a flatter than usual distribution, and these are found for the more sparse species (e.g. Dartford warbler) and a surprisingly large number of raptors (e.g. osprey, goshawk, and hobby).

Discussion

The aim of this study was to explore how incorporating concepts of dispersal in SDM affects the accuracy and uncertainty of projected distributions. As it is impossible to assess accuracy of future projections, we assessed the accuracy of models calibrated with past data and projected to the current time period in an attempt to simulate many of the issues such as interactions, feedbacks, and novel climates that are problematic in modelling future species' distributions. Due to these added uncertainties, our expectations of accuracy were lower than they would have been for other modelling scenarios (e.g. modelling distributions in current time), and we did observe this difference in our results, recording higher accuracies for the SDMs fit and projected in 1990 (t_1) than compared to 2010 (t_2). However, this result is not uncommon (Araújo *et al.* 2005; Veloz *et al.* 2012), and moreover, perfect validation of SDMs fit in future time could be conceptually impossible due to the added uncertainties and the fact that the modelled system is not closed (Araújo *et al.* 2005). However, as species and environmental data collection and management are improving dramatically, we are now beginning to have available data at a relevant temporal extent needed to conduct more rigorous validation of this type of study. Therefore, this research should foster subsequent studies which explicitly address both the uncertainty and accuracy associated with methods of simulating dispersal alongside species' future distributions.

The selection of a statistical method was one of the most variable aspects of this research. The difference in outputs derived from the statistical methods used has long been noted as being important (Guisan and Zimmermann 2000), and several studies have identified the uncertainty in the results of different statistical methods (Reese *et al.* 2005, Graham *et al.* 2008, Elith and Graham 2009). MaxEnt better predicts the fundamental distribution of a species (Gi) than the actual distribution (Go) (Figure 1), due to the fact that the algorithm uses presence-only data. GLM and RF incorporate absence data, and often constrain their

predictions accordingly, meaning MaxEnt was the most likely statistical method to over-predict the distribution (as it essentially models Gi). Subsequently, under-prediction of the distribution was an issue with GLM and in particular RF, and was the primary reason the accuracy metrics did not change when the 20 dispersal models were coupled with RF and to a lesser extent GLM (Figure 3). This was because results were based on coupling a restrictive model of dispersal with an already under-predicted distribution. When this occurred, geographically widespread species remained relatively widespread, while the accuracy for under-predicted species couldn't be improved as the new suitable locations were either similar or exactly the same as the previous locations. This issue highlights the importance of testing several statistical models, as if we used only GLM or RF in this analysis, the results would suggest that differences in dispersal models were minimal, whereas when we coupled the dispersal models with MaxEnt, our results varied greatly and we had a number of significant differences.

When the dispersal models were compared with each other (Figure 3, Table 4), in general, the more restrictive methods decreased accuracy when measured as sensitivity and TSS, as the unrealistic lack of accessibility impacted the accuracy. TSS was higher for the one-step fixed rate methods (FR1 and FR2) compared with the two-step methods (FR3 and FR4), and the probabilistic kernels with the inverse exponential PDF (PK3 and PK4) also had higher TSS and sensitivity scores compared with the other PDFs (PK1, PK2, PK5, and PK6). Surprisingly, in many instances, the limited dispersal models (L1 and L2) did not have a significantly lower accuracy than many of the other parameterized constraints (Figure 3, Table 4). These methods only penalize fragmentation in the distribution, so as long as the predicted future distribution is continuous, this method assumes that the species can reach these locations. With the SDMs generated at a 10km resolution, much of the species' distributions are connected. If these dispersal models were implemented at a finer resolution,

then they would most likely have much lower sensitivity and TSS scores, as any gap in the distribution (e.g. urban area or slight change in habitat) could heavily fragment the factors that define the suitable habitat. In these instances, the choice of connectivity (rook's or Queen's) may have an important role in determining future distributions. Some differences between rook's and Queen's cases of connectivity were found in this study, particularly in the southwest of Great Britain, where islands are only connected to the mainland if Queen's case of connectivity was considered. However, with only 3 islands connected to the mainland in this manner, any change in accuracy was minimal. Subsequently, in this study, due to the spatial resolution, limited dispersal models often reported similar accuracies to unlimited dispersal, however these results are unlikely to replicate at finer resolutions and across larger extents.

The variation in area predicted present was notable. For almost every method, some difference in area was observed, and while these differences were not always significant when averaged across all 50 species, small variations in area for a specific species could have large implications on any conservation strategies for individual species. Only three methods did not vary in area predicted present by unlimited dispersal. These were three of the discrete dispersal kernels with fat-tail PDFs (DK3, DK5 and DK6). The discrete kernels are a combination of a dispersal kernel and the fixed rate method, with the maximum value drawn from a PDF used as the fixed rate of dispersal. With the fat-tailed kernels (inverse exponential and Cauchy), a value greater than the length of the country was often generated due to the relatively large number of iterations, regardless as to whether the other 99% of dispersal distances drawn from the PDF were within a 10km radius. Subsequently, every suitable location between the maximum value was considered equal (something which is most likely not realistic of long distance dispersal events). The fact that no differences with unlimited dispersal were found for the inverse exponential and Cauchy PDFs, along with the

expensive computing time and resources needed to generate these models, implies that the use of this method may be redundant (particularly for birds which are capable of travelling extensive distances). This method has been used in plant studies across much larger spatial and temporal timescales (Clark *et al.* 2001, Cunze *et al.* 2013), so future research should focus on if differences between the implementations of discrete dispersal kernels and unlimited dispersal exist for different taxa and spatio-temporal scales.

In contrast, the probabilistic kernels often resulted in less predicted area to unlimited dispersal and significantly lower TSS scores for the Gaussian and Cauchy PDFs. However, the probabilistic kernels with inverse exponential PDFs varied in area predicted present compared to unlimited dispersal, but did not differ significantly in accuracy, suggesting that this may be a more realistic method of simulating dispersal for birds compared to the discrete kernel implementation as long distance dispersal events are controlled by probabilities. In contrast to the discrete kernels, almost all of the comparisons among the probabilistic kernels resulted in a significant change in accuracy and in predicted area. The choice of PDF (and in particular the presence or absence of a fat-tail) when using a probabilistic kernel can substantially impact the accuracy of the final model. More resources should be expended for the collection of empirical data to fit a dispersal kernel, so that the choice of PDF (and any uncertainty in the user decisions) is negated. However, if empirical data collection is not an option, effort should be directed to identifying a general framework for PDF generation (e.g., see Vittoz and Engler 2007 for a detailed discussion on the creation of dispersal kernels for European flora).

From the comparison, no dispersal (XD) appeared to outperform the other dispersal models in terms of achieving the highest accuracy scores (Figure 4), and this was consistent across all the accuracy metrics except for sensitivity. This was due to XD's ability to correctly predict absences, recording the highest specificity for all 50 species, as well as the

highest Kappa, TSS and PCC scores for the same reasons (Figure 4). However, the ability to correctly predict absences may not be as important when projecting the distribution of rare species, as a disproportionately high number of absences can exert too much influence in the metrics that consider both (Araújo et al. 2005). This issue is particularly pertinent when the test dataset used to validate the SDMs is representative of every observation across the entire study area, meaning that for sparse species, the accuracy metrics would effectively favour correctly predicting absences. This explains why XD scored so highly across many of the accuracy metrics, and why there were relatively lower Kappa and TSS scores for MaxEnt compared to GLM and RF (Table 3).

The rationale behind ensemble modelling in SDM is that by calculating the ensemble score, the 'signal' that one is concerned with emerges from the 'noise' associated with individual model errors and uncertainties (Araújo and New 2007). A lot of the current work with ensemble models in SDM is 'pre-thresholding', whereby suitability indices are averaged across various models and these values are used in the generation of presence/absence models (Thuiller *et al.* 2013, Barbet-Massin *et al.* 2012). For many scenarios, this type of ensemble forecast is desirable; however, many of the dispersal models used in this study require a binary presence/absence output from the statistical model in their input, and produce only a binary output. Therefore, we developed the Ensemble Agreement Index (EAI) with which to analyse these ensemble models. This index ranks full agreement for every observation (i.e. an ensemble score of 20 out of 20 in every presence observation) as 1, and full disagreement for every observation (i.e. an ensemble score of 1 out of 20 in every presence observation) as 0. Each species is now associated with an EAI score, and researchers can discuss dispersal potential with a greater understanding of the uncertainty of how the dispersal models align with each other.

Many of the introduced species (e.g., wood duck, ring-necked parakeet) have a relatively lower EAI score than the native species (Table 5). In part, this is because these species tended to have smaller original distributions, and the fact that they are not in equilibrium with the environment in 1990 due to their recent establishment. Therefore, the potential area with which they can disperse is greater than those native to the country and subsequently already occupying their niche. Raptors such as the hobby, osprey and goshawk all have platykurtic dispersion of EAI scores, suggesting that their dispersal capability varied. Similar to the introduced species, these species were most likely not in equilibrium with their environment in 1990 due to persecution (e.g. Marquiss *et al.* 2003), and so their predicted distribution is more fragmented, causing the slight differences in dispersal models to be exaggerated, particularly differences between the restrictive and expansive methods. For example, the areal difference between limited dispersal with rook's connectivity (L1) and Queen's connectivity (L2) for the osprey was 3,800km^2, which was 1,000km^2 greater than the average of all 50 species (Table 4).

There are no really low EAI scores for any of the 50 birds. In part this could be due to a relatively low uncertainty surrounding these methods, although more likely this is due to the inclusion of very similarly defined methods and possibly inflated ensemble scores (e.g., the six discrete dispersal kernel methods). When the six discrete kernel values were removed, we observed lower scores for the species with moderate uncertainty (e.g. wood duck), whereas the species with low uncertainty (e.g. blackcap) did not change. Likewise, the inclusion of unlimited dispersal at this spatial extent almost negates the opportunity for an EAI score of 0, as it is relatively unlikely that no other dispersal method will predict all the observations as absent. In practice, research will not compare as many different dispersal models with slight differences in implementation as we did in this extensive study.

It should be noted that low uncertainty measured by the EAI does not mean that the future projections have a high accuracy. For example, Figure 3 shows high agreement among the 20 dispersal models when coupled with RF, but the accuracy is substantially lower than GLM or MaxEnt. However, for projections into the future (e.g. 2100) researchers will have to evaluate the uncertainty of their projections because there is no test data with which to validate. In these instances, agreement among dispersal models and other decisions in the SDM framework (e.g. statistical models) should be considered within the EAI, so that a better understanding of the output is achieved. Therefore, when generating ensemble models, different methods of implementing dispersal (or any other user-defined aspect which can be ensembled) should be selected carefully and specifically, rather than simply inputting every possible implementation.

The coarse resolution at which the land cover is generated (1km) compared to the resolution at which actual bird movements occur was insufficient to generate meaningful comparisons if we used landscape derived metrics. Similarly, demographic models are very rare in SDM studies due to the paucity of comparable abundance data, and subsequently have only been applied in a few studies (e.g. Midgley *et al.* 2010). As such, it was not practical to include these conceptualizations of dispersal in the analysis. However, for many terrestrial animals and plants, these notions of movement may be more suitable, and more research should be conducted to see how incorporating these methods alongside SDM impacts results.

The variation in accuracy among dispersal models suggests that the choice of dispersal model should therefore reflect the underlying purpose of the research being conducted. No dispersal (which performs well for specificity) would therefore be recommended for studies trying to identify future suitable habitat for species which have low dispersal capabilities (e.g. reptiles), or for studies aiming to find definitive locations of future abiotic suitability (without introducing the uncertainty of dispersal). While many dispersal

methods scored high sensitivity (Figure 4), if the aim of the research is to find the potential future distribution of a species, then unlimited dispersal (UD) should be used due to its conceptual underpinnings and ability to identify every suitable location in the study area. We found the use of a probabilistic dispersal kernel and limited dispersal with rook's connectivity (L1) resulted in higher TSS for five of the seven non-native species. These dispersal models also recorded sensitivity scores equal to or fractionally lower (<0.1 difference) than unlimited dispersal. From this, we can infer that the statistical models for invasive species are projecting inaccessible abiotically suitable areas, and that a dispersal model that removes or controls the possibility of long distance dispersal eliminates these false positives, and improves the accuracy of metrics such as TSS. Therefore, the use of a probabilistic dispersal kernel or limited dispersal model should be used when studying invasive spread under changing climates. The use of a probabilistic dispersal kernel with an inverse exponential PDF (PK3 and PK4) resulted in slightly smaller areal extents predicted as present compared to UD and DK implementations, but no significant changes in accuracy (Table 4). By controlling for long distance dispersal events through probabilities, rather than the assumption that every observation between the minimum and maximum dispersal distances is equally accessible (as UD and DK implementations do), the probabilistic dispersal kernel is perhaps the most accurate representation to how birds disperse with their projections resulting in equally high accuracies.

Conclusion

The use of the 'BAM' framework within the SDM discipline to identify the factors that drive the geographic distributions of species is becoming increasingly popular. Within this framework, movement factors that refer to the processes that lead to an area being accessible (e.g., via dispersal or migration) are an important yet understudied component. The importance of incorporating dispersal alongside SDMs projecting into the future cannot be

overstated, as the results of SDMs which ignore dispersal are subject to high levels of uncertainty. This is the first study that has extensively compared the accuracy and uncertainty of the methods of incorporating dispersal in SDM, and as such should serve as a foundation for studies projecting into future climates. Alongside the dispersal models, we also compared the statistical methods, evaluated the projected 2010 distributions using multiple accuracy metrics, deconstructed species indices by species traits and reported both the accuracy and uncertainty of the models. Many of the methods of dispersal differed greatly in terms of their accuracy, particularly between the restrictive and the expansive methods, while other methods of dispersal did not differ (e.g. discrete kernels and unlimited dispersal). The use of no dispersal yielded significantly lower accuracy (TSS) when averaged across the 50 species and compared to every other method of dispersal, while conversely also recording the highest scores for the accuracy metrics which favour correct prediction of absences. Subsequently XD should only be used if the researcher has a valid reason to do so, and even then other simulations of dispersal should be incorporated alongside this. The development of the Ensemble Agreement Index allowed for the quantification of uncertainty among the different dispersal models, but will also provide researchers with a quantitative tool to assess the variations between their inputs for other areas of uncertainty in SDM (e.g. use of statistical method, threshold classification) or any environmental or geographic research where the main output can be binary (e.g. flood risk, urban growth). For the first time in SDM research, we have been able to compare these dispersal models based on how well they predict future geographic distributions. Not only has this research provided practitioners with a product with which to select a dispersal model to use, saving their time, resources and research efforts, it has also resulted in a better understanding of the effects of both the accuracy and uncertainty on projected distributions, extinction rates and dispersal patterns.

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Table 1. The 20 dispersal models used in this study and their reference code.

Method	**Code**
No dispersal	XD
Limited dispersal (rook's)	L1
Limited dispersal (Queen's)	L2
Fixed rate 1 step (arithmetic mean)	FR1
Fixed rate 1 step (geometric mean)	FR2
Fixed rate 2 steps (arithmetic mean)	FR3
Fixed rate 2 steps (geometric mean)	FR4
Discrete dispersal kernel (Gaussian arithmetic)	DK1
Discrete dispersal kernel (Gaussian geometric)	DK2
Discrete dispersal kernel (inverse exponential arithmetic)	DK3
Discrete dispersal kernel (inverse exponential geometric)	DK4
Discrete dispersal kernel (Cauchy arithmetic)	DK5
Discrete dispersal kernel (Cauchy geometric)	DK6
Probabilistic dispersal kernel (Gaussian arithmetic)	PK1
Probabilistic dispersal kernel (Gaussian geometric)	PK2
Probabilistic dispersal kernel (inverse exponential arithmetic)	PK3
Probabilistic dispersal kernel (inverse exponential geometric)	PK4
Probabilistic dispersal kernel (Cauchy arithmetic)	PK5
Probabilistic dispersal kernel (Cauchy geometric)	PK6
Unlimited dispersal	UD

Table 2. Threshold-dependent accuracy measures for species presence/absence models. TP = True Positive, TN = True Negative, FP = False Positive, FN = False Negative

Metric	Equation
Sensitivity	TP / (TP + FN)
Specificity	TN / (TN + FP)
Proportion Correctly Classified (PCC)	(TP + TN) / n
True Skill Statistic (TSS)	(Sensitivity + Specificity) - 1
Kappa	$\frac{[(\mathrm{TP}+\mathrm{TN})-(\frac{\left((\mathrm{TP}+\mathrm{FN})(\mathrm{TP}+\mathrm{FP})+(\mathrm{FP}+\mathrm{TN})(\mathrm{FN}+\mathrm{TN})\right)}{\mathrm{n}})]}{[n-\left(\frac{(\mathrm{TP}+\mathrm{FN})(\mathrm{TP}+\mathrm{FP})+(\mathrm{FP}+\mathrm{TN})(\mathrm{FN}+\mathrm{TN})}{\mathrm{n}}\right)]}$

Table 3. Mean and standard deviation (SD) of accuracy metric scores for the three statistical methods fitted on the 1990 environmental data and projected using the 2010 environmental data, with the assumption of unlimited migration across the 50 species. Abbreviations stand for Proportion Correctly Predicted (PPC), True Skill Statistic (TSS) and Area Under the Curve (AUC).

	Sensitivity	**Specificity**	**PPC**	**Kappa**	**TSS**	**AUC**
	Mean (SD)	**Mean (SD)**	**Mean (SD)**	**Mean (SD)**	**Mean (SD)**	**Mean (SD)**
GLM	0.532 (0.209)	0.855 (0.108)	0.738 (0.121)	0.325 (0.180)	0.386 (0.180)	0.693 (0.090)
MaxEnt	0.601 (0.208)	0.828 (0.137)	0.732 (0.115)	0.343 (0.168)	0.286 (0.168)	0.714 (0.084)
RF	0.563 (0.251)	0.857 (0.142)	0.803 (0.101)	0.403 (0.185)	0.420 (0.197)	0.710 (0.098)

Table 4. Pairwise comparison of the performance of the 20 migration methods. The value represents the average change in area (km^2) predicted present averaged for the 50 species between the method in the row compared to the method in the column. Green represents a significant increase in accuracy (True Skill Statistic – TSS) and red represents a significant decrease in accuracy (TSS) between the methods. Significance of $\alpha = 0.05$ calculated using a paired sample t-Test. XD is no dispersal, L is limited dispersal (1 = rook's, 2 = Queen's), FR is fixed rate (1 = 1 step arithmetic, 2 = 1 step geometric, 3 = 2 step arithmetic, 4 = 2 step geometric), DK is discrete kernel, PK is probabilistic kernel, UD is unlimited dispersal. For Kernels, 1 = Gaussian Probability Density Function (PDF) arithmetic, 2 = Gaussian PDF geometric, 3 = inverse exponential PDF arithmetic, 4 = inverse exponential PDF geometric, 5 = Cauchy PDF arithmetic, 6 = Cauchy PDF geometric.

	XD	L1	L2	FR1	FR2	FR3	FR4	DK1	DK2	DK3	DK4	DK5	DK6	PK1	PK2	PK3	PK4	PK5	PK6	UD
XD																				
L1	31848																			
L2	34010	2162																		
FR1	36276	4428	2266																	
FR2	33588	1740	-422	-2688																
FR3	35616	3768	1606	-660	2028															
FR4	29708	-2140	-4302	-6568	-3880	-5908														
DK1	36382	4534	2372	106	2794	766	6674													
DK2	35698	3850	1688	-578	2110	82	5990	-684												
DK3	36640	4792	2630	364	3052	1024	6932	258	942											
DK4	36322	4474	2312	46	2734	706	6614	-60	624	-318										
DK5	36640	4792	2630	364	3052	1024	6932	258	942	0	318									
DK6	36640	4792	2630	364	3052	1024	6932	258	942	0	318	0								
PK1	30382	-1466	-3628	-5894	-3206	-5234	674	-6000	-5316	-6258	-5940	-6258	-6258							
PK2	31104	-744	-2906	-5172	-2484	-4512	1396	-5278	-4594	-5536	-5218	-5536	-5536	722						
PK3	36552	4704	2542	276	2964	936	6844	170	854	-88	230	-88	-88	6170	5448					
PK4	35316	3468	1306	-960	1728	-300	5608	-1066	-382	-1324	-1006	-1324	-1324	4934	4212	-1236				
PK5	31016	-832	-2994	-5260	-2572	-4600	1308	-5366	-4682	-5624	-5306	-5624	-5624	634	-88	-5536	-4300			
PK6	31452	-396	-2558	-4824	-2136	-4164	1744	-4930	-4246	-5188	-4870	-5188	-5188	1070	348	-5100	-3864	436		
UD	36640	4792	2630	364	3052	1024	6932	258	942	0	318	0	0	6258	5536	88	1324	5624	5188	

Table 5. Ensemble Agreement Index (EAI) scores for the 50 species. A value of 1 indicates all 20 methods made the same predictions for all locations. –lk represents a significant lepokurtic distribution. –pk represents a significant platykurtic distribution. A kurtosis value twice the standard error was considered significantly different from a normal distribution.

Species	EAI with Discrete Kernels	EAI without Discrete Kernels
Blackcap (*Sylvia atricapilla*)	0.999^{-lp}	0.998^{-lp}
Great Spotted Woodpecker (*Dendrocopos major*)	0.997^{-lp}	0.995^{-lp}
Grey Heron (*Ardea cinerea*)	0.996^{-lp}	0.993^{-lp}
Grey Wagtail (*Motacilla cinerea*)	0.993^{-lp}	0.990^{-lp}
Common Buzzard (*Buteo buteo*)	0.992^{-lp}	0.989^{-lp}
Oystercatcher (*Haematopus ostralegus*)	0.992^{-lp}	0.989^{-lp}
Red-legged Partridge (*Alectoris rufa*)	0.992^{-lp}	0.988^{-pk}
Canada Goose (*Branta canadensis*)	0.991^{-lp}	0.987^{-lp}
Green Woodpecker (*Picus viridis*)	0.990^{-lp}	0.986^{-lp}
Nuthatch (*Sitta europea*)	0.990^{-lp}	0.986^{-lp}
Raven (*Corvus corax*)	0.990^{-lp}	0.985^{-lp}
Kingfisher (*Alcedo atthis*)	0.988^{-lp}	0.982^{-lp}
Tree Sparrow (*Passer montanus*)	0.988^{-lp}	0.982^{-lp}
Sand Martin (*Riparia riparia*)	0.985^{-pk}	0.978^{-pk}
Herring Gull (*Larus argentatus*)	0.985^{-lp}	0.978^{-lp}
Lesser Black-backed Gull (*Larus fuscus*)	0.985^{-lp}	0.978^{-lp}
Siskin (*Spinus spinus*)	0.985^{-lp}	0.977^{-lp}
Barn Owl (*Tyto alba*)	0.982^{-lp}	0.973^{-lp}
Peregrine Falcon (*Falco peregrinus*)	0.982^{-lp}	0.973^{-lp}
Reed Warbler (*Acrocephalus scirpaceus*)	0.982^{-lp}	0.974^{-pk}
Common Eider (*Somateria mollissima*)	0.981^{-lp}	0.972^{-lp}
Goosander (*Mergus merganser*)	0.981^{-lp}	0.973^{-lp}
Stonechat (*Saxicola rubicola*)	0.979^{-lp}	0.970^{-lp}
Little Grebe (*Tachybaptus ruficollis*)	0.978^{-lp}	0.967^{-lp}
Shelduck (*Tadorna tadorna*)	0.977^{-lp}	0.967^{-lp}
Quail (*Coturnis coturnix*)	0.974^{-lp}	0.962^{-lp}
Cormorant (*Phalacrocora carbo*)	0.973^{-lp}	0.961^{-lp}
Grasshopper Warbler (*Locustella naevia*)	0.971^{-lp}	0.958^{-lp}
Common Tern (*Sterna hirunda*)	0.970^{-lp}	0.955^{-lp}
Greylag Goose (*Anser anser*)	0.966^{-lp}	0.951^{-lp}
Long-eared Owl (*Asio otus*)	0.951^{-lp}	0.928^{-lp}
Hobby (*Falco subbuteo*)	0.950^{-pk}	0.926^{-pk}
Water Rail (*Rallus aquaticus*)	0.946^{-lp}	0.921^{-lp}
Gadwall (*Anas strepera*)	0.944^{-lp}	0.917^{-pk}
Mandarin Duck (*Aix galericulata*)	0.938^{-lp}	0.910^{-lp}
Goshawk (*Accipter gentilis*)	0.937^{-lp}	0.909^{-pk}
Wigeon (*Anas penolope*)	0.935^{-lp}	0.905^{-lp}
Little Ringed Plover (*Charadrius dubius*)	0.927^{-lp}	0.894^{-lp}
Nightjar (*Caprimulgus europaeus*)	0.917^{-lp}	0.879^{-lp}
Great Skua (*Stercorarius skua*)	0.895^{-pk}	0.847^{-pk}
Garganey (*Anas querquedula*)	0.879^{-pk}	0.823^{-pk}

Egyptian Goose (*Alopochen aegyptiaca*)	0.856^{-lp}	0.793
Osprey (*Pandion haliaetus*)	0.825^{-pk}	0.744^{-pk}
Cetti's Warbler (*Cettia cetti*)	0.802^{-lp}	0.715^{-lp}
Firecrest (*Regulus ignicapilla*)	0.788^{-lp}	0.719
Ring-necked Parakeet (*Psittacula krameri*)	0.784	0.691^{-pk}
Barnacle Goose (*Branta leucopsis*)	0.782^{-lp}	0.689^{-lp}
Woodlark (*Lullula arborea*)	0.775^{-pk}	0.676^{-pk}
Wood Duck (*Aix sponsa*)	0.769^{-lp}	0.675^{-pk}
Dartford Warbler (*Sylvia undata*)	0.740^{-pk}	0.634^{-pk}

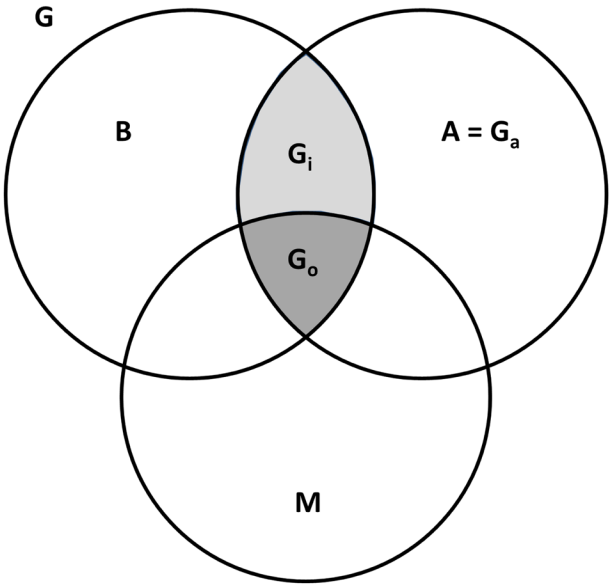
Figure 1. The 'BAM' diagram, which depicts the interaction between biotic (B), abiotic (A), and movement (M) factors. Four areas are represented: G, the geographical space within which the analyses are developed, Ga, the abiotically suitable area, Go, the occupied distributional area, and Gi, the invadable distribution (if movement limitation is reduced). Modified from Soberón (2007).

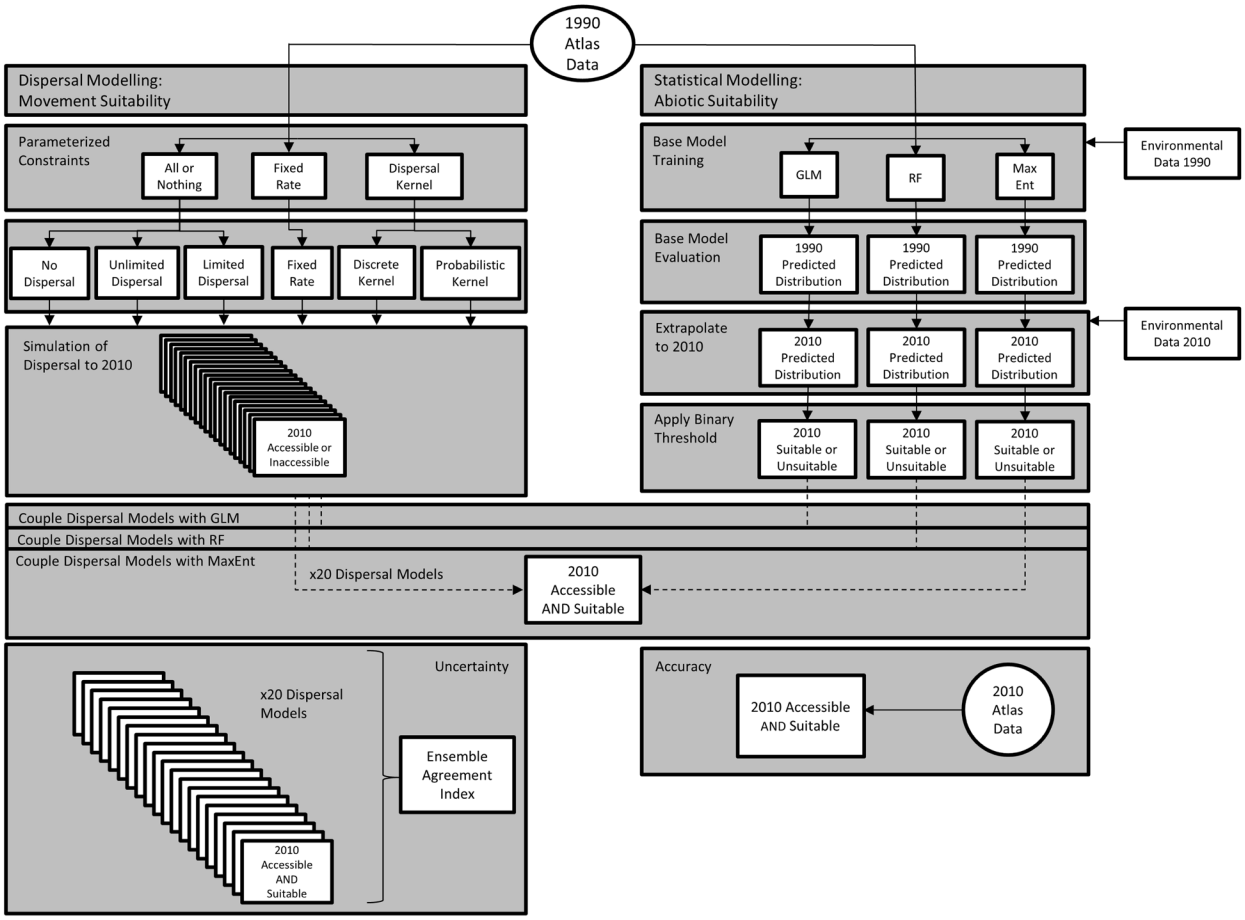
Figure 2. Conceptual diagram of workflow.

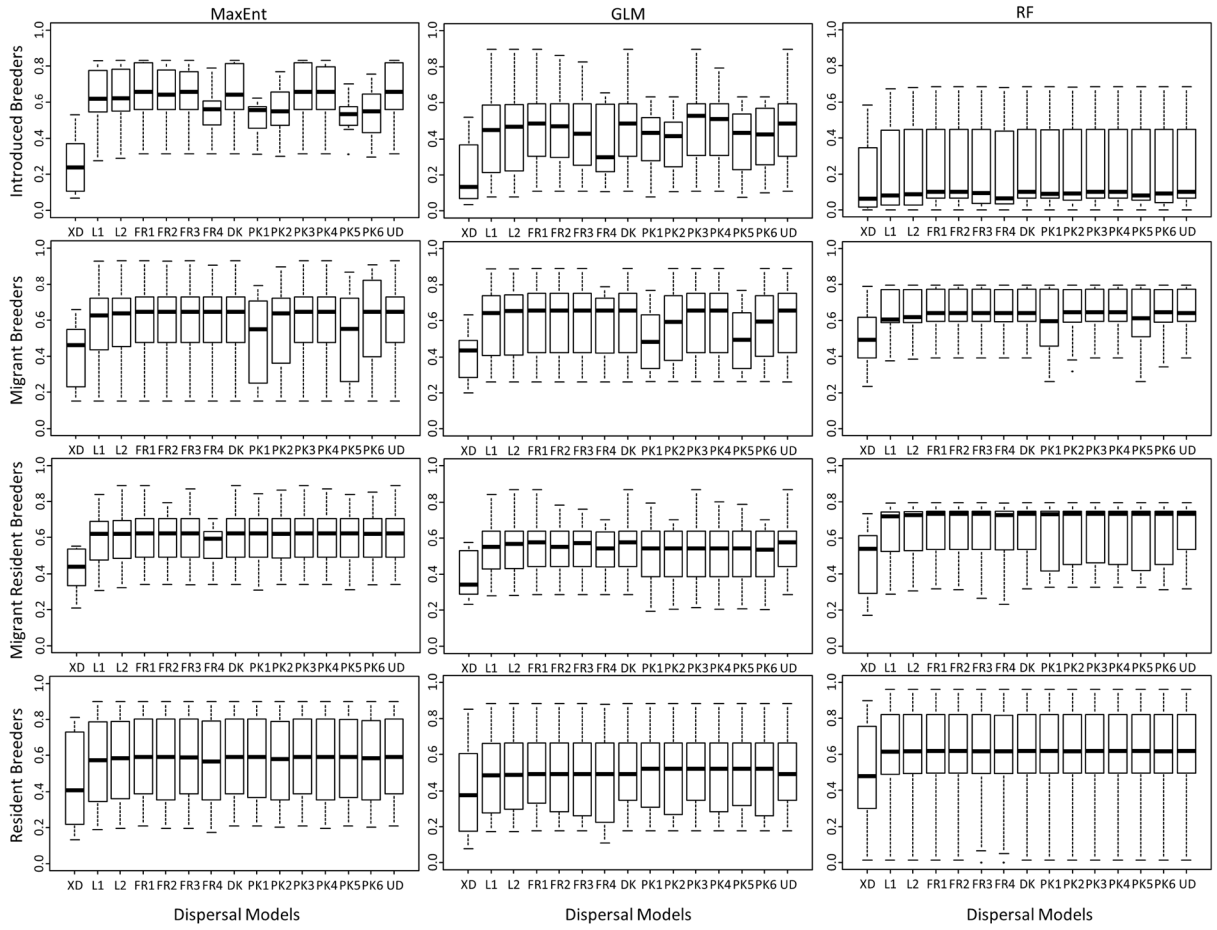
Figure 3. Sensitivity scores for the 20 dispersal models for the three statistical methods and four breeding groups. XD is no dispersal, L is limited dispersal (1 = rook's, 2 = Queen's), FR is fixed rate (1 = 1 step arithmetic, 2 = 1 step geometric, 3 = 2 step arithmetic, 4 = 2 step geometric), DK is discrete kernel, PK is probabilistic kernel, UD is unlimited dispersal. For Kernels, 1 = Gaussian PDF arithmetic, 2 = Gaussian PDF geometric, 3 = inverse exponential PDF arithmetic, 4 = inverse exponential PDF geometric, 5 = Cauchy PDF arithmetic, 6 = Cauchy PDF geometric (n.b. DK1 to DK6 are consolidated under DK due to no visible variation).

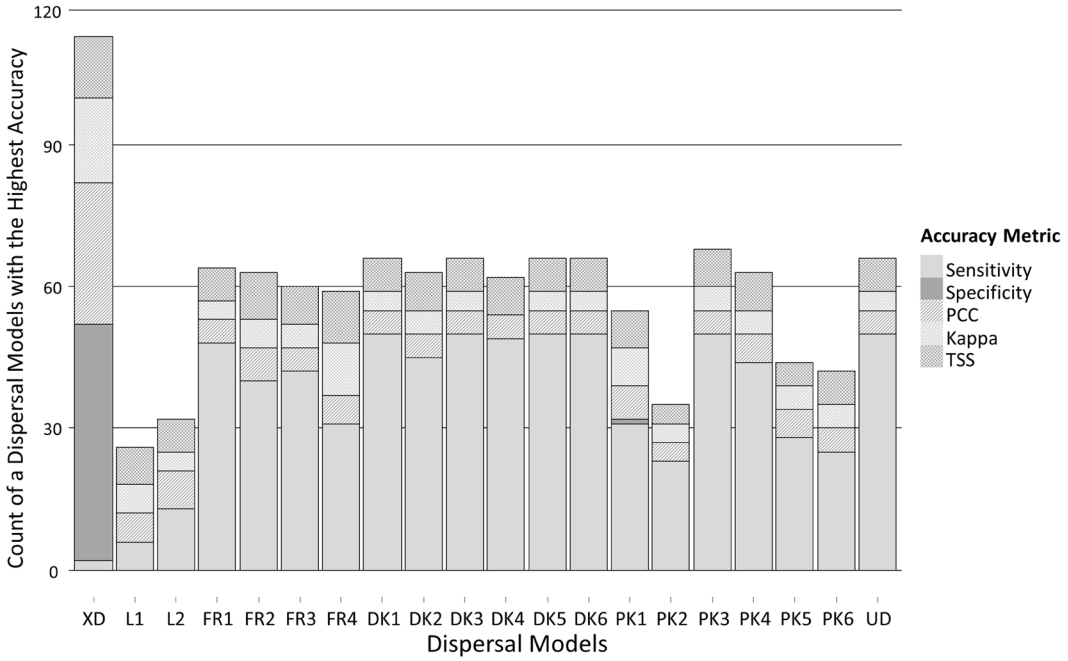
Figure 4. Number of times each dispersal model recorded the highest value for a particular accuracy metric for each individual species. Across the 50 species and five accuracy metrics, the highest possible value could have been 250.

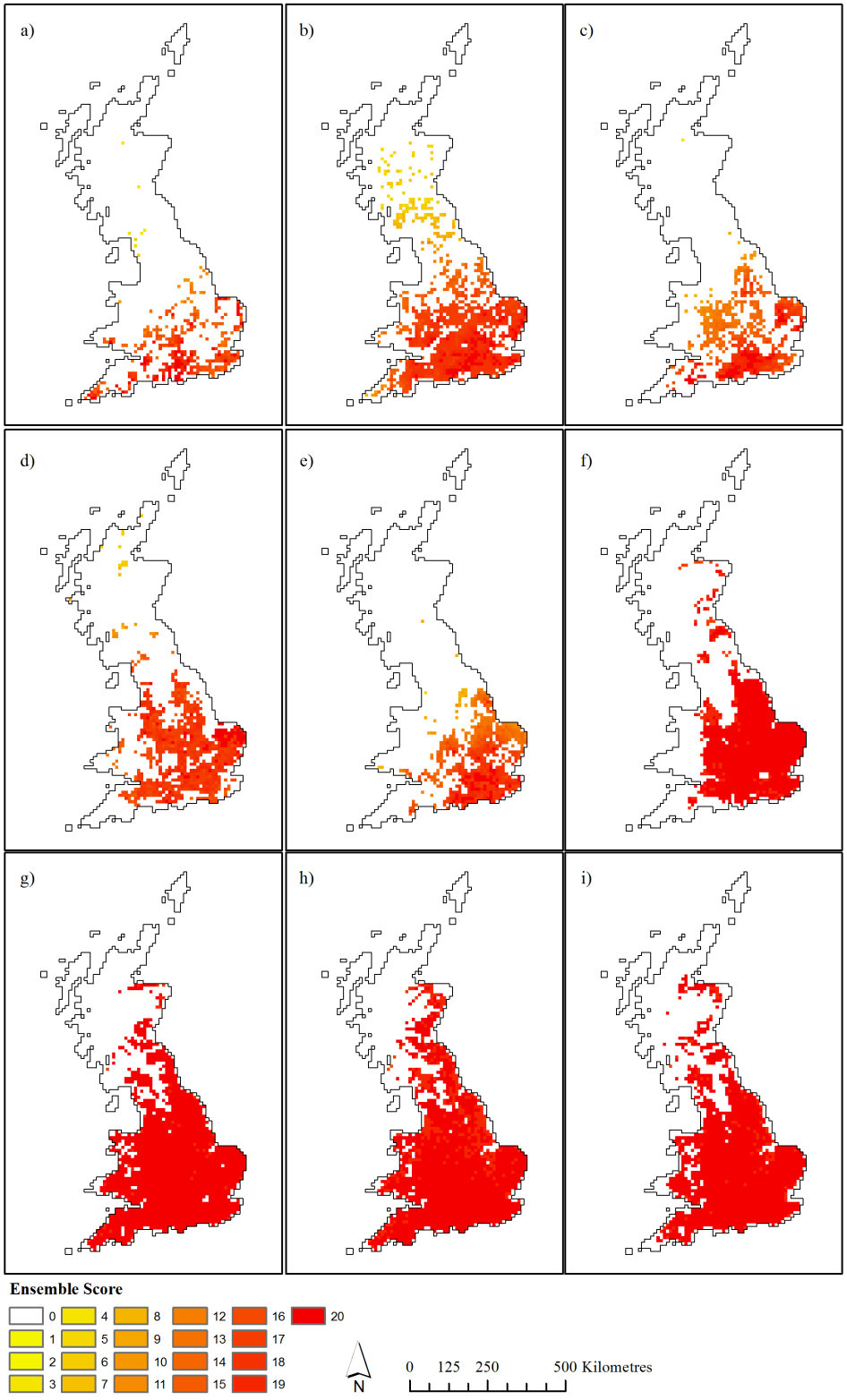
Figure 5. Ensemble maps of predicted presence based on environmental suitability (using MaxEnt) and the 20 dispersal models for 2010 for a–c) three species with high uncertainty (Cetti's Warbler, Firecrest, Woodlark), d–f) three introduced species (Egyptian Goose, Ring-necked Parakeet, Red-legged Partridge) and g–i) three with high modelling certainty (Blackcap, Green Woodpecker, Great Spotted Woodpecker).


G
B
G_i
A = G_a
G_o
M


1990 Atlas Data
Dispersal Modelling: Movement Suitability
Parameterized Constraints
All or Nothing
Fixed Rate
Dispersal Kernel
No Dispersal
Unlimited Dispersal
Limited Dispersal
Fixed Rate
Discrete Kernel
Probabilistic Kernel
Simulation of Dispersal to 2010
2010 Accessible or Inaccessible
Statistical Modelling: Abiotic Suitability
Base Model Training
GLM
RF
Max Ent
Environmental Data 1990
Base Model Evaluation
1990 Predicted Distribution
1990 Predicted Distribution
1990 Predicted Distribution
Extrapolate to 2010
Environmental Data 2010
2010 Predicted Distribution
2010 Predicted Distribution
2010 Predicted Distribution
Apply Binary Threshold
2010 Suitable or Unsuitable
2010 Suitable or Unsuitable
2010 Suitable or Unsuitable
Couple Dispersal Models with GLM
Couple Dispersal Models with RF
Couple Dispersal Models with MaxEnt
x20 Dispersal Models
2010 Accessible AND Suitable
Uncertainty
x20 Dispersal Models
Ensemble Agreement Index
2010 Accessible AND Suitable
Accuracy
2010 Accessible AND Suitable
2010 Atlas Data


MaxEnt
GLM
RF
Introduced Breeders
Migrant Breeders
Migrant Resident Breeders
Resident Breeders
XD L1 L2 FR1 FR2 FR3 FR4 DK PK1 PK2 PK3 PK4 PK5 PK6 UD
Dispersal Models


Count of a Dispersal Models with the Highest Accuracy
120
90
60
30
0
XD L1 L2 FR1 FR2 FR3 FR4 DK1 DK2 DK3 DK4 DK5 DK6 PK1 PK2 PK3 PK4 PK5 PK6 UD
Dispersal Models
Accuracy Metric
Sensitivity
Specificity
PCC
Kappa
TSS


a)
b)
c)
d)
e)
f)
g)
h)
i)
Ensemble Score
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
N
0 125 250 500 Kilometres