5

6   **Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species**

7

8   Chloe Bellamy, Christopher Scott & John Altringham

9   School of Biology, University of Leeds

10   bsccb@leeds.ac.uk   c.d.scott@leeds.ac.uk   j.d.altringham@leeds.ac.uk

11   Corresponding author:

12   John Altringham   j.d.altringham@leeds.ac.uk

13   School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT

14   Tel. +44 (0)113 343 2832

15

16   Running title: Multiscale habitat suitability modelling for bats

17   Word count: Total 7,000

18   Summary 363, main text 5,151, acknowledgements 120, references 1077, table and figure legends 289

19   The number of tables and figures: 6 figures

20   The number of references: 39

21

22

24   **Summary**

25   1. To manage anthropogenic environmental change for the benefit of biodiversity we must improve our

26   understanding of the complex relationships between organisms and their environment. We have

27   developed multiscale habitat suitability models (HSMs) for bats, a mobile group of mammals, for a

28   geographically varied region of the UK. We ask if the models have sufficient accuracy to contribute to

29   informed decision-making in habitat management and in minimizing the impact of climate change and

30   human infrastructural development.

31   2. We used acoustic surveys supplemented by catching to gather presence data for eight species from

32   30 sites across the south of the Lake District National Park in NW England. Species were identified by

33   manual and automated extraction and analysis of echolocation calls. Fine-resolution (50 and 100 m)

34   habitat maps were generated at twelve spatial scales by calculating the variables across squares of

35   increasing size, from 100–6000 m, around each focal 50 or 100 m square. Presence-only HSM software,

36   MaxEnt, was used to determine the predictive power of each habitat variable at each scale. Multiscale

37   models included data for each variable at the scale at which it had the strongest relationship with the

38   presence of each species.

39   3. The best multiscale models were selected using 5-fold cross-validation, with backwards, stepwise

40   variable removal, whilst minimising residual spatial autocorrelation and sampling bias. Further tests with

41   independent field data indicated good model transferability across the entire National Park.

42   4. Foraging bats were generally most strongly associated with variables measured at small spatial scales

43   and distance measures. However, each species responded differently across the range of scales, and

44   strong associations were also found at the largest scale of analysis (6000 m).

45   5. *Synthesis and applications*. The best models for determining habitat suitability had few variables,

46   making them easy to interpret and use in practical conservation planning. The approach is applicable to

47   any taxa for which reliable presence records are available, providing insight into the potential impacts of

48   land use and environmental change. Maps identify areas of conservation concern, such as hotspots for

49   diversity, rare or vulnerable species and potential or threatened network corridors, making them useful

50   for ecological impact assessment of proposed developments, and to conservation managers planning

51   habitat creation or improvement.

52

53   Key words

54   Bats, Habitat Suitability Model, MaxEnt, multiscale model, presence-only model, spatial scale, Species

55   Distribution Model

Introduction

To protect our natural heritage in the face of climate change and increasingly intensive land-use, conservation management must operate on a landscape scale (e.g. Lindenmayer *et al*. 2008; Heller & Zavaleta 2009; Lawton *et al*. 2010). In addition to retaining and managing existing protected areas, we must improve the ecological connections between them and, where possible, improve the surrounding matrix of agricultural and urban landscapes. This management, whether for a species, community or ecosystem, should be driven by an understanding of how the target species interact with their abiotic and biotic environment, since it is by changing this environment that management is achieved. To develop the best management solutions, we need to be able to predict the consequences of performing a particular task in a particular place. This could be deciding where to plant new woodland, or choosing the line of a new road to cause minimal ecological disturbance. This requires tools that facilitate decision-making in complex environments at a landscape scale. This paper uses bats to explore the usefulness of Habitat Suitability Modelling (HSM, or Species Distribution Modelling, SDM), generated by the program MaxEnt, as such a tool.

Habitat Suitability Modelling is a statistical technique that predicts the distribution of a species over large areas from environmental data and occurrence records. It has been usefully applied using few presence-only data (e.g. Pearson *et al.* 2007), giving it considerable potential in practical conservation, since large presence/absence datasets are frequently unavailable or unreliable. GIS-based HSM can produce large extent, fine-resolution maps that encapsulate many of the interactions between species and environment. Maps can be generated from small datasets, are easily interpreted by conservation practitioners, and can be updated easily. However, HSMs can also have poor, and often over-estimated, predictive performance, due to residual spatial autocorrelation in the data, sampling bias, and inadequate testing with independent data (Phillips *et al*. 2009; Veloz 2009; Merckx *et al*. 2011). Residual spatial autocorrelation (rSAC) can result from factors not studied, such as a species' gregariousness, or when distribution is not adequately explained by the ecological variables in the model. Use of spatially autocorrelated data violates the assumptions of many tests. We explicitly test the effects of failing to account for these in models.

83   The interaction between an organism and its environment occurs on many scales (e.g. Wiens 1989). In the case

84   of bats, habitat choice on a small scale is typically driven by the constraints of echolocation and flight:

85   extremes include slow flying bats that feed by gleaning from the leaves and trunks of woodland trees and bats

86   adapted for aerial hawking during rapid, efficient flight in the open. The distribution of many of the

87   invertebrates that bats feed on is also likely to be determined by fine scale factors: insects with aquatic larvae

88   will be close to water, flying insects more often in the lee of woodland trees. On a larger scale, the presence or

89   absence of a species in a locality will be determined by such factors as woodland perimeter for edge habitat

90   specialists, the permeability of the typically 'disturbed' landscape between their multiple roosts and foraging

91   sites, and the distances between summer roosts and hibernacula. Our ecological understanding may therefore

92   need to encompass many scales. To date, most studies on foraging bat-habitat relationships have been at a

93   fixed spatial scale (e.g. Jaberg & Guisan 2001; Wickramasinghe *et al*. 2003; Rebelo & Jones 2010; Rainho &

94   Palmeirim 2011). These studies tell us which habitat factors are important determinants of bat-habitat

95   suitability, but only in relation to the scale considered. Multiscale models are now being used and a recent

96   paper by Razgour, Hanmer & Jones (2011) used such models to predict the distribution of a rare UK bat.

97

98   We have used field data collected specifically to develop multiscale HSMs for eight bat species in the Lake

99   District National Park, NW England. Our aims were two-fold. (1) To investigate multiscale species-habitat

100 relationships and provide accurate and easily interpretable habitat suitability maps for environmental impact

101 assessment and conservation management. (2) To explicitly test the effects of sampling bias and rSAC on

102 measures of model performance. The work thus serves as a template for HSMs for temperate bats in general,

103 and since bats are increasingly recognised as good bioindicators (Jones *et al* 2009) the maps have value

104 beyond bat conservation.

105

106 **Materials and methods**

107 STUDY SITES AND SPECIES

108 The study was carried out in the Lake District National Park, NW England (subsequently referred to as "Park";

109 Fig. 1). It has wide post-glacial valleys filled with a rich mosaic of woodland, plantations, lakes, farmland and

110 open grassland, turning into moorland and rocky, mountainous terrain at higher elevations (up to 977 m a.s.l.).

111 Built areas vary from scattered farms linked by unlit tracks to small towns and well-lit, busy roads. Nine bat

112 species were recorded: *Pipistrellus pipistrellus*, *P. pygmaeus*, *Plecotus auritus*, *Myotis daubentonii*, *M.*

113 *nattereri*, *M. brandtii*, *M. mystacinus* and *Nyctalus noctula* and the locally rare *N. leisleri*. We used acoustic

114 surveys to gather presence from thirty 1-km^2 sites across the southern part of the Park from May to August

115 inclusive in 2008 and 2009, walking two transects in each site each year (Fig.1 and Supplementary Appendix

116 S1). Sites were chosen by aligning a 5 x 6 grid of 25 km^2 squares with the Ordnance Survey grid. At the centre

117 of each 25-km^2 square was the 1-km^2 study site, making the sites 5 km apart, centre to centre. Two sites were

118 repositioned to overcome access problems. Sites were highly varied in habitat composition, structure and

119 altitude. Within each site, 2–3 km transects encompassed this variation. Full transect methodology is given in

120 S1. Species were identified by manual and automated extraction and analysis of full-spectrum echolocation

121 calls (S1). We captured bats to obtain additional data from *Plecotus auritus* since their low intensity calls are

122 difficult to detect. Bats were captured as a component of other work at a single woodland site in over half of

123 the study squares, using mist nets and harp traps. To assess how robust models were to geographic transferral,

124 we collected independent data using the same methods in eight sites west and north of the training sites,

125 selected to encompass a range of habitat types (Fig. 1, S1).

126

127 ENVIRONMENTAL VARIABLES

128 GIS data from multiple sources were used to create gridded environmental variables (50 or 100 m resolution

129 rasters; Tables S1.1–1.3). Data were validated by comparing them with recent (2005) aerial photographs,

130 provided by Natural England. GIS manipulation was performed in ArcGIS 9.3 (www.esri.com). In brief, two non-

131 scalar environmental variables were used in each model (distance to water and woodland edge) and all other

132 variables were measured at 12 scales (100–6000 m) by measuring cell statistics within different sized windows

133 centred on each raster cell using the focal statistics tool (details in S1).

134

135 MODELLING

136 **Model fitting**

137 MaxEnt is a program that predicts the geographical distribution of a species based on the environmental

138 conditions at locations where the species is known to occur, using the maximum entropy method (Phillips,

139 Anderson & Schapire 2006). All models were run in MaxEnt Version 3.3.3e

140   (http://www.cs.princeton.edu/~schapire/maxent), using primarily default settings and one species record per

141   cell (see S1). Models were evaluated using 5-fold cross validation: study site data were randomly partitioned

142   into five roughly equal subsets, four being used to train a model and one to test the model. The process was

143   repeated five times, using a different subset each time for testing, and the results averaged.

144

145   **Sampling bias and spatial autocorrelation**

146   Moran's correlograms were used to check for significant spatial autocorrelation of residuals (1 – predicted HSI

147   for each species record; de Marco, Diniz-Filho & Bini 2008) using Spatial Analysis in Macroecology (SAM;

148   Rangel, Diniz-Filho & Bini 2006). Significance of Moran's I was calculated using a randomisation test with 9,999

149   Monte Carlo permutations, correcting for multiple testing. If significant residual spatial autocorrelation (rSAC)

150   was detected we spatially constrained testing and training data: the first distance lags found to be positively

151   spatially autocorrelated were used to set a distance threshold and data pairs closer to each other than this

152   were placed in the same data partition (Parolo, Rossi & Ferrarini 2008). Models were also run using random 5-

153   fold cross validation for comparison.

154

155   To prevent MaxEnt from using background data from environmental conditions outside the range sampled, we

156   included a mask, forcing MaxEnt to calibrate models with data from each field site and a surrounding 0.5-km

157   buffer. To factor out any bias introduced by sampling habitats more or less often than they were available

158   within these sites, a bias file was created by scoring cells every time they were sampled by either a transect or

159   catching. When given the data, MaxEnt will correct for non-uniform sampling effort (Dudík, Schapire & Philips

160   2005).

161

162   Models were also run without measures to counteract sampling bias and rSAC, to explicitly determine the

163   consequences. We hypothesised that this would result in falsely inflated measures of test performance. This

164   was analysed using paired t-tests on Area Under Curve (AUC) scores, the most commonly used HSM

165   performance parameter (Merckx *et al*. 2011; Parolo, Rossi & Ferrarini 2008) and assessing changes in

166   individual variable performance with and without measures to control for sampling bias for selected species

167   (details in S1). AUC measures the probability that a randomly chosen presence point will rank above a

168   randomly chosen background point (AUC = 0.5 = random; the closer to 1.0 the better the discrimination).

8

169 Presence-only models vary in their maximum achievable AUC between species because of differences in the

170 likelihood that background samples will be drawn from suitable habitat (Phillips, Anderson & Shapire 2006).

171 Although this limits the ability to contrast model performance between species, scores can be used for

172 comparing the performance of model settings and parameters for a particular species. Other measures of

173 accuracy are available and are discussed in depth by Elith & Graham (2009).

174

175 **From univariate to multivariate models**

176 The predictive power of environmental variables was assessed using the MaxEnt jackknife measure of test

177 AUC. The scale at which an environmental variable had the highest test AUC in a univariate model was entered

178 into a species' multivariate model, to create 'full models' of all variables at their best performing scale.

179 Environmental variables with test AUC ≤0.5 were removed and those remaining were checked for

180 multicollinearity ($r \geq 0.70$) using ENMTools (www.ENMTools.com; Warren, Glor & Turelli 2008; 2010). Collinear

181 variables were pruned by retaining those with higher test AUC scores. Models were further pruned to yield a

182 set of variables with the highest predictive power, using a jackknife, leave-one-out stepwise approach (Parolo,

183 Rossi & Ferrarini 2008). Environmental variables causing the smallest decrease (or largest increase) in test AUC

184 when removed were pruned in turn until only one environmental variable remained. The 'pruned model' with

185 the highest test AUC was used for further analysis. The contribution each remaining environmental variable

186 made to a species' pruned model was determined by randomly permuting the value of each environmental

187 variable in turn at the presence and background locations and re-testing the model. The resulting, normalised

188 drop in training AUC was compared between variables (Phillips 2011).

189

190 **Model selection**

191 The fit of full and pruned models were compared using Akaike Information Criteria corrected for small sample

192 sizes (AICc), in ENMTools (Warren & Seifert 2011). Models for each species were ranked by calculating the

193 difference (ΔAICc) between a model's AICc and the minimum AICc (minAICc). Models were considered

194 equivalent if ΔAICc was ≤ 2 values of the minAICc model, or potential alternatives if ≤ 10 of minAICc (Burnham

195 & Anderson 2002). AICc was calculated using all records unique to a single raster cell from study and test sites

196 separately. We could only assess fit when a species sample size was greater than the number of model

197 parameters (Burnham & Anderson 2002).

198

Model transferability: evaluation using independent data

200 Models were trained with all data and predictions were projected to the entire Park. Their performance was

201 assessed with new, independent field data from test sites. AUC was calculated in R (version 2.12.2, package

202 ROCR; Sing *et al.* 2009), comparing Habitat Suitability Index (HSI) values at presence sites (one species record

203 per cell) and at each cell within the eight test sites plus a 0.5-km buffer (background HSI values). Data were

204 bootstrapped 2,000 times to generate 95% confidence intervals. We created multivariate environmental

205 similarity surface (MESS) maps for the Park to highlight areas with habitat values outside the range

206 encountered within the study sites (Elith, Kearney & Phillips 2010; Rodda, Jarnevich & Reed 2011).

207

208 Pruned models have been found to perform better on independent test data, suggesting that they may be less

209 prone to overfitting (Parolo, Rossi & Ferrarini 2008). One-tailed paired t-tests, comparing species' distributions

210 predicted by the full and pruned models within the study and test sites, examined whether model pruning

211 resulted in higher test AUC values, larger areas of suitable habitat, and lower and more statistically significant

212 extrinsic omission rates after accounting for the size of the suitable area (lower binomial test *P*-values). The

213 extrinsic omission rate is the proportion of all test points that fall outside the area predicted to be suitable for

214 the species.

215

216 *Plecotus auritus*, **a special case**

217 Due to the low intensity of *P. auritus* echolocation calls we recorded only eight independent bat passes. This

218 species was therefore modelled using records from all 38 study and test sites, incidental records made during

219 other fieldwork and reliable county records. A target background approach was adopted rather than a bias file

220 (Phillips *et al*. 2009). We used 9,827 six-figure grid referenced mammal records held by the county records

221 office to extract background data (pseudoabsences) and a 100 x 100 m resolution**.** The principle is that these

222 records will have been collected using similar, and therefore similarly biased, methods to the bat records so

223 that differentiation between bat habitat and background is possible.

224

225 **Estimating species richness**

226   Species' habitat suitability maps were combined in ArcGIS to generate richness maps. Each species' binary

227   presence-absence (suitable-unsuitable habitat) maps, generated by two threshold rules, were overlaid to

228   estimate the number of species predicted to be present at each cell. The Minimum Training Presence (MTP)

229   threshold uses the lowest predicted HSI value for a known species location in the training data, and therefore

230   always has a training omission rate of zero. The tenth percentile rule discards the lowest ten percent of

231   predicted habitat suitability indices at training locations, so that ten percent of training locations fall outside of

232   the suitable area. Alternative threshold rules are discussed in Liu *et al*. (2013).

233   **Results**

234

235   Presence data are summarised in Table S2.1. *Pipistrellus* records accounted for approximately 75% of all

236   recordings. Since *N. leisleri* is rare in the study area we assumed all *Nyctalus* calls were *N. noctula*. Models built

237   with random and spatially constrained data showed significant rSAC between data pairs at ≤3,000 m, i.e. those

238   within a study site. Since all data from separate sites were separated by ≥4,000 m, data from within each site

239   were placed in the same 20% partition of the data for 5-fold cross validation. *P. auritus* were modelled using

240   random 5-fold cross validation because residuals were not found to be spatially autocorrelated.

241

242   UNIVARIATE SPECIES–HABITAT ASSOCIATIONS

243   Figure 2 shows the strength of association (test AUC as an estimate of predictive power) from univariate

244   models, across the scales, between each species. Only the most important environmental variables are shown,

245   those retained in the final, multivariate pruned models. Further results are shown in Appendix S2, Fig. S2.1, in

246   the online Supporting Information. Representative MaxEnt response curves in Fig. 3 show the relationship

247   between the probability of a species presence and the values of the more important environmental variables.

248   Generally, habitat features measured at 100–500 m scales were the most important predictors of foraging

249   habitat suitability (Fig.2, Fig.S2.1), but there was considerable variation between species and variables. Most

250   species had strong, positive associations with cover of inland water (Fig. 2), and were negatively associated

251   with slope (Fig. 3c) and distance to woodland edge and water (Fig. 3 a, b). Deciduous woodland cover was also

252   a strong, positive predictor (Fig. 3d). Bats responded in more complex ways to other variables, such as cover of

253   roads and buildings (Fig. 3e, f).

254

255 *Pipistrellus* species showed similar associations across scales, but variable predictive power was usually higher

256 for *P. pygmaeus*. Power tended to decrease with increasing scale, although slope maintained a strong negative

257 association across scales. *P. pygmaeus* had an association with most environmental variables at small spatial

258 scales, but was most likely to be found within short distances of woodland edge and water in areas with high,

259 small scale, deciduous woodland cover and medium woodland edge densities. It was positively related to

260 water cover at all scales < 6,000 m, but this relationship was strongest at 1,000–1,500 m. *P. pipistrellus* showed

261 the same relationships with woodland edge distance and density. Small-scale road, building, and water cover

262 were the only other useful (positive) habitat predictors for this species.

263

264 The cover of water (positive) and average slope (negative) were important predictors for all *Myotis* species at

265 small scales. The distance to water (negative), and the cover of roads (negative) and ancient woodland

266 (positive) were also useful predictors for *M. nattereri*. Altitude (negative), distance to water and woodland

267 edge (negative) and deciduous woodland cover (positive), had a strong association with *M. daubentonii*

268 presence, and *M. brandtii/mystacinus* were strongly associated with areas close to woodland edge with

269 medium densities of this edge habitat within small extents (≤ 500 m).

270

271 *Nyctalus noctula* presence was best predicted by altitude (negative at all scales, but strongest ≥ 1,000 m) and

272 road cover (positive, small scales). Deciduous woodland cover (positive) and structural variables (all negative:

273 richness, woodland edge density and maximum woodland patch) were most important at small scales (200–

274 1,000 m).

275

276 *P. auritus* presence was strongly and negatively associated with slope at all scales. Variable importance

277 typically increased from 100 m to 400–500 m with little variation at larger scales. However, the positive effect

278 of building cover decreased with increasing scale, and the negative effect of water and positive effect of mixed

279 woodland became more important predictors at large scales. The positive relationships between *P. auritus* and

280 ancient woodland cover, deciduous woodland cover and maximum woodland patch size were strongest at

281 small scales.

282

283   MULTIVARIATE MODELS

284   Only the final pruned models are discussed here. A comparison of the performance of full and pruned models

285   can be found in S2. Removing poor performing variables and subsequent pruning significantly increased

286   model performance in study sites (test AUC increase = 0.20 ± 0.13 (mean ± s.d.); test gain = 0.90 ± 0.53; Fig. 4;

287   Table S2.2). This process also increased the area predicted to be suitable for each species by a mean of 7.8%

288   (MTP) and 12.7% (tenth percentile), suggesting pruning reduced overfitting (Tables S2.2, S2.3). Extrinsic

289   omission rates fell from 9–36% to 0.002–8% (MTP) and from 29–73% to 8–22% (tenth percentile). Binomial

290   test *P*-values also decreased significantly between full and pruned models, with fewer test points falling

291   outside the suitable area than predicted by chance alone.

292

293   *rSAC and sampling bias*

294   The final models we present minimise the effects of rSAC and sampling bias. Failing to control for rSAC in full

295   models (random cross-validation) significantly decreased training AUC (0.017 ± 0.02) and inflated test AUC

296   (0.198 ± 0.10) relative to models with spatially constrained testing and training data (Table S2.4 & S2.5). A

297   similar, significant increase in test AUC scores (0.104 ± 0.05) was found when the spatially constrained models

298   were run without the bias file. Training AUC also increased slightly, but not significantly. The selection of

299   random background data for *P. auritus*, rather than accounting for bias using the target background approach,

300   resulted in higher model training and test AUC (Table S2.4). Only small changes in the predictive power of all

301   variables in the full *P. pipistrellus* model were found on removal of the bias file, whereas use of a random

302   background increased test AUC for all variables in the *P. auritus* model, except coniferous woodland (Table

303   S2.6).

304

305   *Environmental variables in the pruned models*

306   The pruned models with the highest test AUC retained only 2–4 primarily small scale variables and at least one

307   distance variable (Fig. S2.2). *Pipistrellus* pruned models contained only 2–3 variables (Fig. 2), with distance to

308   woodland edge contributing 74% to *P. pygmaeus* and 64% to *P. pipistrellus* pruned models. The importance of

309   water to *P. pygmaeus* was evident in the contributions made by large scale water cover and distance to water.

310   The *P. pipistrellus* model included a positive effect of small scale (100 m) road cover. However, only roads close

311   to woodland (<100 m) increased habitat suitability and roads >500 m from woodland decreased suitability.

312   *Myotis* pruned models contained similar environmental variables: all included distance to water or woodland

313   edge, and small scale (100–500 m) variables describing slope, water cover, and woodland composition or

314   structure (Fig. 2). Distance to woodland edge contributed 73% to the *M. brandtii/mystacinus* model, and

315   woodland edge density was the next most important variable (Fig. S2.2). Distance to water made the highest

316   contribution to the *M. daubentonii* model and high deciduous woodland cover (200 m) was also important.

317   Water cover was an important positive predictor of *M. nattereri* presence at the 100 m scale. However, the

318   distance to water response curve suggests that the species forages close to, but not over water, preferring flat

319   areas of ancient woodland (Fig. S2.2). The last variable to be pruned from the *N. noctula* model was average

320   altitude measured at 4,000 m. Favoured habitat is land <250 m a.s.l. with small woodland patches (500 m), ~1

321   km km^{-2} of woodland edge (400 m), and high road cover (200 m)(Fig. S2.2). The variable response curves for *P.*

322   *auritus* indicate a preference for areas with high mixed woodland and low water cover (5,000 m), close to

323   buildings on landscapes with gentle slopes (1,000 m) (Fig. S2.2).

324

325   MODEL TRANSFERABILITY

326   Pruned models performed well within new field sites (test AUC: 0.70–0.84). The pruned models gave the

327   highest test AUC scores, except for *N. noctula* and *M. brandtii/mystacinus*, when full models had slightly higher

328   test AUCs (Table S2.7). Low MTP thresholds produced larger areas of suitability and lower extrinsic omission

329   rates for independent data than the tenth percentile rule (Table S2.7). Error rates were lower than expected by

330   chance for 11 out of the 12 full and pruned species models using the tenth percentile rule, indicating good

331   model performance. Pruning significantly increased the area predicted to be suitable for a species and

332   decreased extrinsic omission rates (Fig. S2.3; Table S2.8).

333

334   MODEL SELECTION

335   AICc results indicate that *Pipistrellus* pruned models fitted better to independent test data compared to full

336   models (Table S2.9). Although we were not able to perform this test on other species' independent data

337   because their sample size outweighed the number of model parameters, we were able to show that all

338   species' pruned models fit best to their training data (Table S2.9). This illustrates the positive effect of pruning

339   on model transferability.

340

341 HABITAT SUITABILITY MAPS

342 Pruned, multiscale models were used to create habitat suitability maps for all seven species or species groups.

343 The maps (Fig. 5) show that the lowland networks of inland water and woodland were most suitable for most

344 species. This pattern was emphasised by the species richness maps (Fig. 6). The lower MTP threshold

345 generated more generous predictions of species richness across the Park compared to the tenth percentile

346 threshold. Less than 0.1% of the Park held environmental conditions outside the range recorded in the training

347 sites.

348

349 **Discussion**

350

351 We built useful habitat suitability models for eight species of UK bat from data collected on acoustic transects.

352 The best results were obtained from multiscale models from which poor predictor variables had been removed

353 and backward stepwise deletion had identified the most useful subsets of variables. Steps taken to minimise

354 sampling bias and residual spatial autocorrelation led to significant improvements. Final models for the study

355 area, when tested using independent field data, had test AUCs in the range 0.70–0.84, making them useful

356 predictors of bat distributions. The small number of variables in the final models makes them easier to

357 interpret by practitioners when using them to inform planning or practical management decisions. A

358 discussion of the more technical aspects of the modelling process will be found in Appendix S2 and this

359 discussion will focus on the ecological and practical aspects of the study.

360

361 SPECIES–HABITAT RELATIONSHIPS AND THE IMPORTANCE OF SCALE.

362 Presence was best predicted by a set of variables that varied significantly between species. However, water

363 and ancient and deciduous woodland variables were generally the most important positive predictors of

364 habitat suitability in univariate tests and the pruned models of most species included these variables. It is

365 striking how similar the responses are among species for many variables. For example the probability of

366 occurrence decreased with distance to water in all species in a very similar way (Fig.3a), yet the community

367 includes a fast open-air forager (*N. noctula*), a trawler (*M. daubentonii*) woodland gleaners (e.g. *M. nattereri*)

368 and a generalist (*P. pipistrellus*). Several ecologically different species also show a similar relationship with

369   deciduous woodland cover (Fig. 3d). This indicates that many habitat management interventions have the

370   potential to benefit broad communities, not just individual species.

371

372   Woodland structure (distance to woodland, woodland edge density, patch size) was particularly important at

373   small spatial scales. In common with most small insectivorous bats, the species studied typically forage within

374   1–3 km of their roost, rarely more than 6 km, and once established at a foraging site, many occupy 'beats' of

375   less than 100 m (e.g. Senior, Butlin & Altringham 2005). The strongest relationships with environmental

376   variables were typically observed at smaller spatial scales (100–500 m), coinciding with foraging beat and small

377   home range distances (see e.g. Graf *et al.* (2005) who drew similar conclusions for capercaillie). Small-scale

378   bat–habitat relationships will therefore reflect the decisions made by bats from local roosts on where to feed

379   within their home range. Relationships at larger scales are more likely to reflect the 'carrying capacity' of a

380   locality: how many colonies, of what size, an area can support. However, with the ability to fly, bats can exploit

381   patchily distributed resources, so small areas of suitable habitat may still be important (and should be

382   conserved), particularly in marginal habitat (Gorresen & Willig 2004; Meyer & Kalko 2008). Because different

383   processes may be operating at different scales, it is not surprising that the relative importance of variables

384   often changed with scale. For example, in the *N. noctula* model, area of road cover and urban development

385   becomes less important, and altitude more important, with increasing scale. Deciduous woodland cover and

386   woodland edge density show more a complex, but similar pattern.

387

388   Road and urban cover was a useful predictor at small scales: positive for *N. noctula* and *Pipistrellus*, negative

389   for *Myotis* and *P. auritus*. As road cover increased above 5–10% it became a negative predictor for most

390   species at large scales, highlighting the complex relationships bats have with roads. Bat activity and diversity

391   are reduced by major roads, probably through a barrier effect (Berthinussen & Altringham 2012). However,

392   the hedges and woodland lining many of the predominantly minor roads in the study area are utilised by open-

393   air foragers such as *N. noctula* and *Pipistrellus*. Woodland bats, such as many *Myotis* and *Plecotus* species, are

394   likely to avoid all but the most minor roads, since roads are associated with high levels of noise, light and open

395   space (Stone, Jones & Harris 2009; Siemers & Schaub 2011). Dense road cover, however small the roads may

396   be, is associated with urban development, habitat loss and disturbance, so it is not surprising that all species

397   avoid such areas. All species had a negative relationship with altitude, which is not surprising since higher

398   altitudes at the latitude of the study are associated with lower temperature, higher wind speed and higher

399   rainfall. However, the only pruned model to retain altitude was that of *N. noctula,* in which it was an important

400   negative predictor. Because *N. noctula* is a large bat that feeds in the open, it may be particularly prone to

401   these climatic effects. It should not be forgotten that the two scale-independent variables, distance to

402   woodland and water, were important components of most species' models.

403

404   SPECIES RICHNESS PATTERNS

405   Richness maps based on presence should be interpreted with the occupancy thresholds in mind. The MTP

406   threshold is low for all species, suggesting large portions of the study area were suitable habitat. The tenth

407   percentile threshold is probably more useful at identifying critical foraging habitat. Generating species richness

408   maps by overlaying species HSM maps may overestimate richness since factors that limit species distributions,

409   such as competition and dispersal, are not accounted for (Graham & Hijmans 2006), but these effects are not

410   likely to be significant for bats (e.g. Bloch, Stevens & Willig 2011), and indeed more intensive survey work may

411   increase species richness (e.g. MacSwiney, Clarke & Racey 2007). Species richness is, as expected, high in the

412   lower elevation valleys that hold most of the woodland and water. The south-east quadrant of the study area

413   is strikingly rich compared to other areas, reflecting the generally lower elevations and the abundance of

414   woodland patches of varying size. This is despite the higher (although still low) human population density with

415   its associated development.

416
417
418   **Conclusions, recommendations and applications**

419   We have shown that useful bat HSMs can be built across a large and diverse area based on relatively limited

420   data collected on acoustic transects. Multiscale HSMs perform better than single scale models and will

421   therefore have greater practical value. Model building should account for sampling bias and spatial

422   autocorrelation. The most important variables for most species relate to distance to and coverage of woodland

423   and water. Our study provides a methodology for future bat population monitoring and the updating and

424   refining of the maps. The methodology also provides a template for mapping projects for a wide range of

425   localities and taxa. How can the maps and models be used? In scientific terms, the models improve our

426   understanding of how bats use large and complex habitats and help us to predict the consequences of climate

427   change and more direct anthropogenic alteration of the landscape. Conservation practitioners can make use of

428 the maps in several ways. Cost path analysis can identify the least disruptive routes for new or upgraded roads,

429 or locations for new developments that minimise impact. The maps can also be used to make more informed

430 judgements about the most effective mitigation methods and locations by modelling proposed changes in the

431 landscape. HSMs can be used in opportunity mapping for planning both large- and small-scale habitat

432 management for maximum effectiveness by identifying, for example, critical locations for corridors and

433 networks, hotspots for diversity and the location of rare or vulnerable species. The maps can also help in the

434 identification of unknown populations of rarer species (e.g. Razgour, Hanmer & Jones 2011), or in the

435 identification of sites for reintroduction.

436

437

447

448 **References**

449 Berthinussen, A. & Altringham, J. (2012) The effect of a major road on bat activity and diversity. *Journal of*

450 *Applied Ecology*, **49**, 82-89.

451 Bloch, C.P., Stevens, R.D. & Willig, M.R. (2011) Body size and resource competition in New World bats: a test of

452 spatial scaling laws. *Ecography*, **34**, 460-468.

453 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: A practical information-*

454 *theoretic approach.* pp. 49 - 96. Fort Collins, USA.

455   de Marco, P., Diniz-Filho, J.A.F. & Bini, L.M. (2008) Spatial analysis improves species distribution

456   modelling during range expansion. *Biology Letters*, **4**, 577-80.

457   Dudík, M., Schapire, R.E. & Phillips, S.J. (2005) Correcting sample selection bias in maximum entropy density

458   estimation. *Advances in Neural Information Processing Systems 18.* (eds Y. Weiss, B. Schölkopf & J.

459   Platt), pp. 323–330. MIT Press, Cambridge, Massachusetts, USA.

460   Elith, J. & Graham, H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing

461   performances of species distribution models. *Ecography* **32**, 66–77.

462   Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and*

463   *Evolution*, 1, 330-342.

464   Gorresen, P.M. & Willig, M.R. (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of

465   Paraguay. *Journal of Mammalogy*, **85**, 688-697.

466   Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. (2005). The importance of spatial scale in habitat models:

467   capercaillie in the Swiss Alps. *Landscape Ecology*, **20**, 703-717.

468   Graham, C.H. & Hijmans, R.J. (2006) A comparison of methods for mapping species ranges and species

469   richness. *Global Ecology and Biogeography*, **15**, 578-587.

470   Heller, N. & Zavaleta, E. (2009) Biodiversity management in the face of climate change: a review of 22 years of

471   recommendations. *Biological Conservation*, **142**, 14–32.

472   Jaberg, C. & Guisan, A. (2001) Modelling the distribution of bats in relation to landscape structure in a

473   temperate mountain environment. *Journal or Applied Ecology*, **38**, 1169-1181.

474   Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as

475   bioindicators. *Endangered Species Research*, **8**, 93-115.

476   Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J., Haddow, R.W., Hilborne, S.,

477   Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland, W.J., Tew, T.E., Varley, J., & Wynne, G.R. (2010)

478   *Making Space for Nature: a review of England's wildlife sites and ecological network*. Report to Defra.

479   Lindenmayer, D., Hobbs, R. J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun,

480   A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., Haila, Y., Hunter, M., Gibbons,

481   P., Lake, S., Luck, G., MacGregor, C., McIntyre, S., Mac Nally, R., Manning, A., Miller, J., Mooney,

482   H., Noss, R., Possingham, H., Sanders, D., Schmiegelow, F., Scott, M., Simberloff, D., Sisk, T., Tabor,

483   G., Walker, B., Wiens, J., Woinarski, J. & Zavaleta, E. (2008) A checklist for ecological management of

484   landscapes for conservation. *Ecology Letters*, **11**, 78–91.

485 Liu, C., White, M. & Newell, G. (2013) Selecting thresholds for the prediction of species occurrence with

486   presence-only data. *Journal of Biogeography*, **40**, 778-789.

487 MacSwiney, M.C., Clarke, F.M. & Racey, P.A. (2008) What you see is not what you get: the role of ultrasonic

488   detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied*

489   *Ecology*, **45**, 1364-1371.

490 Merckx, B., Steyaert, M., Vanreusel, A., Vincx, M. & Vanaverbeke, J. (2011) Null models reveal preferential

491   sampling, spatial autocorrelation and overfitting in habitat suitability modelling. *Ecological Modelling*,

492   **222**, 588-597.

493 Meyer, C.F.J. & Kalko, E.K.V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest

494   fragmentation: land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711-1726.

495 Parolo, G., Rossi, G. & Ferrarini, A. (2008) Toward improved species niche modelling: *Arnica montana* in the

496   Alps as a case study. *Journal of Applied Ecology*, **45**, 1410-1418.

497 Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from

498   small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of*

499   *Biogeography*, **34**, 102-117.

500 Phillips, S.J. (2011) A brief tutorial on Maxent. AT&T Research, pp. 32. Available from

501   http://www.cs.princeton.edu/~schapire/maxent/

502 Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic

503   distributions. *Ecological Modelling*, **190**, 231-259.

504 Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J.R. & Ferrier, S. (2009) Sample

505   selection bias and presence-only distribution models: implications for background and pseudo-absence

506   data. *Ecological Applications*, **19**, 181-197.

507 Rainho, A. & Palmeirim, J.M. (2011) The importance of distance to resources in the spatial modelling of bat

508   foraging habitat. PLoS ONE, **6** (4): e19227. doi:10.1371/journal.pone.0019227.

509 Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis

510   in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321-327.

511   Razgour, O., Hanmer, J. & Jones, G. (2011) Using multi-scale modeling to predict habitat suitability for species

512   of conservation concern: the grey log-eared bat. *Biological Conservation*, **144**, 2922-2930.

513   Rebelo, H. & Jones, G. (2010) Ground validation of presence-only modelling with rare species: a case study on

514   barbastelles *Barbastella barbastellus* (Chiroptera: Vespertilionidae). *Journal of Applied Ecology*, **47**, 410-

515   420.

516   Rodda, G.H., Jarnevich, C.S. & Reed, R.N. (2011) Challenges in identifying sites climatically matched to the

517   native ranges of animal invaders. *PLoS ONE*, **6** (2): e14670.

518   Senior, P., Butlin, R.K. & Altringham, J.D. (2005) Sex and segregation in temperate bats. *Proceedings of The*

519   *Royal Society B-Biological Sciences*, **272**, 2467-2473.

520   Siemers, B.M. & Schaub, A. (2011) Hunting at the highway: traffic noise reduces foraging efficiency in acoustic

521   predators. *Proceedings of The Royal Society B-Biological Sciences*, **278**, 1646–1652.

522   Sing, T., Sander, O., Beerenwinkel, N., & Lengauer, T. (2011) ROCR: visualizing the performance of scoring

523   classifiers. R package version 1.0-4. 2009.

524   Stone, E.L., Jones, G. & Harris, S. (2009) Street lighting disturbs commuting bats. *Current Biology*, **19**, 1–5.

525   Veloz, S.D. (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only

526   niche models. *Journal of Biogeography*, **36**, 2290–2299.

527   Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative

528   approaches to niche evolution. *Evolution*, **62**, 2868-2883.

529   Warren, D. L., Glor, R.E. & Turelli, M. (2010) ENMTools: a toolbox for comparative studies of environmental

530   niche models. *Ecography*, **33** (3), 607 – 611.

531   Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity

532   and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.

533   Wickramasinghe, L.P., Harris, S., Jones, G. & Vaughan, N. (2003) Bat activity and species richness on organic

534   and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology*, **40**, 984–993.

535   Wiens, J.A. (1989) Spatial scaling in Ecology. *Functional Ecology*, **3**, 385-397.

536
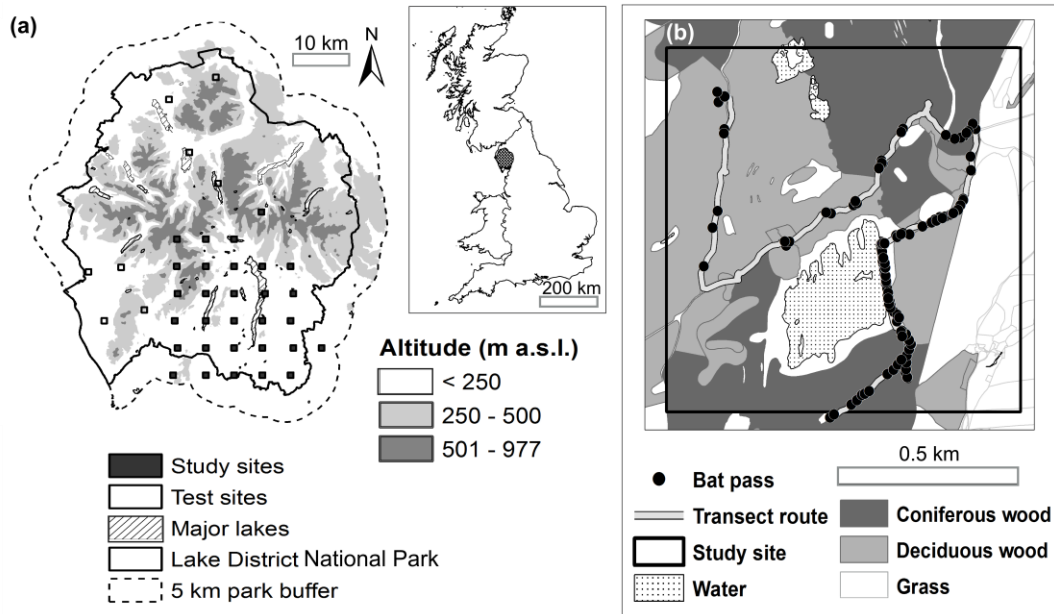
Fig. 1. (a) Lake District National Park, showing 5 km buffer, major lakes, relief, and study and test sites. (b) Typical transect, showing route and ba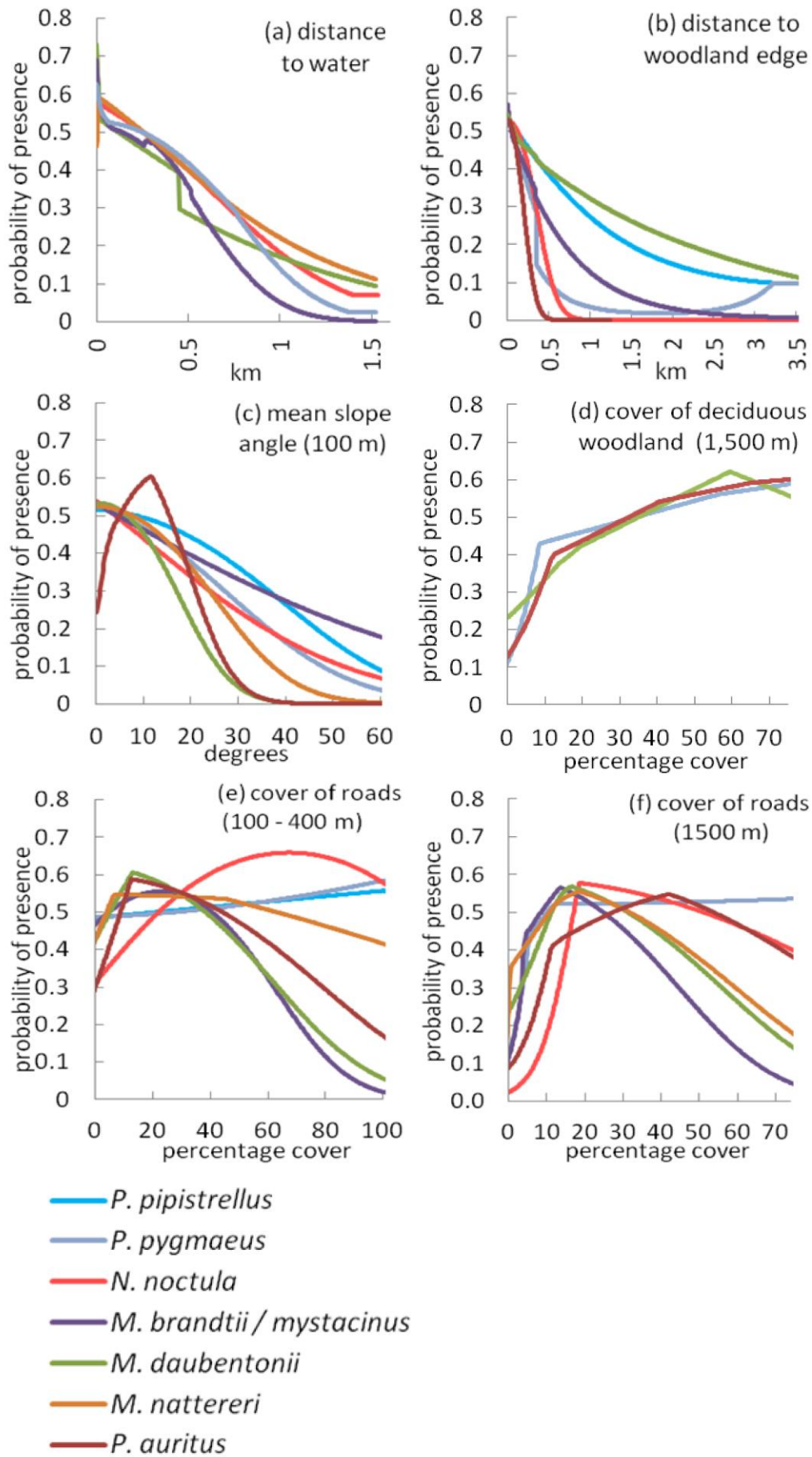t records. An Ordnance Survey/EDINA supplied service © Crown Copyright/database right 2008. Inset based on data provided through EDINA UKBORDERS with support of ESRC and JISC, boundary material © Crown Copyright and the Post Office.
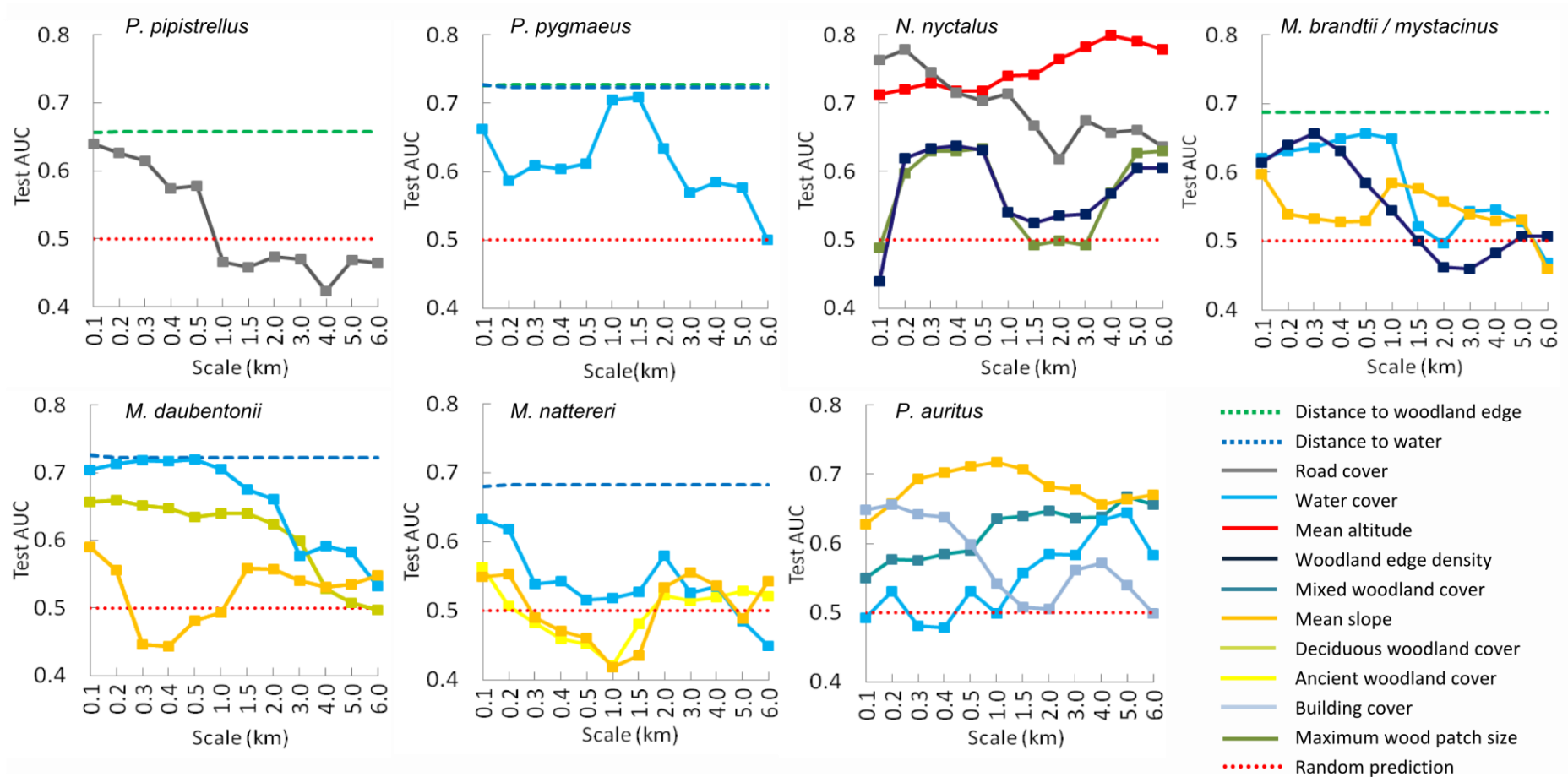
542
543   Fig. 2. The strength of association (as test AUC) between each species' presence and individual environmental variables at different spatial scales. The average predictive power of

544   the distance variables is shown as a dashed line: these were independent of scale. Environmental variables with a predictive power ≤ 0.5 are no better than random. Only variables

545   retained in pruned models are shown (see S2 for others). NB. The scale range is not linear for improved clarity at small scales.

(a) distance to water

(b) distance to woodland edge

(c) mean slope angle (100 m)

(d) cover of deciduous woodland (1,500 m)

(e) cover of roads (100 - 400 m)

(f) cover of roads (1500 m)

P. pipistrellus
P. pygmaeus
N. noctula
M. brandtii / mystacinus
M. daubentonii
M. nattereri
P. auritus

546

547   Fig. 3. Representative MaxEnt response curves showing the probability of a species' presence at a

548   location for a range of parameters. (d) shows response curves at a species' best performing small scale

549   (100–500 m). These graphs are based on univariate models to prevent interacting or collinear variables

550   from affecting the relationships modelled. Variables found to have poor predictive power at a particular

551   scale (AUC ≤ 0.5) are not shown.
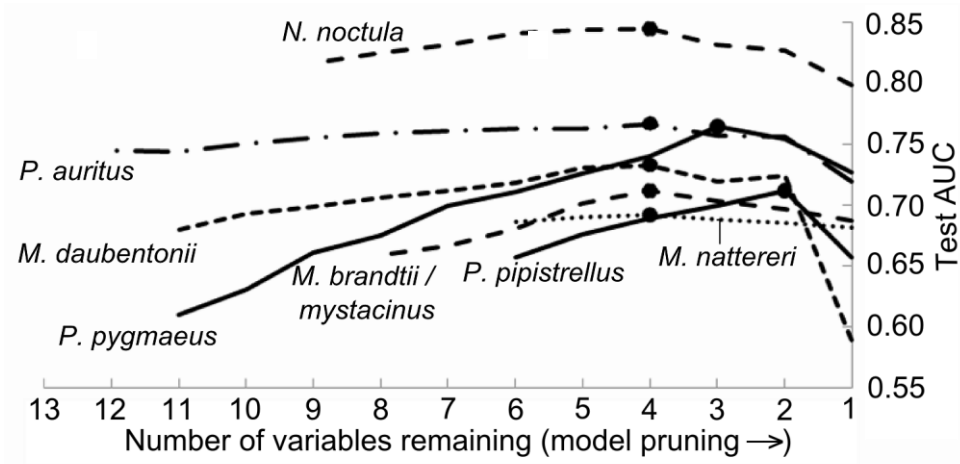
Fig. 4. Effect of model pruning on test AUC scores after removal of collinear variables and poor predictors (AUC≤0.5) from a species full model. The best test AUC values are marked with a circle.
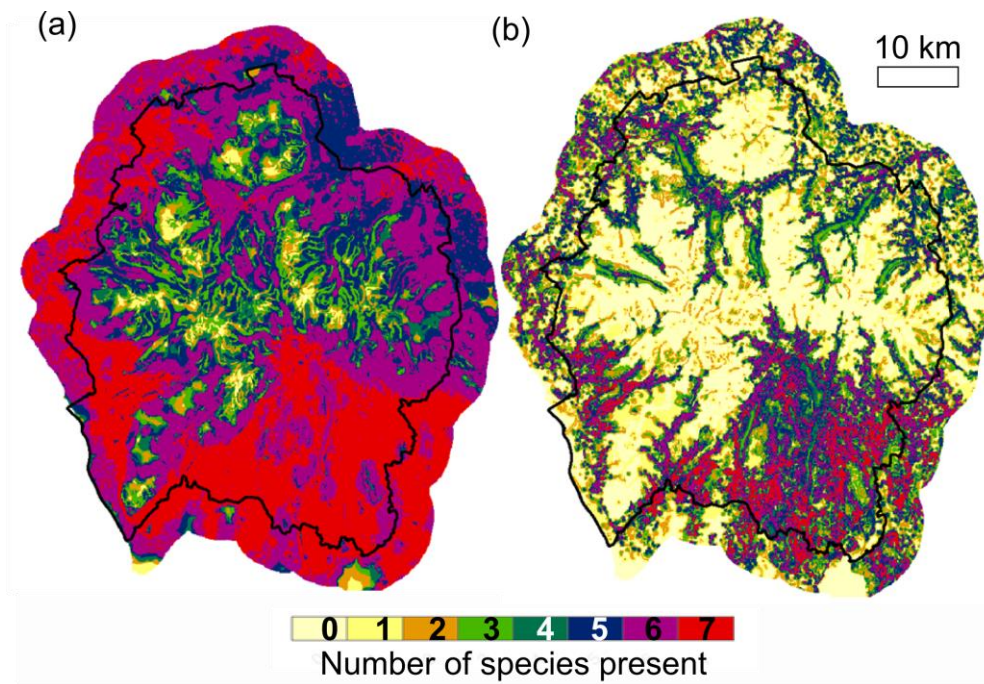
555
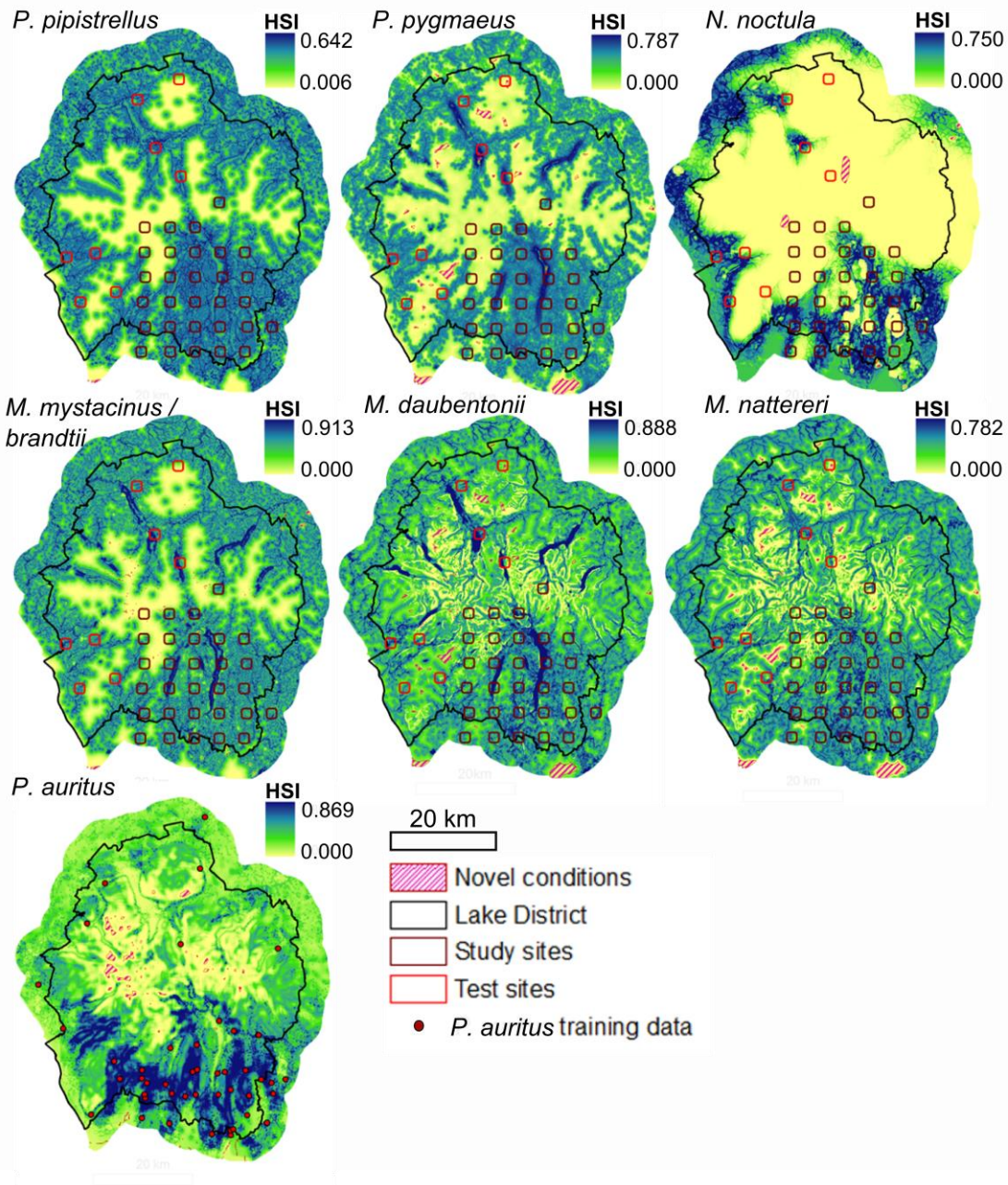
Fig 5. Habitat suitability maps made using each species' pruned set of variables. Novel conditions are areas

containing variables outside of the range on which a model was trained. HSI = Habitat Suitability Index.

Number of species present

558

559   Fig.6. Species richness maps using occupancy thresholds MTP (a) and tenth percentile (b).

560

561   **Supporting Information**

562   Additional Supporting Information may be found in the online version of this article:

563   **Appendix S1:** Methods.

564   **Appendix S2:** Results and technical discussion

565