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Deposited in DRO:

04 June 2014

Version of attached file:

Accepted Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Huntley, B. and Allen, J.R.M. and Barnard, P. and Collingham, Y.C. and Holliday, P.R. (2013) 'Species' distribution models indicate contrasting late-Quaternary histories for southern and northern hemisphere bird species.', Global ecology and biogeography., 22 (3). pp. 277-288.

Further information on publisher's website:

http://dx.doi.org/10.1111/j.1466-8238.2011.00751.x

Publisher's copyright statement:

Additional information:

Species' distribution models indicate contrasting late-Quaternary histories for southern and northern hemisphere bird species

Brian Huntley[1*], Judy R.M. Allen[1], Phoebe Barnard[2,3], Yvonne C. Collingham[1], and Phyllida R. Holliday[1]

[1] School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, United Kingdom

[2] Birds & Environmental Change Partnership, Climate Change and BioAdaptation Division, South African National Biodiversity Institute, Kirstenbosch Research Centre, P/Bag X7, Claremont 7735, Cape Town, South Africa

[3] Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

* Corresponding author: brian.huntley@durham.ac.uk

Word count: 294 (Abstract, including 10 keywords); 4953 (Introduction to Discussion); 77 (Acknowledgements); 110 (Biosketch); 57 references; 2 tables; 2 figures.

15 **Abstract**

16 **Aim:** To test hypotheses: that Fynbos species had more extensive distributions at the Last Glacial

17 Maximum (LGM), extending onto the exposed 'Agulhas Plain'; that genetically distinct British taxa could

18 have persisted through the LGM on adjacent areas of exposed shelf.

19 **Location:** Southern Africa; Europe.

20 **Methods:** Climatic response surfaces were fitted for 14 Fynbos and two European birds. These models

21 were used to hindcast species' distributions for palaeoclimates simulated using a fully-coupled

22 atmosphere–ocean general circulation model. LGM annual net primary productivities (ANPP) of two plant

23 functional types upon which the European birds depend were simulated using a dynamic vegetation model

24 and compared to potential LGM bird distributions.

25 **Results:** Fynbos birds' potential LGM distributions mostly extended southwards onto the exposed

26 Agulhas Plain and consistently were more extensive than at present. This contrasts with conventional

27 expectations for temperate species based upon northern hemisphere evidence. North-west European

28 taxa potentially had LGM ranges on exposed shelf and ice-free areas west and south-west of the British

29 Isles ice sheet. This is consistent with available genetic evidence, supporting the long-standing

30 hypothesis that these taxa persisted through the LGM in this region. In both regions, results allow

31 generation of new testable hypotheses about species' evolution and palaeobiogeography.

32 **Main Conclusions:** Bird species found today in Fynbos likely had more extensive ranges under glacial

33 conditions, with many species' potential ranges extending onto the Agulhas Plain. Bird taxa today

34 restricted to the British Isles probably survived the LGM with limited distributions on exposed shelf and ice-

35 free areas south-west of the British Isles ice sheet. Areas of shelf exposed under glacial conditions are

36 likely to have been important components of glacial distributions of species in both northern and southern

37 hemispheres. The contrasting history of northern and southern hemisphere species has important

38 conservation implications, especially in relation to conserving intra-specific genetic diversity.

39 **Keywords**

1. Introduction

Species' distribution models (SDMs), relating species' present recorded distributions to present climatic conditions (Pearson & Dawson, 2003), are widely used to explore species' potential distributions under future climatic conditions projected using general circulation models (GCMs), first being applied in this way >15 years ago (Huntley *et al.*, 1995; Lenihan & Neilson, 1995). Only recently, however, have SDMs been used to explore species' potential past distributions under GCM-simulated palaeoclimatic conditions (Martínez-Meyer & Peterson, 2006; Garzon *et al.*, 2007; Carnaval & Moritz, 2008; Alba-Sanchez *et al.*, 2010), or to identify areas where species' may have persisted during periods of the late Quaternary when conditions were unfavourable for their wider occurrence (Buckley *et al.*, 2009; VanDerWal *et al.*, 2009). To a large extent this can be attributed to historical limitations of GCM palaeoclimatic simulations. Until recently, these predominantly were made using atmospheric GCMs that required sea surface temperatures (SSTs) to be specified, usually on the basis of summer and winter season reconstructions made from microfossil evidence (CLIMAP Project Members, 1984). Furthermore, neither ocean circulation nor seasonal sea-ice cover generally were simulated. Even when refined using a nested regional climate model (RCM), using the RCM output to drive palaeovegetation simulations revealed substantial biases with respect to the palynological record of past vegetation, (Huntley *et al.*, 2003). Similar biases were revealed when comparing simulated climates with conditions inferred from dated permafrost features (van Huissteden *et al.*, 2003). As Alfano *et al.* (2003) showed, these biases were likely a result largely of how reconstructed seasonal SSTs were used to derive an annual cycle of SSTs.

As computing power increased, however, and the imperative for more reliable projections of future climate drove the development of fully-coupled ocean–atmosphere GCMs, these models have also begun to be applied to simulate late Quaternary palaeoclimates. Singarayer and Valdes (2010) used a version of the Hadley Centre Unified Model to make a consistent set of simulations for a series of time slices extending back through the last glacial to the last interglacial. These simulations provide the basis for palaeovegetation simulations that are sufficiently robust to be used to supplement information from the palynological record, allowing exploration of the drivers of past forest dynamics (Miller *et al.*, 2008) and of the character and productivity of last glacial vegetation throughout northern Eurasia (Allen *et al.*, 2010).

69 Such series of GCM simulations provide a basis for applying SDMs to explore the late-Quaternary

70 history of taxa that have a limited, or no, fossil record. They can also be used to explore how the different

71 glacial palaeogeography, as a result of eustatic depression of sea-level by a maximum of *ca.* 120 m at the

72 last glacial maximum (LGM; *ca.* 21 ka BP), may have been important in providing areas of distribution that

73 are now submerged (Sakaguchi *et al.*, 2010). In addition, they are a potentially valuable basis for testing

74 and generating hypotheses in historical biogeography. Here we illustrate this potential using SDMs fitted

75 to bird species of two regions, southern Africa and north-west Europe, that provide several marked

76 contrasts. In particular, southern Africa experienced no extensive development of last glacial ice sheets,

77 whereas large parts of northern Europe and the European mountains were covered by ice sheets at the

78 LGM (Ehlers & Gibbard, 2005). Prevalent climatic constraints also differ today between the two regions:

79 Nowhere in north-west Europe experiences any significant degree of seasonal moisture deficiency,

80 whereas much of the region is typified by sub-zero winter temperatures and snow cover even in the

81 lowlands. In contrast, seasonal drought typifies most of southern Africa, whilst sub-zero temperatures and

82 snow are features generally only of the higher mountains (e.g. Mulder & Grab, 2010).

83 Exploring how palaeoclimatic conditions potentially impacted upon species in these two regions allows

84 us to examine whether the paradigm, based upon northern hemisphere evidence, of temperate species

85 having more restricted glacial distributions applies also in the southern hemisphere. We also apply our

86 SDMs to address two specific hypotheses:

87 • That LGM palaeoclimatic conditions enabled bird species associated today with the Fynbos

88   Biome of southern and south-western South Africa to have more extensive LGM distributions,

89   including southward range extensions onto the 'Agulhas Plain' that was exposed at that time.

90 • That species or races today restricted to the British Isles, including the endemic *Loxia scotica*

91   (Scottish Crossbill) and *Lagopus lagopus scoticus* (Red Grouse), as well as the genetically

92   distinctive *Pinus sylvestris* (Scots Pine) found today in Scotland (Ennos, 1997), could have

93   persisted through the LGM on ice-free areas and areas of exposed continental shelf south-west

94   of the British Isles (Huntley & Birks, 1983; Huntley, 1989).

2. Methods

To address the first hypothesis, we examined the 39 bird species listed by Hockey et al. (2005) as primarily associated with the Fynbos Biome.   Fourteen species were selected (Table 1) on the basis that: (1) they are southern African endemics;   (2) they do not range extensively beyond the Fynbos; and   (3) they were mapped as individual taxa by Harrison et al. (1997).   Distribution and reporting rate data, the latter a proxy for abundance, were mapped for southern African birds by Harrison et al. (1997) on a 0·25° grid, except in Botswana where a 0·5° grid was used.   Reporting rate data for the 14 selected species were obtained from the Animal Demography Unit, University of Cape Town, and used to fit quantitative climatic response surface (CRS) models.

To address the second hypothesis, distribution data for Loxia scotica and Lagopus lagopus (Red / Willow Grouse), were obtained from the European Bird Census Council (EBCC).   These data, mapped by Hagemeijer and Blair (1997), were recorded on a ca. 50 km grid.   Unfortunately L. l. scoticus, endemic to the British Isles and distinguished from other sub-species principally by its uniform and seasonally invariant plumage and its diet principally of Calluna vulgaris (Ling) shoots (Cramp & Simmons, 1980), was not mapped separately.   Qualitative CRSs were fitted using data for the entire area mapped by the EBCC.

CRS models describe species' recorded distributions or abundances in relation to a series of bioclimatic variables derived from present climatic data.   Both the quantitative models for Fynbos species and the qualitative models for European species were fitted by locally-weighted regression following methods described by Huntley et al (1995; 2011).   We favour this approach because: it requires an a priori choice of a limited number of biologically relevant bioclimatic variables;   it makes no assumptions about the form of the relationships between species' probability of occurrence or abundance and the bioclimatic variables;   it allows for interacting effects of bioclimatic variables and for these interactions to be non-stationary in climatic space;   the fitted response surface is readily visualised, which is of great benefit in model interpretation;   and extrapolation of the models into climatic space not represented in the training dataset is both conservative and predictable.   Goodness-of-fit and robustness of the models were assessed using the measures and validation procedures described by Huntley et al. (2011).   With the exception of species recorded from ≤25 grid cells, model validation was performed by fitting and testing models on 100 random

123   70:30 splits of the data;   in the case of the more sparsely recorded species models were fitted omitting and

124   predicting each grid cell in turn.   Threshold values for determining suitable grid cells were taken as those

125   values that maximised Cohen's kappa (Cohen, 1960; Huntley *et al.*, 1995).

126   Bioclimatic variables were derived from climatic variables in the CRU CL 1.0 0·5° dataset

127   (http://www.cru.uea.ac.uk/~timm/grid/CRU_CL_1_0.html, New *et al.*, 1999) and/or the WorldClim 2·5′

128   dataset (http://www.worldclim.org/, Hijmans *et al.*, 2005).   Bioclimatic variables used were chosen to

129   reflect primary constraints on bird species' distributions and abundance, whether acting directly or

130   indirectly.   As discussed by Huntley *et al.* (2006), appropriate variables differ between the two regions:

131   Coldest month mean temperature, annual thermal sum above a 5°C threshold and annual ratio of actual to

132   potential evapotranspiration were used for European species, whereas for Fynbos species, coldest and

133   warmest month mean temperatures, annual ratio of actual to potential evapotranspiration and a measure of

134   the intensity of either the dry or wet season, according to which gave the better model for each species,

135   were used.   Calculation of the measures of dry and wet season intensity is described by Huntley *et al.*

136   (2006).

137   Palaeoclimate scenarios used were derived from the series of simulations made by Singarayer and

138   Valdes (2010) using the HadCM3 fully-coupled atmosphere–ocean GCM (Gordon *et al.*, 2000; Pope *et al.*,

139   2000).   Whereas many simulations made with different GCMs are available for the LGM and Holocene

140   'optimum' (6 ka BP), this consistent series of 68 simulations spanning the past 120 ka offers a unique

141   opportunity to explore species' potential distributions and abundances for a range of past conditions.

142   Atmospheric composition, orbital forcing, ice-sheet extent and altitude, and the land–sea mask were

143   prescribed, respectively, on the basis of ice-core data, orbital calculations, ice-sheet modelling and sea-

144   level depression inferred from ice-volume evidence.   Past values of climatic variables were derived from

145   the GCM outputs following Allen *et al.* (2010), but were extended to include shelf areas exposed by eustatic

146   sea-level depression.   To do this we first calculated the potential present (i.e. 1961–90) climate of grid

147   cells exposed by the maximum 120 m sea-level depression.   This was achieved by fitting thin-plate spline

148   surfaces (Hutchinson, 1989) relating each of the 36 relevant climatic variables from the CRU CL 1.0

149   dataset (i.e. 12 monthly means of temperature, precipitation and percentage cloud cover) concurrently to

150   longitude, latitude and altitude.   Climatic variables were then interpolated for shelf grid cells, altitudes for

151 which were calculated as means of the relevant grid cells in the GEBCO 1′ resolution global altitudinal and

152 bathymetric grid (IOC *et al.*, 2003). Interpolated anomalies for the palaeoclimate scenario were then

153 applied to these values, and finally bioclimatic variable values were calculated. Species' potential past

154 distribution and/or abundance patterns were simulated using the CRS models. Potential late Quaternary

155 distribution and/or abundance patterns were then mapped and compared with those simulated for the

156 present.

157 To explore the extent to which *Pinus sylvestris* and *Calluna vulgaris*, specific food plants required by the

158 two north-west European bird taxa, may have been present in western Europe at the LGM, and their likely

159 productivity, we used results from a simulation of LGM vegetation north of 35° N made using the LPJ-

160 GUESS dynamic vegetation model (Smith *et al.*, 2001). This simulation (Allen *et al.*, 2010) used 47 plant

161 functional types (PFTs), including one parameterised to represent *P. sylvestris*. Although *C. vulgaris* was

162 not specifically represented as a PFT, the PFT parameterised to represent dwarf shrubs in the Ericaceae

163 can be taken as an adequate representation of this species because it is the dominant representative of

164 this PFT in most areas where the PFT has high productivity. The principal advantages of this approach,

165 rather than of fitting CRS models for the plant taxa and using them to simulate their LGM distributions, are:

166 (1) that direct effects upon plant performance of the lower atmospheric CO_2 concentration at the LGM,

167 compared to prior to the industrial revolution, are accounted for by LPJ-GUESS; and (2) that LPJ-GUESS

168 provides quantitative simulations of annual net primary productivity (ANPP) for each PFT, whereas CRSs,

169 and the data to which they could be fitted, provide only qualitative information about where the species

170 potentially might occur. Details of the LGM palaeovegetation simulation, including boundary conditions

171 used, are given by Allen *et al.* (2010).

3. Results

3.1 Fynbos birds

174 CRS models for the 14 species all gave goodness-of-fit measures indicating high performance, values for

175 the area under the curve (AUC) for a receiver operating characteristic plot all being > 0·97 (Table 1). The

176 models were also shown to be robust (for details see Huntley *et al.*, 2011). When used to simulate

177 species' potential LGM distribution and abundance patterns, they revealed evidence supporting the

178   hypothesised southward range extensions onto exposed shelf areas, although with individualistic species'

179   responses (Figure 1).

180   The species examined fall into four groups on the basis of their present distributions (see

181   Supplementary Figure S1(a – d) for species' recorded and simulated potential present distributions). The

182   first group comprises seven species at present limited to a greater or lesser extent to Western Cape (see

183   Supplementary Information Figure S2 for place names referred to in the text) and adjacent parts of the

184   surrounding provinces (*Pternistis capensis* (Cape Spurfowl), Figure 1(a); *Chaetops frenatus* (Cape

185   Rock-jumper), Figure 1(c); *Cryptillas victorini* (Victorin's Warbler), Figure 1(f); *Promerops cafer* (Cape

186   Sugarbird), Figure 1(g); *Anthobaphes violacea* (Orange-breasted Sunbird), Figure 1(i); *Crithagra totta*

187   (Cape Siskin), Figure 1(k); and *C. leucopterus* (Protea Seedeater), Figure 1(n)). These species

188   generally had much enlarged potential LGM ranges, extending eastwards, northwards and also southward

189   onto the Agulhas Plain, although in the case of *Chaetops frenatus* and *Cryptillas victorini* extension onto the

190   Agulhas Plain is simulated only in the east of their potential LGM ranges.

191   Three species have present distributions confined largely to the east, often principally in the

192   Drakensberg and surrounding mountainous areas (*Chaetops aurantius* (Drakensberg Rock-jumper), Figure

193   1(d); *Promerops gurneyi* (Gurney's Sugarbird), Figure 1(h); and *Crithagra symonsi* (Drakensberg

194   Siskin), Figure 1(l)). All three had potential LGM distributions of increased extent, with increases

195   especially towards the north and, to a lesser extent, east. Southward range extension was limited, with

196   potentially suitable grid cells on the Agulhas Plain an order of magnitude further from the species' principal

197   potential range (500 – 1000 km) than typical dispersal distances observed for Fynbos species, and thus

198   unlikely to have been occupied.

199   A further three species have more widespread present distributions (*Geocolaptes olivaceus* (Ground

200   Woodpecker), Figure 1(b); *Cinnyris afer* (Greater Double-collared Sunbird), Figure 1(j); and *Crithagra*

201   *scotops* (Forest Canary), Figure 1(m)). All three again had potentially more extensive LGM distributions,

202   extending in almost all directions, including southwards onto the Agulhas Plain. In two cases they

203   exhibited a tendency potentially to retreat from more inland parts of their present range, the exception being

204   *G. olivaceus* that potentially also expanded its range inland.

205   For several species in these groups, suitable conditions are simulated at the LGM also in markedly

206   disjunct areas far to the north or north-east of the remainder of the species' potential LGM range, notably in

207   northern Namibia and/or South Africa.   Given their isolation, it is unlikely, albeit not impossible, that such

208   areas would have been occupied.

209   The final species, *Bradypterus sylvaticus* (Knysna Warbler), Figure 1(e), has a very restricted present

210   distribution close to the south coasts of Western and Eastern Cape.   Although at 0·5° resolution the CRS

211   model simulates rather few occurrences, these are in the appropriate areas.   At the LGM the species'

212   distribution is simulated to shift eastwards and also to extend southwards onto the narrow shelf areas south

213   of Eastern Cape.   Interestingly, however, there is no suggestion of any extension northwards, in contrast

214   to what is seen for most other species.

215   Median range extent for the 14 species, calculated as the number of grid cells simulated as potentially

216   suitable, is *ca.* 2·6 x greater for LGM climate than for present climate.   Only one species, *Crithagra*

217   *scotops*, has a potential LGM range virtually identical in extent to that for the present, whilst three species

218   (*Chaetops frenatus*, *Cryptillas victorini* and *Crithagra leucopterus*) have potential LGM range extents ≥ 4 x

219   those simulated for the present.   These LGM results can be placed in context by considering simulations

220   made for palaeoclimate scenarios derived from simulations made by Singarayer and Valdes (2010) for a

221   series of other past intervals (6, 9, 12, 15, 18, 42 and 120 ka BP, and three Heinrich Events (Andrews,

222   1998):   H1 (17 ka BP), H2 (24 ka BP) and H4 (38 ka BP)) (see Supplementary Information, Figures S2 –

223   15).   These reveal that glacial palaeoclimates generally result in simulated range extents greater than at

224   present, the most extreme potential range increases being simulated for Heinrich Event palaeoclimates.

225   The latter all give median range extents > 4 x those simulated for the present, H1 (*ca.* 17k BP) with a

226   median range extent of 5·6 x, being the most extreme.   Strikingly, the last interglacial palaeoclimate

227   (120 ka BP) was the only one to give a reduction, albeit marginally, in median range extent.   Species most

228   reduced in potential range at that time compared to the present were *Promerops gurneyi* (0·53), *Chaetops*

229   *aurantius* (0·63) and *Crithagra symonsi* (0·67), the three species with present distributions principally in the

230   Drakensberg and other mountainous eastern areas.

231 **3.2 North-west European birds and their habitats**

232 CRS models for both species had excellent goodness-of-fit measures (Table 2). That for *Loxia scotica*

233 accurately simulated the species' distribution in Scotland (see Supplementary Figure S17 for the species'

234 recorded distribution), although also simulating one grid square in England and two in Norway as potentially

235 suitable under present climatic conditions (Figure 2(a)). For the LGM the species is simulated potentially

236 to occupy a series of grid cells south-west of the ice sheet that covered most of the British Isles. In

237 addition, areas in the Cantabrian mountains and eastern Pyrenees are simulated as potentially suitable,

238 along with isolated grid cells in Cornwall and Brittany. Persistence of the species in these areas would

239 have required presence of *Pinus*, preferably *P. sylvestris*, its principal food plant. As Figure 2(c)

240 illustrates, simulated ANPP for the *P. sylvestris* PFT at the LGM is high in the areas simulated as potentially

241 suitable for *L. scotica*. Most importantly, high ANPP of *P. sylvestris* is simulated throughout the exposed

242 shelf and ice-free continental areas west and south-west of the British Isles ice sheet.

243 The model for *Lagopus lagopus* accurately simulates the species' present range that includes Britain

244 and Ireland (*L. l. scoticus*) and the Boreal zone, its range in the latter extending from western Norway (*L. l.*

245 *variegatus*) eastwards across Fennoscandia and northern Russia (*L. l. lagopus*) to Siberia and Boreal North

246 America (see Supplementary Figure S17 for the species' recorded north-west European distribution). In

247 addition, however, areas in the Alps, and a single grid cell in the Pyrenees, remote from the species'

248 present range, are simulated as suitable for the species under present climatic conditions. The potential

249 range simulated for the LGM extends throughout ice-free areas of the exposed shelf and British Isles, as

250 well as across the southern North Sea basin and southwards through eastern Europe. In addition, most of

251 the Cantabrians, parts of the Pyrenees, the Massif Central and the margins of the Alps are simulated as

252 potentially suitable. Strikingly, the ice-free area of shelf north-east of Scotland also is simulated as

253 potentially suitable, whilst the area of suitable conditions is constricted in central southern England, with

254 highly suitable conditions to west and east but only a limited link between the two where conditions are less

255 suitable.

256 Whereas most *Lagopus lagopus* sub-species feed primarily upon *Salix* (Willow) and *Betula* (Birch)

257 catkins and buds, or on berries of various dwarf shrubs, including *Vaccinium* spp. (Bilberry, Cowberry, etc.)

258 and *Empetrum nigrum* (Crowberry), *L. l. scoticus* feeds primarily upon *Calluna vulgaris* shoots.

259   Accordingly, the key habitat requirement for the latter sub-species is presence of *Calluna*-dominated

260   heathlands and related communities. The most relevant PFT simulated by Allen *et al*. (2010) is the

261   Ericaceae (dwarf shrub) PFT, parameterisation of which results in behaviour similar to that of *C. vulgaris* in

262   terms of the ANPP pattern simulated for present climate. Simulated ANPP for this PFT for the LGM

263   (Figure 2(d)) is high on the exposed shelf and land areas to the west and south-west of the British Isles. It

264   is also high in northern Iberia, around the Massif Central and western Alps, in the southern North Sea and

265   in parts of eastern Europe. The coincidence between the high productivity area simulated to the south-

266   west of the British Isles and the high suitability of the same area for *L. lagopus* provides additional support

267   for the hypothesis that *L. l. scoticus* persisted in this region through the LGM.

268   **4. Discussion**

269   On the basis of northern hemisphere evidence, there is a paradigm expectation that temperate species'

270   ranges were reduced in extent under glacial conditions, species being constrained to what frequently are

271   referred to as 'glacial refugia'. Simulated LGM ranges of Fynbos species, however, are generally more

272   extensive, or at least no less extensive, than those simulated for present climatic conditions. This reflects

273   the absence of extensive continental ice sheets or mountain glaciation in southern Africa (Boelhouwers &

274   Meiklejohn, 2002), coupled to limited cooling and reduced spatial extent of the summer rainfall regime, the

275   latter likely associated with a general reduction in monsoon strength under glacial conditions. This

276   potential for more, rather than less, extensive LGM ranges has important implications for Fynbos species,

277   and perhaps also for other southern hemisphere temperate species. In particular, present distributions

278   and populations of Fynbos species are likely reduced compared to their ranges and populations during

279   most of the Pleistocene, perhaps rendering them even more vulnerable than northern hemisphere

280   temperate species to the impacts of projected future climatic changes. The overall range reduction

281   simulated for the last interglacial serves to underline this issue. That this reduction was potentially most

282   severe for species of the eastern mountains provides a striking parallel to simulated impacts of projected

283   future climatic changes upon species with this general distribution (Huntley *et al.*, 2011; Huntley & Barnard,

284   submitted).

285   Our results for most of the 14 Fynbos species modelled also uphold our hypothesis that these species'

286   more extensive LGM ranges would have included areas on the exposed Agulhas Plain. Given the

287 paradigm expectation that temperate species' ranges shifted equatorward during glacial stages, the overall

288 southward shift of potential range at the LGM exhibited by several species is striking.   This expectation

289 arises primarily from evidence for northern hemisphere regions where seasonal temperatures are a

290 principal determinant of species' range limits.   In South Africa, however, remoteness from any sea-ice

291 cover at the LGM, even in winter, and persistence of the warm Agulhas Current during glacial stages

292 (Gersonde *et al.*, 2003), even if somewhat weakened (Franzese *et al.*, 2006), would have limited the

293 degree of cooling.   Furthermore, the differing seasonal patterns of precipitation and drought, with winter

294 rains predominating in the south-west but summer rains in the east (see e.g. South Africa Rain Atlas,

295 http://134.76.173.220/rainfall/index.html), are of much greater importance in determining species' present

296 distribution patterns (Cowling *et al.*, 1997).   Changes in seasonal precipitation patterns thus are likely to

297 have been at least as important as, if not more important than, temperature changes in driving species'

298 range changes in this region during the Pleistocene.   The general potential range expansion of Fynbos

299 species associated with the region of predominantly winter rainfall is consistent with projections of

300 increased winter rainfall in the region at the LGM (see e.g. PMIP2 results, http://pmip2.lsce.ipsl.fr/).

301 Centres of diversity in the northern hemisphere temperate zone, in terms of both species richness and

302 intra-specific genetic diversity, frequently are associated with the limited areas in which species of this zone

303 occurred during the LGM (Hampe & Petit, 2005).   Fynbos species, however, potentially experience their

304 greatest range restriction under peak interglacial conditions, with the most extreme recent 'bottle-neck'

305 being during the last interglacial.   We can thus hypothesise that both the species richness of Fynbos

306 species and their intra-specific genetic diversity should be greatest in their potential 'interglacial refugia'.

307 We also postulate that closely related species pairs with vicariant distributions centred in the Western Cape

308 and the eastern mountains, especially the Drakensberg (e.g. *Chaetops frenatus / C. aurantius*, *Promerops*

309 *cafer / P. gurneyi*, *Crithagra totta / C. symonsi*) likely diverged from common ancestors as a consequence

310 of isolation in these two 'refugial' regions, most probably during successive Pleistocene interglacials but

311 alternatively during the early Pleistocene when glacial cooling was less strongly expressed.

312 To-date, Fynbos birds have attracted little attention from geneticists and phylogeographers.   The

313 results of our simulations, however, suggest a number of specific testable hypotheses, as well as the

314 general hypotheses outlined above, that could be addressed using genetic approaches.   For example,

315   species of the eastern mountains, whose potential last interglacial ranges are simulated to have been

316   particularly reduced, might be hypothesised to show genetic evidence of a more marked 'bottleneck' at that

317   time.   Given that the majority of species potentially had increased range extents and populations during

318   the LGM, they can be expected to show population genetic evidence of recent contraction of both range

319   and population.   The simulated potential suitability of disjunct areas at the LGM for species that have

320   vicariant sister species (e.g. *Chaetops frenatus* and *C. aurantius*, *Promerops cafer* and *P. gurneyi*) whose

321   LGM range potentially overlapped with, or was at least adjacent to, these disjunct areas, raises an

322   intriguing possibility.   If these disjunct potential LGM range components were occupied, then there may be

323   a genetic legacy of inter-breeding in populations of the sister species if, as a result of their relatively recent

324   origins, the species were not by then completely isolated.

325   In the case of the hypothesised LGM survival on areas of exposed shelf and ice-free continent south-

326   west of the British Isles of taxa such as the endemic *Loxia scotica*, the Scottish genetic variant of *Pinus*

327   *sylvestris*, *Lagopus lagopus scoticus* and *Calluna vulgaris*, the simulations provide compelling supporting

328   evidence.   Palaeoecological evidence long ago pointed to the likelihood of survival of *P. sylvestris* in this

329   region (Huntley & Birks, 1983; Birks, 1989), a hypothesis subsequently supported by genetic evidence

330   (Ennos, 1997; Sinclair *et al.*, 1998; Sinclair *et al.*, 1999; Kinloch *et al.*, 1986).   Survival of this species

331   would imply survival of communities similar to those in which it is found today, such communities often

332   having an understorey in which *C. vulgaris* is a dominant species, even close to the north-westernmost limit

333   of *P. sylvestris* today in northern Norway (Jalas & Suominen, 1973) that closely coincides with the northern

334   limit of *C. vulgaris* in the same region (Gimingham, 1960).   In this case the genetic evidence (Rendell &

335   Ennos, 2002) also points to the glacial survival of *C. vulgaris* in northern Europe, consistent with the model

336   evidence of areas of high ANPP of the Ericaceae (dwarf shrub) PFT south-west of the British Isles ice

337   sheet at the LGM.

338   Although the status of the endemic Scottish Crossbill has long been debated, it is now accorded

339   specific status as *Loxia scotica*.   It is considered most closely related to *L. pytyopsittacus* (Parrot Crossbil),

340   another *Pinus* specialist, rather than to *L. curvirostra* (Common Crossbill) that generally specialises upon

341   *Picea* (Spruce).   Although Knox (1989) speculated that *L. scotica* may have originated as recently as the

342   Holocene, from a population of *L. pytyopsittacus* that reached the British Isles during the Pleistocene and

343 subsequently became isolated, the simulation of suitable conditions for the species south-west of the British

344 Isles ice sheet at the LGM suggests that the species may have a longer history. Furthermore, the

345 simulated potential range at 120 ka BP, during the last interglacial, is closely similar to that occupied during

346 the Holocene, leading us to hypothesise that the species has a history extending back at least to the that

347 time, and perhaps much further into the Pleistocene. Such an hypothesis is amenable to testing using

348 genetic evidence.

349 The status of *Lagopus lagopus scoticus* is similarly the subject of debate. Genetic evidence, however,

350 suggests that this taxon is as distinct from other races of *L. lagopus* as is *L. lagopus* from *L. mutus*

351 (Ptarmigan) in Scandinavia (Quintela *et al.*, 2010). The simulation of an extensive potential range for *L.*

352 *lagopus* south-west and south of the British Isles ice sheet at the LGM, the near isolation of this area from

353 other areas simulated as potentially suitable for *L. lagopus* at the LGM, and the coincidence that this area

354 also is simulated to have a high ANPP for the Ericaceae (dwarf shrub) PFT at the LGM, together support

355 the proposition that *L. l. scoticus* originated no later than the LGM, and potentially earlier in the late

356 Pleistocene. The genetic evidence indicates that divergence between *L. l. scoticus* and *L. l. lagopus*

357 occurred between 12,500 and 125,000 years ago (Quintela *et al.*, 2010). Such a divergence time would

358 be consistent with an origin for *L. l. scoticus* as a result of isolation during the last glacial stage, and hence

359 with the simulated range for *L. lagopus* at the LGM. That the population from which *L. l. scoticus* evolved

360 was isolated also in an area with high ANPP of the Ericaceae (dwarf shrub) PFT might well have

361 contributed to the evolution of the sub-species' dietary specialisation.

362 The simulated potential LGM range of *L. lagopus* also includes an isolated area of suitable conditions

363 north-east of Scotland. This leads us to hypothesise that *L. l. variegatus* may have originated in this

364 region during the last glacial stage, shifting to its present range in south-west Norway as the Scandinavian

365 ice sheet retreated. Genetic evidence could again test this hypothesis.

366 Our simulations have provided support for both of our specific hypotheses, and have also led to the

367 important conclusion that, in contrast to northern hemisphere temperate species, Fynbos species, and

368 potentially also other southern hemisphere temperate species, potentially had LGM distributions that were

369 more extensive than their present distributions. In the case of the north-west European species, available

370 genetic evidence is consistent with our results and conclusions. These results also lead to new

371   hypotheses about the time of origin of *Loxia scotica* and the place and time of origin of both *Lagopus*

372   *lagopus scoticus* and *L. l. variegatus*, all of which could be tested by new genetic data.   In the case of the

373   Fynbos species, our results also enable us to generate hypotheses that could be tested using new genetic

374   evidence.   From a biodiversity conservation viewpoint, and in the context of anthropogenic climatic

375   change, the contrasting history of northern and southern hemisphere temperate species has important

376   implications: Whereas it has been argued that "the rear edge matters" (Hampe & Petit, 2005) in relation to

377   conserving intra-specific genetic diversity of northern hemisphere temperate species, almost the opposite

378   may be true for southern hemisphere species if climatic change parallels previous interglacial maxima in

379   terms of the resulting range restriction.

380   As Nogues-Bravo (2009) has argued, this and similar studies have limitations in terms of the

381   assessment of uncertainties.   This largely reflects a lack of means adequately to quantify the many

382   sources of uncertainty, and thus realistically to assess the overall uncertainty of simulated distributions.

383   These studies, nonetheless, are valuable because of their capacity to generate testable hypotheses.

384   Improvements in modelling approaches, realistic assessments of uncertainties, and iterative interactions

385   with other approaches together can advance our understanding of how species responded to past climatic

386   changes.   This is especially true of genetic approaches, and where taxa are poorly represented in the

387   fossil record, such as most birds, and/or indistinguishable in the fossil record, such as the genetic races of

388   *Pinus sylvestris*.   Such advances are crucial to improving our ability to predict the consequences of

389   present and projected future climatic changes.

390 **Acknowledgements**

397 **Biosketch**

398 Brian Huntley is a palaeoecologist, ecologist and biogeographer with research interests in the interactions

399 between species, ecosystems and their changing environment. His current work spans a range of

400 taxonomic groups and ecosystems, from conifers forming New Zealand treelines to extinct Pleistocene

401 mammals of Eurasia, although he has a particular interest in birds and climatic change. Judy Allen is a

402 palaeoecologist with particular interests in Quaternary vegetation history. Phoebe Barnard is a

403 conservation biologist with a particular interest in birds of the Fynbos Biome. Yvonne Collingham is a

404 biologist who researches the responses of species to climatic changes. Phyllida Holliday is a biologist

405 who is currently researching the history of the distributions of *Loxia* spp. worldwide.

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541 **SUPPLEMENTARY MATERIAL**

542 The online supplementary material comprises 17 Figures as follows:

543 Figure S1: Recorded and simulated distributions of 14 Fynbos bird species.

544 Figure S2: Map of southern Africa showing South African province names and neighbouring countries as

545 referred to in the text.

546 Figures S3 – S16: Potential distributions for the present, 6, 9, 12, 15, 18, 21, 42 and 120 ka BP, and for

547 Heinrich Events H1 (17 ka BP), H2 (24 ka BP) and H4 (38 ka BP), for 14 Fynbos bird

548 species.

549 Figure S17: Recorded breeding distributions of *Loxia scotica* and *Lagopus lagopus* in north-west Europe.

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551 authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-

552 edited or typeset. Technical support issues arising from supporting information (other than missing files)

553 should be addressed to the authors.

554 **Tables**

555 **Table 1: Goodness-of-fit of models fitted to the full data for Fynbos species**

556 **Table 2: Goodness-of-fit of models fitted to the full data for North-west European species**

557   **Table 1:   Goodness-of-fit of models fitted to the full data for Fynbos species**

Scientific name	Common name	No. of grid cells from which recorded[1]	Goodness-of-fit of the climatic response surface model		
			AUC[2]	TSS[3]	K[4]
Pternistis capensis	Cape Spurfowl	207	0·973	0·817	0·775
Geocolaptes olivaceus	Ground Woodpecker	484	0·973	0·839	0·730
Chaetops frenatus	Cape Rock-jumper	50	0·993	0·957	0·635
C. aurantius	Drakensberg Rock-jumper	80	0·997	0·971	0·796
Bradypterus sylvaticus	Knysna Warbler	25	0·992	0·950	0·529
Cryptillas victorini	Victorin's Warbler	58	0·996	0·970	0·712
Promerops cafer	Cape Sugarbird	134	0·992	0·918	0·822
P. gurneyi	Gurney's Sugarbird	93	0·982	0·897	0·682
Anthobaphes violacea	Orange-breasted Sunbird	123	0·993	0·925	0·810
Cinnyris afer	Greater Double-collared Sunbird	464	0·984	0·877	0·793
Crithagra totta	Cape Siskin	118	0·992	0·927	0·754
C. symonsi	Drakensberg Siskin	49	0·999	0·984	0·867
C. scotops	Forest Canary	195	0·986	0·918	0·733
C. leucopterus	Protea Seedeater	69	0·992	0·916	0·710

558

559   [1] The number of 0·25° grid cells from which the species was recorded as present in the Southern

560   African Bird Atlas Project dataset (Harrison *et al.*, 1997).

561   [2] Area under the curve for a receiver operating characteristic plot (Metz, 1978).

562   [3] True skill statistic (Allouche *et al.*, 2006).

563   [4] Cohen's kappa (Cohen, 1960; Monserud & Leemans, 1992).

564 **Table 2:   Goodness-of-fit of models fitted to the full data for North-west European species**

Scientific name	Common name	No. of grid cells from which recorded[1]	Goodness-of-fit of the climatic response surface model		
			AUC[2]	TSS[3]	K[4]
Lagopus lagopus	Willow / Red Grouse	552	0·995	0·956	0·899
Loxia scotica	Scottish Crossbill	14	0·998	0·993	0·800

565

566   [1] The number of *ca*. 50 km grid cells from which the species was recorded as present in the

567   European Bird Census Council dataset (Hagemeijer & Blair, 1997).

568   [2] Area under the curve for a receiver operating characteristic plot (Metz, 1978).

569   [3] True skill statistic (Allouche *et al.*, 2006).

570   [4] Cohen's kappa (Cohen, 1960; Monserud & Leemans, 1992).

571 **Figures**

572 **Figure 1:   Potential distributions and abundances of Fynbos birds at the last glacial maximum**

573 On each panel cyan rings indicate 0·5° grid cells simulated as potentially occupied under present climatic

574 conditions, whilst shaded dots indicate cells potentially occupied at the LGM, darker shading indicating

575 higher simulated reporting rates;   cells simulated as suitable under both sets of climatic conditions have a

576 shaded dot enclosed by a cyan ring.   (a) *Pternistis capensis* – Cape Spurfowl;   (b) *Geocolaptes olivaceus*

577 – Ground Woodpecker;   (c) *Chaetops frenatus* – Cape Rock-jumper;   (d) *Chaetops aurantius* –

578 Drakensberg Rock-jumper;   (e) *Bradypterus sylvaticus* – Knysna Warbler;   (f) *Cryptillas victorini* –

579 Victorin's Warbler;   (g) *Promerops cafer* – Cape Sugarbird;   (h) *P. gurneyi* – Gurney's Sugarbird;

580 (i) *Anthobaphes violacea* – Orange-breasted Sunbird;   (j) *Cinnyris afer* – Greater Double-collared Sunbird;

581 (k) *Crithagra totta* – Cape Siskin;   (l) *C. symonsi* – Drakensberg Siskin;   (m) *C. scotops* – Forest Canary;

582 (n) *C. leucopterus* – Protea Seedeater.

583 Topography, including the approximate extent of exposed areas of continental shelf, is shown using the

584 GEBCO 1′ resolution global altitudinal and bathymetric grid (IOC *et al.*, 2003).

585 **Figure 2:   Potential last glacial maximum distributions and ANPP of north-west European species**

586 On the upper panels cyan rings indicate 0·5° grid cells simulated as potentially occupied under present

587 climatic conditions, whilst shaded dots indicate cells potentially occupied at the LGM, darker shading

588 indicating higher simulated probability of occurrence;   cells simulated as suitable under both sets of

589 climatic conditions have a shaded enclosed by a cyan ring.   (a) *Loxia scotica* – Scottish Crossbill;

590 (b) *Lagopus lagopus* (Red Grouse / Willow Grouse).   The lower panels show ANPP (g C m^{-2} yr^{-1})

591 simulated by the LPJ-GUESS dynamic vegetation model for the LGM, darker shaded dots indicating higher

592 productivity.   (c) *Pinus sylvestris* – Scots Pine;   (d) Ericaceae (dwarf-shrub) – Heaths, Ling.

593 Topography, including the approximate extent of exposed areas of continental shelf, is shown using the

594 GEBCO 1′ resolution global altitudinal and bathymetric grid (IOC *et al.*, 2003).   LGM ice sheet extents,

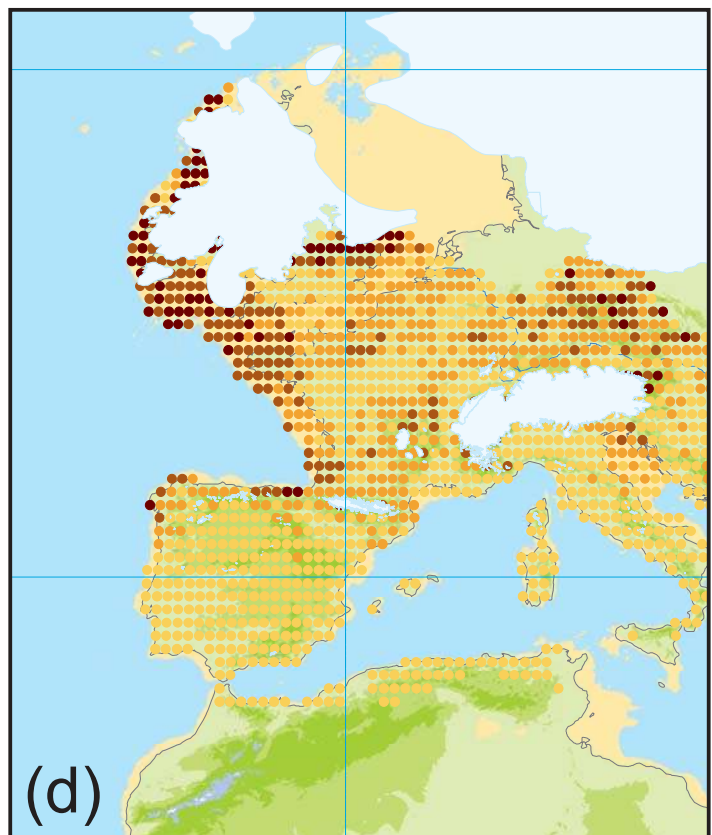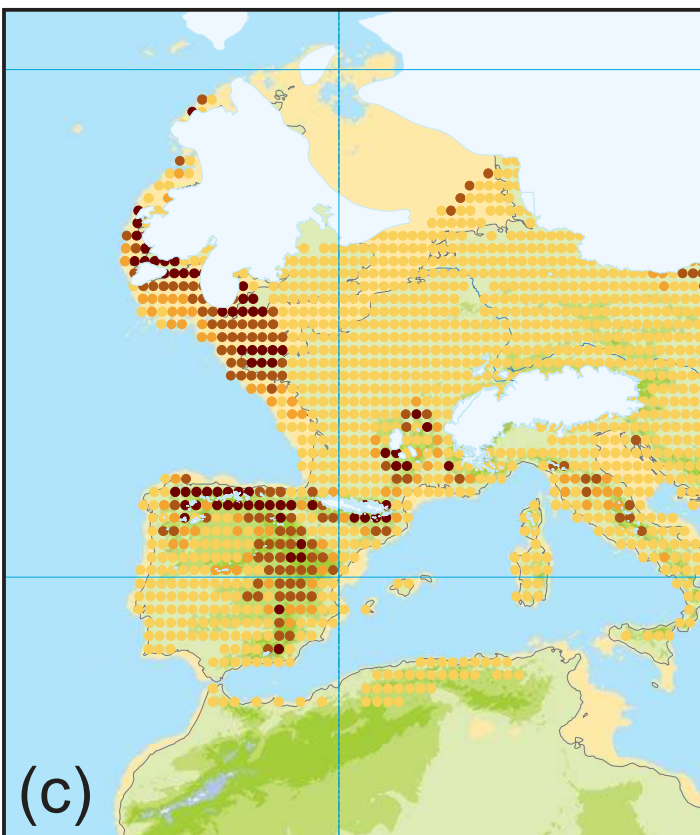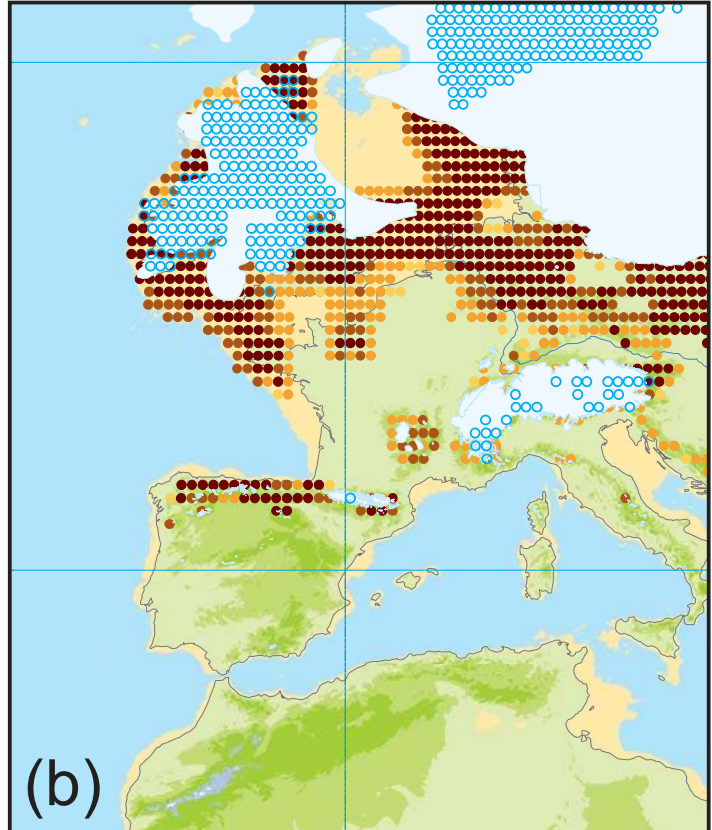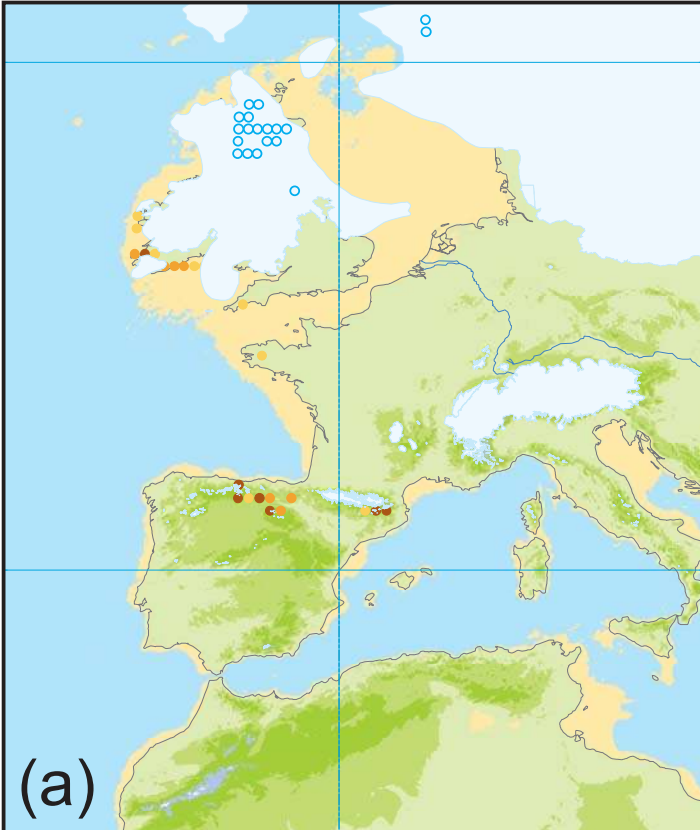595 indicated in blue-white, after Ehlers and Gibbard (2005).

Legend

Altitude (m)

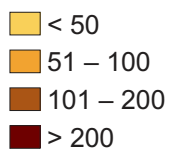|	
-120 – 0	1001 – 2000
1 – 500	2001 – 3000
501 – 1000	≥3001
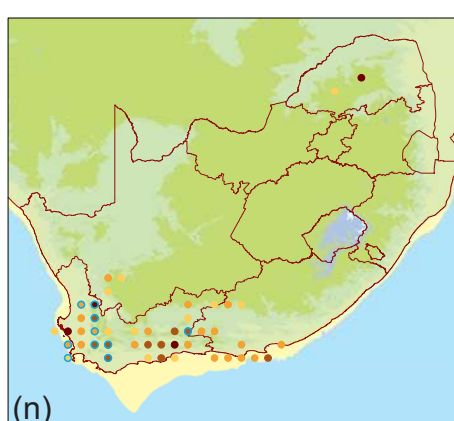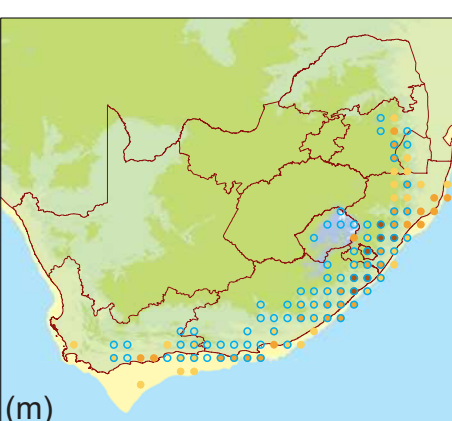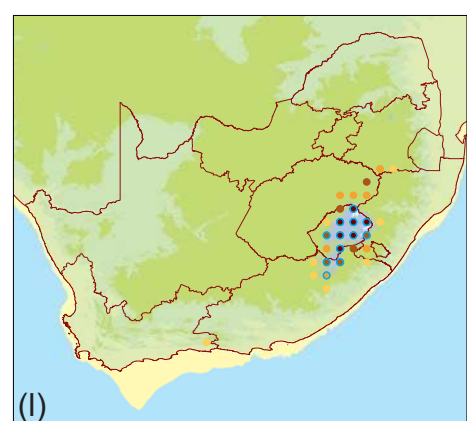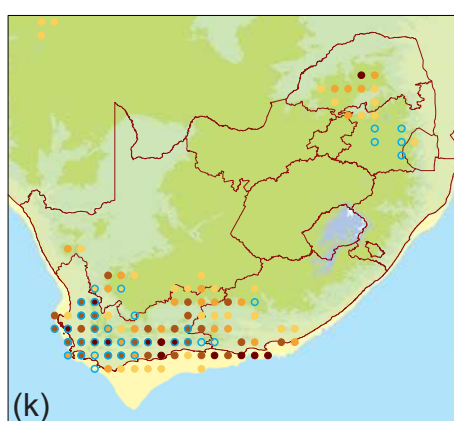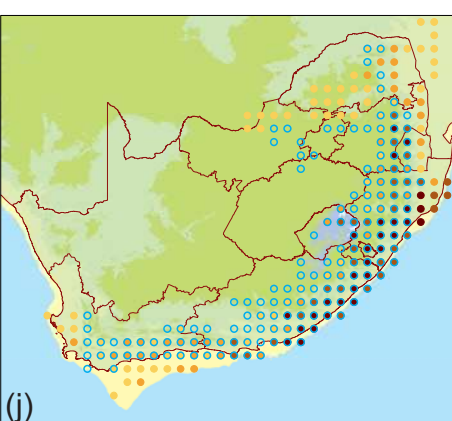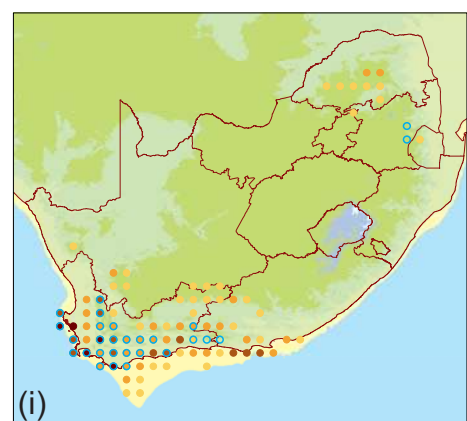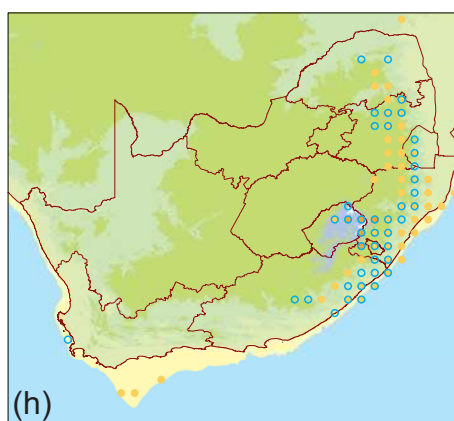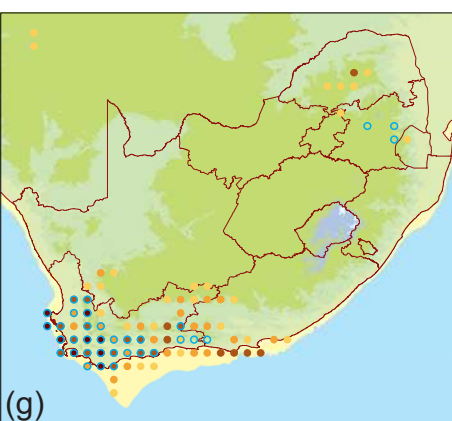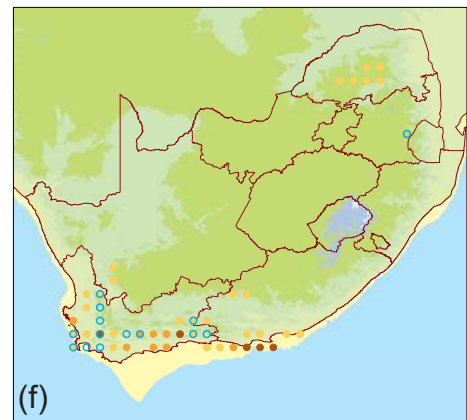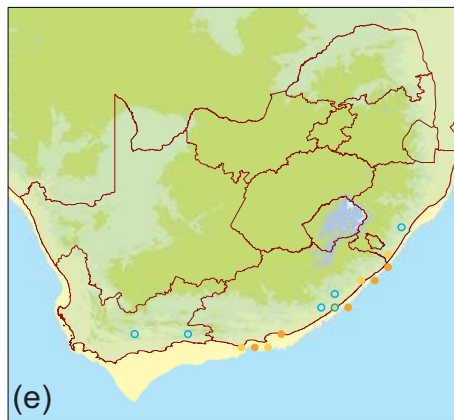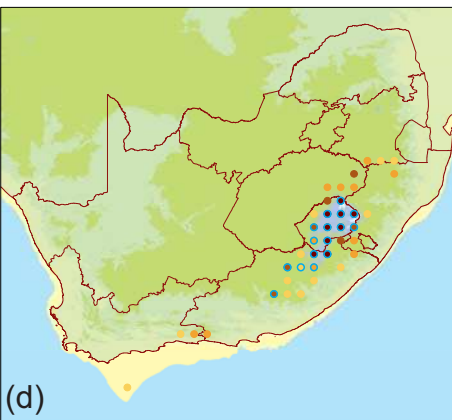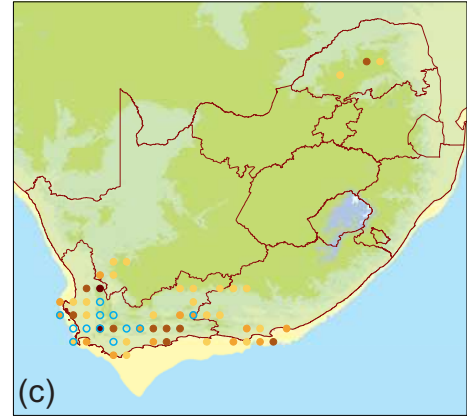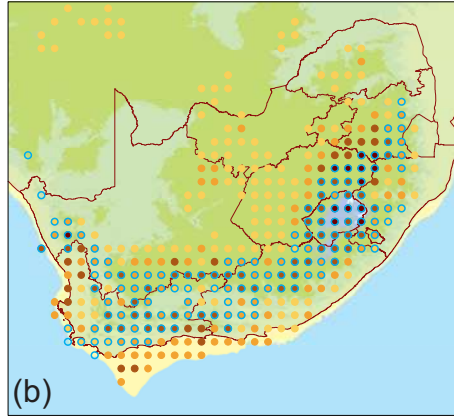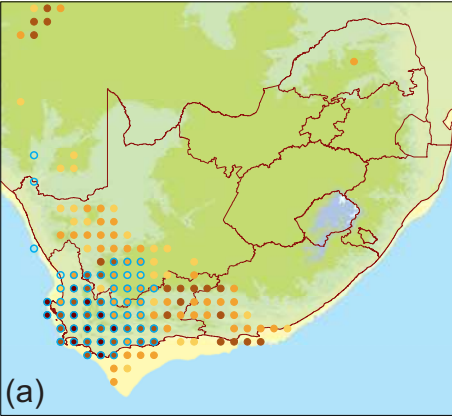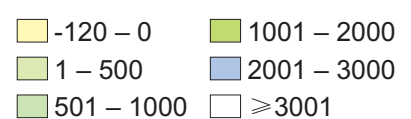
○ Grid cells simulated as suitable under present climatic conditions

● Grid cells simulated as suitable under LGM climatic conditions (Shading indicates simulated reporting rate; darker = higher)
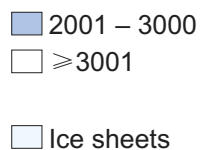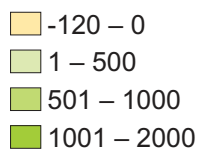
Legend

Pinus sylvestris
ANPP (g C m^{-2} yr^{-1})

- ▢ < 50
- ▢ 51 – 100
- ▢ 101 – 200
- ▢ > 200

Altitude (m)

- ▢ -120 – 0
- ▢ 1 – 500
- ▢ 501 – 1000
- ▢ 1001 – 2000

- ▢ 2001 – 3000
- ▢ ≥3001

- ▢ Ice sheets

Ericaceae (dwarf shrub)
ANPP (g C m^{-2} yr^{-1})

- ▢ < 10
- ▢ 11 – 25
- ▢ 26 – 50
- ▢ > 50