1 **Running head:** *colonisation-extinction under climate and habitat change*

2 **Colonisation and extinction dynamics of a declining migratory bird are influenced by**

3 **climate change and habitat degradation**

4

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18

19 Uncovering the mechanisms involved in the decline of long-distance migrants remains one of

20 the most prominent issues in European conservation. Since the 1980s the British breeding

21 population of Garden Warbler *Sylvia borin* has declined by more than 25%. Here we use data

22 from the Repeat Woodland Bird Survey to show that while the overall population is in

23 decline, the probability of occupancy for this species increased at high latitudes and

24 decreased at low latitudes between the 1980s and 2003-4. Range shifts such as this arise from

25 a change in the ratio of colonisations to extinctions at the range margins, and we therefore

26 relate colonisation and local extinction at the patch level to concurrent changes in climate and

27 habitat. We find that the probability of patch colonisation by this species is significantly

28 lower where the percentage cover of vegetation in the understorey has declined, which

29 reduces habitat quality for this species. The probability of local extinction is significantly

30 correlated with increasing mean May temperature, which may reflect a change in phenology

31 making breeding conditions less suitable. We conclude that changed regimes of grazing and

32 woodland management could be used to increase habitat suitability and therefore increase

33 colonisation probability at the local scale, which may in turn increase the probability of patch

34 occupancy despite future climatic unsuitability.

35

38

39   Long-distance migrants breeding in Europe are in decline and un-covering the mechanisms

40   involved during breeding, migration and over-wintering remains one of the most prominent

41   issues in European conservation (Thaxter *et al.*, 2010). Climate change and habitat

42   degradation on breeding and wintering grounds have been hypothesised as key drivers of

43   population changes within migratory species (e.g. Both *et al.*, 2010, Morrison *et al.*, 2010,

44   Ockendon *et al.*, 2012). Recent theoretical work has shown that spatial variation in both

45   habitat quality at the landscape scale and population processes are likely to be important

46   factors in determining how a species changes its range in response to climate change

47   (McInerny *et al.*, 2007, Anderson *et al.*, 2009, Mustin *et al.*, 2009).

48

49   Empirical work to date has identified a potential pattern of climate-induced range shifts

50   across a number of taxa (e.g. Parmesan *et al.*, 1999, Thomas & Lennon, 1999, Hickling *et al.*,

51   2005, Chen *et al.*, 2009). These studies used a range of metrics including location of the

52   species range margins (Thomas & Lennon, 1999, Hickling *et al.*, 2005), the average altitude

53   of individuals (Chen *et al.*, 2009), probability of occupancy (Wilson *et al.*, 2005) and the

54   balance between low and high temperature dwelling species within a community (Devictor *et*

55   *al.*, 2008). Ultimately, however, range shifts arise from a change in the ratio of colonisations

56   to extinctions at the range margins, such that an advance is caused by more colonisation than

57   extinction, and a contraction by the opposite (Parmesan *et al.*, 1999).

58

59   While climate change is one driver of range shifts, there is evidence that the threshold rate of

60   climate change through which a species can persist may be lowered by changing habitat

61   availability, and specifically that reduced habitat availability through habitat loss,

62   fragmentation and degradation could slow or even halt climate-induced range expansions

63   (Hill *et al.*, 1999, Travis, 2003). However, though work has begun to examine the influence

64   of synergistic interactions between climate change and habitat degradation on population size

65   and distribution (Opdam & Wascher, 2004, Brook *et al.*, 2008, Darling & Cote, 2008), there

66   remain very few empirical studies which consider the impact of both climate change and

67   changing habitat availability on observed changes in distribution.

68

69   The Garden Warbler *Sylvia borin* is a long-distance Afro-Palaearctic migrant passerine which

70   has experienced population declines and changes in distribution throughout Europe over the

71   last 30 years (Hewson *et al.*, 2007, European Bird Census Council, 2013). Declining species

72   often also show declines in the number of sites which are occupied, owing to the so-called

73   'Abundance-occupancy relationship' (Gaston *et al.*, 2000). Concurrent with the population

74   declines and distribution changes, the total area of suitable habitat for this species has

75   declined in parts of its British breeding range (Hopkins & Kirby, 2007, Amar *et al.*, 2010).

76   This species therefore provides an opportunity to explore the relative contributions of climate

77   change and habitat degradation on patch-level colonisation and extinction dynamics and

78   ultimately breeding distribution. We use bird survey data to relate changes in the distribution

79   of this population between the 1980s and 2003-4 to the changing availability of appropriate

80   habitat and suitability of the climate over the same time period. We make suggestions for

81   how this type of analysis can be useful for conservation management in the future.

82

Methods

This study used data from the Repeat Woodland Bird Survey (RWBS), which comprises data collected by The Royal Society for the Protection of Birds (RSPB) and The British Trust for Ornithology (BTO). Each woodland patch was surveyed in one year during the period 1981 to 1988. This broad sampling period reflects the fact that data were being collected for a number of different projects and were not coordinated at the national scale in this first sampling period. Re-survey data from the same 339 patches were collected in either 2003 or 2004. The majority of the analyses presented here used only 240 of the patches surveyed by the RSPB as these have detailed habitat information associated with the bird counts during both periods. The patches range from the south of England to North-West Scotland, although coverage is irregular (see Fig. 1a and Amar *et al.*, 2006).

Bird data

Study species

The Garden Warbler is a long-distance Afro-Palaearctic migrant which has part of its breeding range in the UK. The breeding habitat of Garden Warbler is deciduous or mixed woodland and scrub with an open canopy and a dense understorey; they nest predominantly in low vegetation, particularly bramble (Cramp, 1992). Garden Warblers are insectivorous during the breeding season and forage mainly in the shrub layer below 6 m (Cramp, 1992), and thus foraging efficiency is likely to be higher at patches where there is a well-developed shrub layer. Therefore, local population size may be influenced by changes in vegetation structure. Declines in the British population are more likely to have occurred at patches which have high canopy cover, low levels of bramble and lichen, and where the surrounding landscape is predominantly wooded (Amar *et al.*, 2006).

108   *Point count estimates of Garden Warbler occupancy*

109   The methodology was the same in both sampling time periods (1980 - 1981 and 2003 -

110   2004), but the timing of visits was moved one week earlier in 2003 -2004 to account for

111   potential changes in phenology. A series of randomly located points at each patch (*mean ± se*

112   no. points = 9.76 ± 0.11, range = 2 - 27) were visited twice, once in April or the first week of

113   May and again in the last three weeks of May or the first half of June. Points were separated

114   by at least 100 m and were at least 50 m from the edge of the wood. Counts of all birds seen

115   or heard were recorded over a five minute period. For further details see Amar *et al.* (2006).

116   Garden Warbler were considered to be present at a patch in each time period if they were

117   recorded at any of the survey points at either visit, and absent if they were not recorded.

118   **Habitat data**

119   Habitat recording was undertaken at each point count location within the survey patches.

120   Each point count location formed the centre of a 25 m-radius circle in which habitat

121   recording took place either at that level or in four 5 m radius subplots centred 12.5 m in each

122   of the four cardinal directions from the centre of the plot. A mean value for the point was

123   then calculated across the four sub-plots, and either these point level means or the point level

124   measures were then averaged for the patch.

125

126   Of the habitat variables measured, percentage vegetation cover at 0.5 - 2 m above the ground

127   (measured at the sub-plot level and here-after referred to as vegetation cover) was selected to

128   be used in this study. This variable was considered to be biologically significant for this

129   species based on their known breeding and foraging associations and previous analyses

130   (Cramp, 1992, Smart *et al.*, 2007). In order to assess the effects of change in habitat between

131   the two time periods on patch dynamics (colonisations and extinctions) by Garden Warbler,

132   the difference between time periods in vegetation cover at each patch was calculated and

133   these derived variables were used in subsequent analyses. For full details on survey methods

134   see Amar *et al.* (2006).

135

136   *Climate data*

137   As all climate variables were found to be collinear, May temperature was used as a proxy for

138   spring conditions. Spring conditions were considered to be biologically relevant for this

139   insectivorous species as conditions during the spring are known to influence invertebrate

140   abundance, diversity and phenology (e.g. Brakefield, 1987, Turner *et al.*, 1987, Pollard, 1988,

141   Roy *et al.*, 2001, Conrad *et al.*, 2002). Data for monthly mean May temperature for the years

142   1981-1988 and 2003-2004 were obtained from the Met Office (UKCIP) for the 5 km square

143   in which each patch fell. These values were then averaged to obtain one measure of monthly

144   mean May temperature for each patch for the 1980s and for the second survey period in

145   2003-2004. Again in order to assess the effects of change in temperature between the two

146   time periods on patch level colonisations and extinctions by Garden Warbler the difference

147   between time periods was calculated and this derived variable was used in subsequent

148   analyses.

149

150   *Statistical analyses*

151   The main aim of these analyses was to explore how changes in temperature and habitat relate

152   to variance in the probability of patch-level colonisation and extinction of Garden Warbler

153   from woodland patches between two time periods, in order to infer whether changes in

154   climate and habitat over a twenty year period may have influenced concurrent changes in

155   Garden Warbler distribution. Data exploration, statistical analyses and model validation were

156   carried out using R version 2.12.1 (R Development Core Team, 2009).

157

158 *Latitudinal variation in Garden Warbler occupancy*

159 Latitude and temperature change were correlated ($R^2 = 0.69$), therefore the effect of latitude

160 was modelled separately to the effects of change in vegetation cover and mean May

161 temperature. Binary logistic regression was undertaken to model the probability of patch

162 occupancy in relation to latitude with an interaction with time period to test for a significant

163 directional range change between the two time periods.

164

165 *Influence of temperature and habitat change on Garden Warbler colonisation and extinction*

166 Analyses were then conducted to model the probability of patch colonisation and extinction

167 in relation to the change in climate and habitat. All explanatory variables were standardised

168 using the overall mean and standard deviation (Gelman & Hill, 2007). The dataset was

169 divided into i) patches which were un-occupied in the first time period (which could

170 potentially be colonised by Garden Warbler between the surveys) and ii) patches which were

171 occupied in the first time period (from which Garden Warbler could potentially go locally

172 extinct between the surveys). Both datasets translate to a binary response variable where zero

173 represents no change (patches remain un-occupied or remain occupied respectively) and one

174 represents a change in occupancy status between the time periods (colonisation or extinction

175 respectively). Each of these subsets was analysed separately.

176

177 In this study we aimed to explain the effect of changes in climate and habitat on the processes

178 of colonisation and extinction, and therefore we adopted a null-hypothesis testing framework

179 to test the significance and estimate effect sizes of explanatory variables (Shmueli, 2010),

180 rather than an information theoretical approach that is more applicable to predictive

181 modelling (Burnham & Anderson, 2002). A generalised linear modelling (glm) approach was

182 used, with a binary error structure and a logit link. The full model for both colonisation and

183   extinction contained: 1) change in mean May temperature; 2) change in percentage vegetation

184   cover at 0.5-2m above ground level; and 3) an interaction between temperature and

185   vegetation change. Backwards step-wise deletion was used to remove each non-significant

186   explanatory variable in turn from the full model until only significant terms ($p < 0.05$)

187   remained, and this is considered to be the 'best model'. The coefficient of discrimination (D)

188   (Tjur, 2009) was calculated for each best model, as a measure of the ability of the model to

189   correctly predict higher probabilities of colonisation or extinction for patches which were

190   observed as ones (change in occupancy), compared to patches observed as zeroes (no

191   change):

192                              $$D = F_1 - F_0$$

193   where, F_1 and F_0 are the average fitted probability of colonisation or extinction for patches

194   which were observed to change in occupancy (ones), and patches which were not observed to

195   change in occupancy (zeroes) respectively. D varies between: minus one when all patches are

196   incorrectly assigned as zeroes and ones; and one when patches are all correctly assigned as

197   zeroes and ones. D is zero when all patches have a fitted probability of 0.5. All models were

198   checked for residual spatial auto-correlation using Moran's I.

199

200   **Results**

201   Between 1980 and 2004, Garden Warblers colonised 46 patches and went extinct from 75 of

202   the 339 patches. This represents 13.6% and 22.1% of patches respectively, and is comparable

203   to the changes observed in the restricted dataset (240 patches) upon which subsequent more

204   detailed analyses were conducted (15% and 22.5%). The pattern of colonisation and

205   extinction of patches by Garden Warblers was directional (Fig. 1b). Although low latitude

206   patches were always more likely to be occupied than high latitude patches (Fig. 1 c, 1d, 2a

207   and 2b), between the 1980s and 2003-2004 there was a decrease in the probability of patch

208   occupancy at lower latitudes from approximately 80% to approximately 60%, and an increase

209   in the probability of patch occupancy at higher latitudes from approximately 15% to

210   approximately 35% (Fig. 2; significant interaction with time period: *z-value* = -3.396, *p* <

211   0.001).

212

213   *Relationship between habitat and climate change and patch level colonisations and*

214   *extinctions*

215   The change in vegetation cover was the only explanatory variable retained in the 'best model'

216   distinguishing between patches that were colonised and those which remained unoccupied.

217   The mean vegetation cover at 0.5 - 2 m above ground level had, on average, increased

218   between the two time periods (Fig. 3a – solid line, *mean* = +6.3%). This increase was higher

219   at patches which had been colonised by Garden Warbler (Fig. 3a – short dashes, *mean* of

220   12.89%) than at those which had remained unoccupied (Fig. 3a – long dashes, *mean* of

221   2.81%). The probability of colonisation by Garden Warbler increased significantly where the

222   vegetation cover had increased (Fig. 4 – *p* < 0.01; *D* = 0.08; *β* = 1.42, *se* = ± 0.52).

223

224   Change in mean May temperature (°C) was the only explanatory variable retained in the 'best

225   model' distinguishing between patches from which Garden Warbler went extinct and those

226   which remained occupied. Mean May temperature had increased at all 136 patches between

227   the 1980s and 2003-4 (Fig. 3b - solid line, *mean* = +1.45°C). Patches from which Garden

228   Warbler had gone locally extinct had warmed slightly more, on average, than those which

229   had remained unoccupied (Fig. 3b - short dashes, *mean* of +1.5°C; and Fig. 3b - long dashes,

230   *mean* of +1.41°C respectively). The probability of local extinction of Garden Warbler

231   increased significantly for patches where average temperatures had increased the most (Fig. 5

232   $- p < 0.01; D = 0.08; \beta = 1.51, se = \pm 0.49$).

233

234   **Discussion**

235   Our results suggest that changes in climatic and habitat conditions have contributed to the

236   colonisation and extinction dynamics of a declining long-distance migrant in the UK. As

237   range dynamics are ultimately driven by the ratio of colonisations to extinctions at the range

238   margins, we suggest that taking this approach, as opposed to modelling presence/absence or

239   abundance, can be a powerful tool for understanding the processes through which climate

240   change and other threatening processes impact on range shifts and contractions.

241

242   For Garden Warbler in the UK, in general, more colonisations than extinctions have occurred

243   at high latitudes, and more extinctions than colonisations have occurred at low latitudes

244   between the 1980s and 2003-4 (Fig. 1b and 2). While this pattern fits with the expectation for

245   a climate-induced range shift, we find that the probability of colonisation of a site by Garden

246   Warbler is not significantly related to temperature change, but is highest where sites have

247   shown larger increases in vegetation cover at 0.5-2m above ground level (Fig. 4). Extinctions

248   however are more likely to have occurred where temperatures have increased more (Fig. 5).

249

250   In the UK , changes in woodland management (Morecroft *et al.*, 2001, Gill & Fuller, 2007)

251   and the increasing numbers of native and non-native deer over the past 30 years (Ward, 2005)

252   have contributed to a shift from coppice and scrub towards high forest, with 97% of broad-

253   leaved woodlands falling in to the latter classification by 2002 (Hopkins & Kirby, 2007).

11

254 Canopy closure and browsing by deer have acted to reduce vegetation cover, particularly of

255 species such as bramble and other tall-growing herbs, and open up the understorey (Cooke &

256 Farrell, 2001, Kirby, 2001, Morecroft *et al.*, 2001, Gill & Fuller, 2007, Amar *et al.*, 2010).

257 Declines in woodland birds of conservation concern have been linked to changes in habitat

258 resulting from increases in deer populations in lowland England (Newson *et al.*, 2012).

259 Given their dependence on low vegetation cover, the low probability of colonisation of a site

260 by Garden Warblers where vegetation cover has declined is not unexpected. However, it does

261 highlight a potentially useful management option, as our results indicate that increasing low

262 vegetation cover – either through direct management such as coppicing and pollarding

263 (Plantlife, 2011), or by management of deer numbers where deemed appropriate – should

264 increase the likelihood that Garden Warbler will colonise, or re-colonise woodland sites. This

265 could also be important for other declining woodland birds such as Willow Tit *Poecile*

266 *montanus*, Marsh Tit *Poecile palustris* and Common Nightingale *Luscinia megarhynchos*

267 which nest and forage in the under-storey (Cramp, 1992, Hinsley *et al.*, 2007, Lewis *et al.*,

268 2009). However, it is important to note that management strategies must take into account a

269 whole suite of plant and animal species with differing requirements, and management for

270 woodland birds is only one aspect of an overall management plan.

271

272 The relationship between the probability of site-level extinctions and larger increases in

273 temperature implies that some sites are warming to an extent that they are outside the suitable

274 range for this species. However, notwithstanding the fact that in more extreme parts of its

275 range this species may be confined to microclimates, for example high altitudes in southern

276 Europe, the broad geographical extent of this species' European range means that climatic

277 conditions within the UK are unlikely to exceed those within which this species can breed.

278 However, the timing of spring migration and laying dates for several bird species have been

279   shown to advance in line with climatic changes (e.g. Crick *et al.*, 1997, Jonzén *et al.*, 2006).

280   The extent of these changes may differ from other environmental events at different trophic

281   levels, potentially leading to a phenological mis-match (e.g. Both *et al.*, 2009) which may

282   affect reproductive success or survival at higher trophic levels, leading to population declines

283   (e.g. Møller *et al.*, 2008). An example for insectivorous species such as Garden Warbler is the

284   timing of invertebrate emergence. Spatial variation in the extent of such phenological mis-

285   matching could help to explain the increased extinction risk with greater changes in

286   temperature observed for this species (Fig. 5), for example if mis-match is more extreme at

287   lower latitudes where more extinctions have occured. Indeed, this same pattern has been

288   observed at a European-scale in a study by Both *et al.* (2010). They found that declines in

289   long-distance migrant species, including Garden Warbler, were significantly greater in

290   Western Europe, where spring temperatures have shown considerable increases, than in

291   Northern Europe where temperatures during spring arrival and breeding have not increased to

292   the same extent. They suggest that this is driven by trophic mis-matches resulting from

293   temperature increases in the Spring. They highlight that such mis-matches will affect long-

294   distance migrants to a greater extent than other species owing to their complex annual life-

295   cycle.

296

297   While our results suggest significant relationships between changes in climate and habitat and

298   extinction-colonisation dynamics for Garden Warbler it is important to note that the effect

299   sizes are relatively small, and the coefficients of determination, while positive (indicating that

300   zeroes and ones are correctly assigned more often than not), are also very small. The

301   processes of colonisation and extinction are complex, and likely governed by numerous

302   factors which we were unable to include in our models. For example, the probability of

303   colonisation is related to habitat suitability of the focal patch, and dispersal pressure from the

304 surrounding patches, which means that some sub-optimal patches may be colonised.

305 Furthermore, in the present study we have only considered conditions on the breeding

306 grounds, though it is possible that if migratory connectivity (the extent to which individuals

307 which breed in the same or a different location within the breeding grounds also over-winter

308 in the same or a different location within the wintering range (Marra *et al.*, 1998, Gill *et al.*,

309 2001)) is strong then environmental change in the non-breeding season, such as drought in

310 the Sahel region could create small-scale variation in breeding season population trends as a

311 result of reduced over-winter or passage survival (Morrison *et al.*, 2010).

312

313 Additionally, the spatial distribution of sampling sites is not continuous, but rather consists of

314 two large study regions, one in the south and one in the north (Fig. 1a). These types of

315 limitations may be commonly encountered when using data which were not collected with

316 the specific question in mind, as was the case here. However, The uneven spatial distribution

317 of sites was to some extent compensated for in the analysis of the effect of latitude on the

318 probability of occupancy in each time period (Fig. 2) as a larger dataset was available (339

319 patches, c.f. 240 patches) which gave a more continuous coverage. However, owing to the

320 availability of habitat data the restricted dataset had to be used for all subsequent analyses. As

321 the available data actually represent the geographic extremes of the United Kingdom (Fig. 1a)

322 this uneven coverage is unlikely to have biased the results to a great extent, and as previously

323 stated, if anything it is expected that a more even spatial coverage would strengthen the

324 relationships detected here

325

326 A more serious limitation to the analyses presented here is that each survey only consists of

327 one visit to each site in each time period. Analyses of changes in occupancy would ideally be

328 carried out in an occupancy modelling framework (MacKenzie *et al.*, 2005), which uses

329 multiple visits to the same site to account for detection probability, or the probability that a

330 species which is present is not detected on a given visit and is therefore recorded as absent.

331 This could be particularly problematic at sites where habitat has changed as it may be

332 expected that the ability to detect the species could have been affected. The data presented

333 here consist of two visits to each patch per sampling period. However, the timing of these

334 visits was planned to detect early and late arriving migrants, and as such the first visit

335 recorded almost no Garden Warbler because they had not yet returned from their African

336 wintering grounds. To check for a possible change in detection probability we compared the

337 number of point counts at which Garden Warbler were detected within occupied patches

338 between the two time periods, and found no systematic differences, which increases our

339 confidence that changes in occupancy are true changes in occupancy. However, it is still

340 possible that false negatives, where Garden Warbler were actually present but went un-

341 detected, occurred during both sampling periods. We recommend that the design of any

342 future studies of this nature ensure that repeat visits are made to each site in such a way that

343 detection probabilities could be estimated.

344

345 Given the complex nature of the impacts of climate change on animal abundance and

346 distribution (e.g. Mustin *et al.*, 2007), together with the well recognised limitations of climate

347 envelope models (for review see Hampe, 2004) a more robust approach might be to base

348 management decisions on inferences made on a smaller spatial scale but incorporating more

349 detailed information on factors involved in species distribution. Range shifts arise from the

350 balance of colonisations and extinctions towards the range margins; therefore we recommend

351 that where possible this is the metric used to quantify range shifts, and to explore potential

352 mechanisms of range change. By examining habitat and climate relationships of an organism

353 at different parts of its distribution, and in different time periods, we have been able to infer

354   that while climate change may be reducing the suitability of some woodland patches for this

355   declining species, increasing habitat suitability through management actions can increase

356   colonisation probability at the local scale. It may therefore be possible to halt or even reverse

357   the declines at low latitude patches by changing grazing regimes and woodland management

358   practices, which may in turn increase the probability of patch occupancy despite future

359   climatic unsuitability.

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Figure legends

514 Figure 1: Maps to show: a) the location of all 240 patches surveyed in the RSPB dataset; b)

515 the patches which were colonised by Garden Warbler between the two survey periods (blue

516 squares) and those from which Garden Warbler went locally extinct (red circles); c) the

517 distribution of occupied (black squares) and unoccupied (grey circles) patches in 1981 –

518 1988; and d) the distribution of occupied (black squares) and unoccupied (grey circles)

519 patches in 2003 - 2004.

520

521 Figure 2: The fitted probability of Garden Warbler occupancy of 339 woodland patches in

522 1981-88 (a) and in 2003-4 (b) at differing latitudes within the UK. Histograms show the

523 number of occupied and unoccupied woodland patches. Figure c shows the change in

524 predicted probability of occupancy between 1981-88 and 2003-4 against latitude, and the

525 dashed line shows no change.

526

527 Figure 3: Change, at varying latitudes between the 1980's and 2003-4, in (a) vegetation

528 cover at 36 patches which were colonised by Garden Warbler during that period (closed

529 squares), compared to 68 patches which remained unoccupied (open squares); and (b) mean

530 May temperature at 54 patches from which Garden Warbler went locally extinct (closed

531 triangles), compared to 82 patches which remained occupied (open triangles). Solid line =

532 mean change across all patches; long dashes = mean change across patches which remained

533 unoccupied (a) or occupied (b) by Garden Warbler; short dashes = mean change across

534 patches which were colonised by Garden Warbler (a) or from which Garden Warbler went

535 locally extinct (b).

536

537   Figure 4: The predicted probability of colonisation of 104 woodland patches by Garden

538   Warbler between the 1980's and 2003-4 as a function of change in mean % vegetation cover

539   at 0.5-2m above ground level ($p < 0.01$; $D = 0.08$; $\beta = 0.04$, $se = \pm 0.01$). Histograms show

540   the number of colonised ($n = 36$) and unoccupied ($n = 68$) woodland patches.

541

542   Figure 5: The predicted probability of local extinction of Garden Warbler from 136 woodland

543   patches between the 1980's and 2003-4 as a function of change in mean May temperature (p

544   < 0.01; $D = 0.06$; $\beta = 3.23$, $se = \pm 1.25$). Histograms show the number of woodland patches

545   which remained occupied ($n = 82$) and from which Garden Warbler went extinct ($n = 54$).

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549   Figure 1

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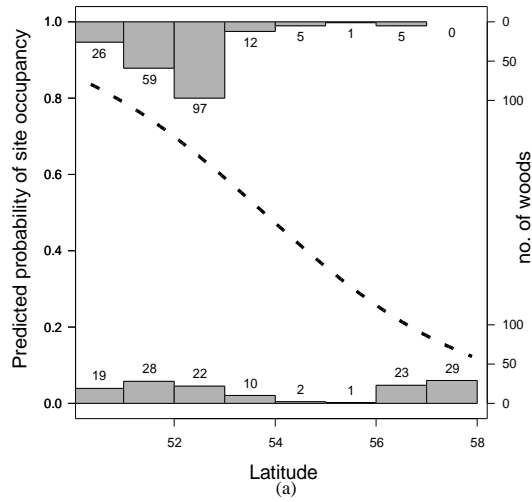
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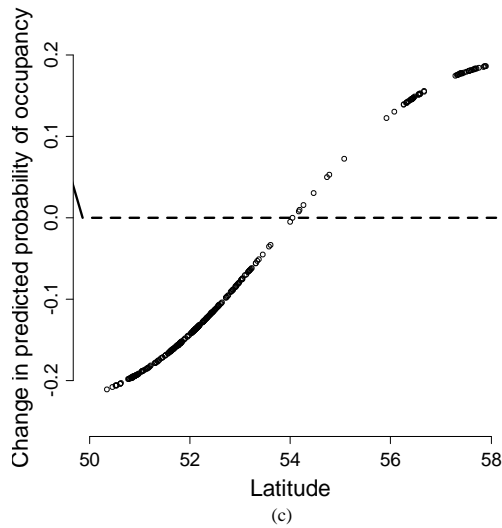
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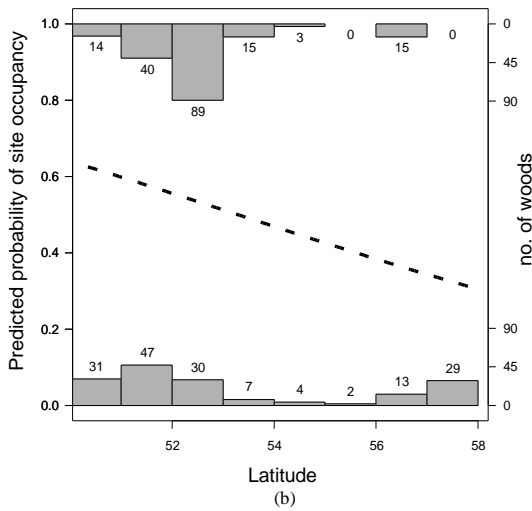
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577   Figure 2

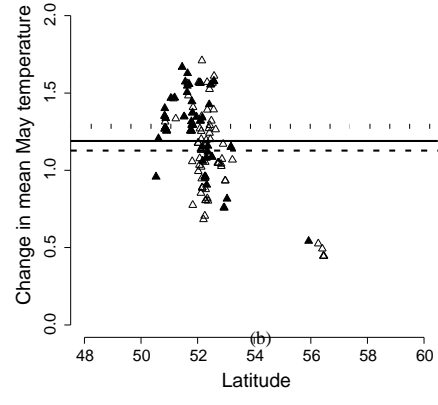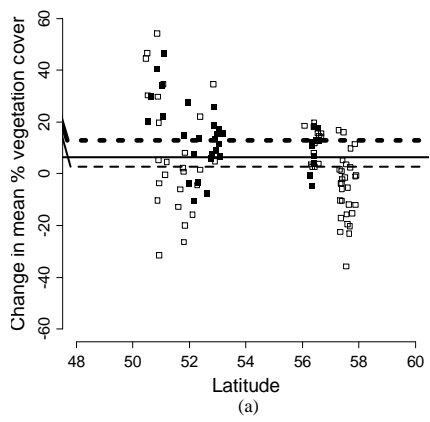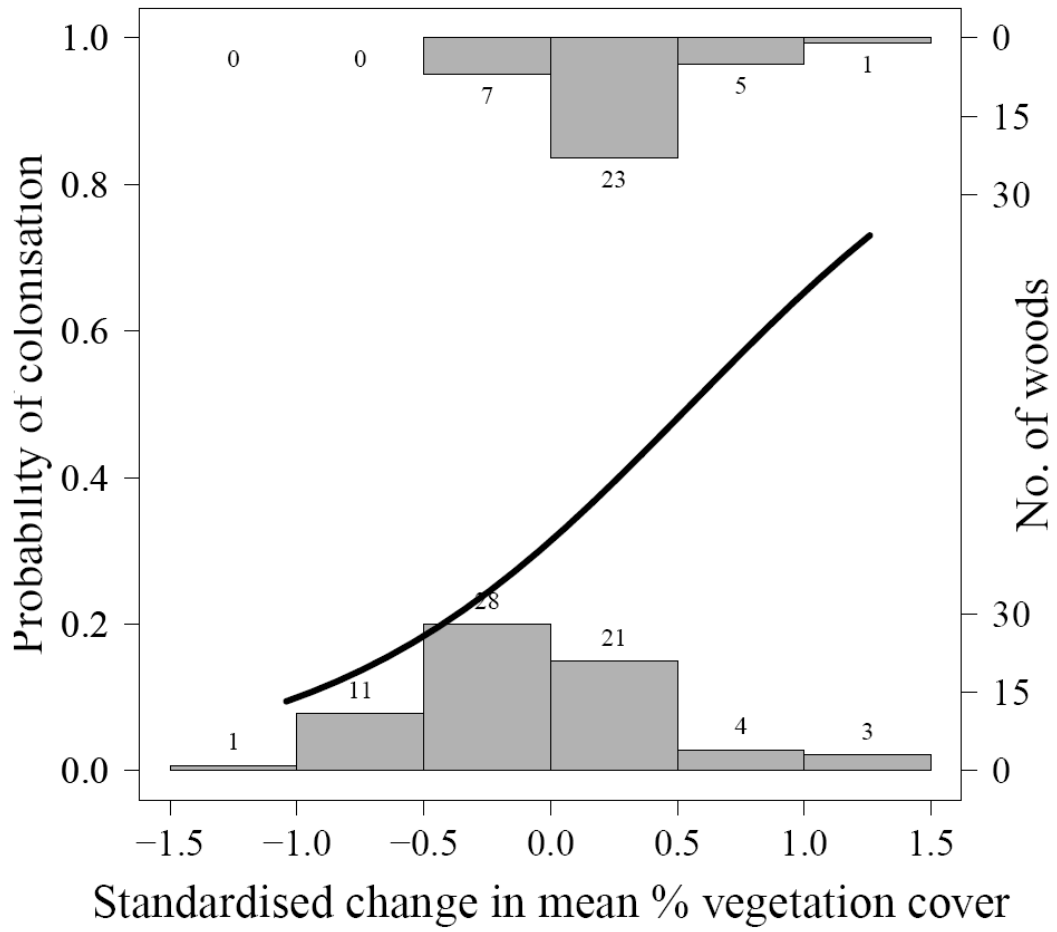578

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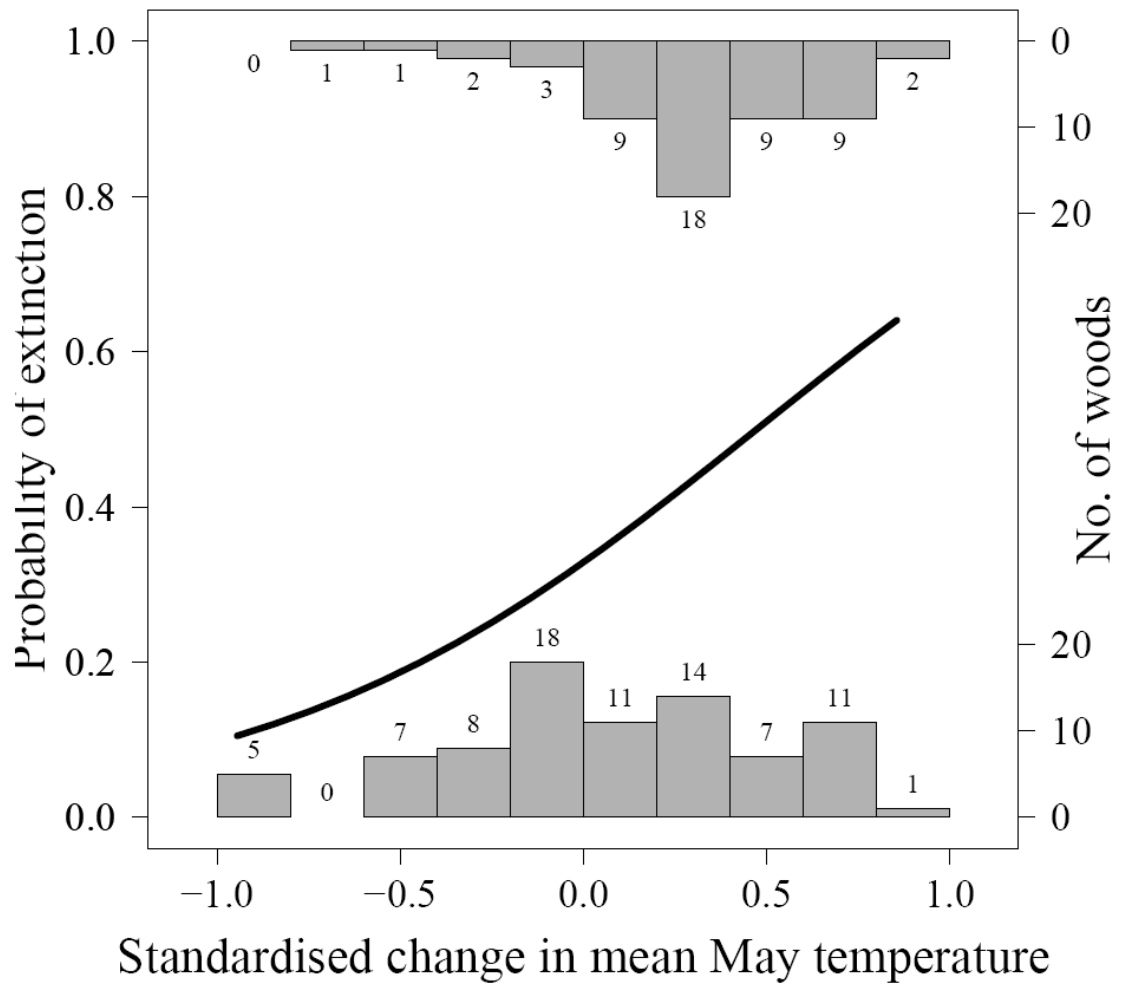
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