1 **Trait correlates of distribution trends in the Odonata of Britain and Ireland: Southern species**

2 **benefit from climate warming**

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12

13 **Abstract**

14 A major challenge in ecology is understanding what enables certain species to persist, while others

15 decline, in response to environmental change. Trait-based comparative analyses are useful in this

16 regard as they can help identify the key drivers of decline, and highlight traits that promote

17 resistance to change. Despite their popularity trait-based comparative analyses tend to focus on

18 explaining variation in range shift and extinction risk, seldom being applied to actual measures of

19 species decline. Furthermore they have tended to be taxonomically restricted to birds, mammals,

20 plants and butterflies. Here we utilise a novel approach to estimate trends for the Odonata in

21 Britain and Ireland, and examine trait correlates of these trends using a recently available trait

22 dataset. We found the dragonfly fauna in Britain and Ireland has undergone considerable change

23 between 1980 and 2012, with 33 and 39% of species showing significant declines and increases

24 respectively. Distribution type was the key trait associated with these trends, where southern

25 species showed significantly higher trends than widespread and northern species. We believe this

26   reflects the impact of climate change as the increased ambient temperature in Britain and Ireland

27   better suits species that are adapted to warmer conditions. We conclude that northern species are

28   particularly vulnerable to climate change due to the combined pressures of a decline in climate

29   suitability, and competition from species that were previously limited by lower thermal tolerance.

30

31   **Introduction**

32   Defaunation, the loss of species and populations (Dirzo *et al.*, 2014), is occurring at an alarming rate

33   with recent estimates suggesting that the current extinction rate is 1000 times that of the historical

34   natural background rate (De Vos *et al.*, 2014). These declines are driven by environmental change,

35   particularly habitat loss and climate change, and can be measured in a number of ways, e.g. changes

36   in distribution and abundance (Thomas *et al.*, 2004; Biesmeijer *et al.*, 2006; Butchart *et al.*, 2010;

37   Chen *et al.*, 2011). Variation in species responses to environmental change has been found across

38   broad taxonomic groups (Hickling *et al.*, 2006; Angert *et al.*, 2011) but also within taxonomic groups,

39   i.e. between species within an order (Hickling *et al.*, 2005). A major challenge in conservation

40   ecology is to gain a better understanding of this interspecific variation in response to environmental

41   change, i.e. what enables certain species to persist while others decline?

42

43   Species traits play an important role in determining species' ability to resist environmental change.

44   For example, several studies have shown that ecological generalists out-perform specialists (Walker

45   & Preston, 2006; Ozinga *et al.*, 2012; Newbold *et al.*, 2013). Such comparative trait-based analyses

46   are popular, as the models help to identify the main drivers of change and allow the prediction of

47   future biodiversity changes based on environmental forecasts (Fisher & Owens, 2004; Cardillo *et al.*,

48   2006). Previous comparative trait analyses have tended to focus on explaining variation in range

49   shift (Angert *et al.*, 2011; Mattila *et al.*, 2011; Grewe *et al.*, 2012) and extinction risk (Purvis *et al.*,

50   2000; Koh *et al.*, 2004; Cardillo *et al.*, 2008; Cooper *et al.*, 2008; Fritz *et al.*, 2009). Despite its

51   popularity, the comparative trait-based approach has seldom been applied to direct measures of

52   species' changing status (i.e. rates of decline or increase). Currently data on such measures of

53   decline are rare, particularly at large (e.g. national) scales and across multiple species. With the

54   increase in public participation in biological recording, the availability of large-scale distribution

55   datasets has increased (Silvertown, 2009). Such data tend to be collected without systematic

56   protocols and thus contain many forms of sampling bias and noise, making it hard to detect genuine

57   signals of change (Tingley & Beissinger, 2009; Hassall & Thompson, 2010; Isaac *et al.*, 2014b).

58   However, recent advances in analytical approaches have improved our ability to estimate reliable

59   trends from these unstructured biological records (Isaac *et al.*, 2014b). In this study we utilise these

60   novel approaches to estimate trends for the Odonata in Britain and Ireland, and use species traits to

61   test hypotheses for the interspecific variation in trends.

62

63   We chose to examine Odonata for a number of reasons. Firstly, previous trait-based comparative

64   analyses have tended to focus on birds, mammals, plants and butterflies. Despite being highly

65   species rich and their crucial role across ecosystems, the non-butterfly invertebrate fauna are

66   comparatively poorly studied (IUCN, 2001; Dirzo *et al.*, 2014). Secondly, Odonata are thought to be

67   excellent bioindicators as they are sensitive to degradation of water ecosystems (Samways &

68   Steytler, 1996; Sahlén & Ekestubbe, 2001; Lee Foote & Rice Hornung, 2005). Thirdly, they provide a

69   valuable ecosystem service as they feed on many insect pests (Brooks & Lewington, 2007). Finally,

70   the publication of a new atlas (Cham *et al.*, 2014) and trait datasets (Powney *et al.*, 2014) for British

71   Odonata together constitute some of the best quality data of any non-butterfly invertebrate group.

72

73   Previous research based on Odonata occurrence data has focussed on the impact of climate change

74   on phenology and distribution. For example Hassall *et al.*, (2007) discovered that emergence from

75   overwintering had significantly advanced over the past 50 years, while Hickling *et al.*, (2005) showed

76   that the upper latitudinal margin shifted north between 1960 and 1995. Outside Britain, Bush *et al.*,

77   (2014) used species distribution models (SDMs) to predict which Australian odonates were under

78   threat from climate change.

79

80   Several studies have utilised traits to explain variation in several aspects of Odonata ecology, but

81   typically focus on explaining variation in species response to climate change. In terms of

82   phenological advancement, Hassall *et al.*, (2007) noted that spring species and those without egg

83   diapause exhibited increased phenological shifts. Angert et al (2011) examined trait correlates of

84   range shift across multiple taxonomic groups, finding that exophytic Odonata species in Britain

85   shifted further north, on average, than endophytic species. These insights, combined with extensive

86   knowledge about their natural history (Brooks & Lewington, 2007), form the basis of seven

87   competing hypotheses (outlined below) that aim at explain the interspecific variation in the

88   distribution trends among British Odonata.

89

90   All traits included in the analysis have been shown to affect species' ability to respond to

91   environmental change. Habitat breadth is frequently related to species trends, where habitat

92   generalists outperform specialists due to their greater ability to adapt to novel environmental

93   conditions (Fisher & Owens, 2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012). Ball-Damerow *et al.*,

94   (2014) found evidence of the widespread expansion of habitat generalists which has led to biotic

95   homogenization in the dragonfly fauna of California and Nevada over the last century. We test the

96   hypothesis that Odonata in Britain and Ireland follow the patterns outlined above, with generalists

97   out-performing specialists. Dispersal ability affects species' ability to respond to environmental

98   pressures, with higher dispersal ability linked to an enhanced ability to respond (Thomas *et al.*, 2001;

99   Pöyry *et al.*, 2011; Grewe *et al.*, 2012). Using SDMs, Hof *et al.*, (2012) found lentic (i.e. pond and lake

100 dwelling) species had a greater ability to track changes in their climatic niche. This was linked to

101 greater dispersal ability, which is essential given the ephemeral nature of their breeding sites (Hof *et*

102 *al.*, 2006). We predict lentic species will have higher (more positive) trend estimates than lotic

103 species as their increased dispersal ability enables them to persist during times of environmental

104 change through the efficient relocation to newly suitable areas. Geographic range size and body size

105 are both frequently used as surrogates for a whole host of traits associated with ecological

106 specialism and competitive ability (Gittleman, 1985; Gaston, 2003; Angert *et al.*, 2011). We predict

107 that widespread species and the larger, therefore more competitive species, are likely to show

108 positive trends. Climate warming has increased the suitability of the landscape to those species that

109 were previously limited by their lower thermal tolerance threshold (Devictor *et al.*, 2008;

110 Dingemanse & Kalkman, 2008; Bellard *et al.*, 2012), therefore we predict that southerly distributed

111 species will show the highest trend estimates. An additional aspect of climate change that has been

112 linked with trends in Odonata is the increase in flood events in Britain. Species which overwinter as

113 larvae are particularly vulnerable to flooding as they can be swept away from ideal habitat areas to

114 unsuitable regions in which they cannot persist (Cham *et al.*, 2014). Alternatively, floods may aid the

115 dispersal of such species that overwinter as larvae and therefore we may expect to see positive

116 trends for such species. Finally we test the hypothesis that flight period will be positively related

117 with species' trend. Grewe *et al.*, (2012) argued that species with longer flight periods have

118 increased dispersal ability, and therefore have a greater capacity to adapt in response to

119 environmental change.

120

121 **Materials & Methods**

Occurrence trends

123 Trends were estimated from Odonata distribution records in Britain and Ireland collected by the

124 Dragonfly Recording Network and coordinated by the British Dragonfly Society. Our analyses are

125 based on 895,022 records of 38 native species collected between 1980 and 2012 where the

126 recording date is known and the location was recorded to 1 km^2 precision or better. As these

127 occurrence records were collected without a specific sampling design they contain a variety of bias

128 which inhibit their use in estimating reliable trends. For example, the number of records collected

129 each year has increased dramatically over time (Cham *et al.*, 2014), such that simply counting the

130 number of occupied sites would produce biased trend estimates (Prendergast *et al.*, 1993; Isaac *et*

131 *al.*, 2014b). To account for these biases we estimated species trends using a method known

132 elsewhere as the 'well-sampled sites' (Isaac *et al.*, 2014a), which aims to remove the noise and bases

133 the statistical inference on a 'well-sampled' subset of the data. We first arranged the records into

134 239,392 visits, which are defined as unique combinations of date and 1 km^2 grid cell (site). For each

135 visit, each of the 38 species was coded as either recorded (1) or not-recorded (0). We then removed

136 all visits where less than three species were recorded, since these short lists probably represent

137 incomplete sampling (van Strien *et al.*, 2010). We then selected sites with at least three years of

138 data, ensuring we retained only the 'well-sampled' sites (Figure 1). Our final dataset contains

139 357,654 records from 67,382 visits to 5,352 sites (30,481 site-year combinations). Different

140 thresholds for defining the well-sampled set (two species recorded and two years of data) produced

141 qualitatively identical results (not shown). For each species, we estimated a linear trend in the

142 probability of being recorded on an average site visit. This was achieved using binomial generalised

143 linear mixed-effects models (GLMMs), implemented by the R package *lme4* (Bates *et al.*, 2011), with

144 the log odds of being recorded modelled as a linear function of a fixed effect for year, and a random

145 intercept for site. We used the slope estimate for the fixed effect of year as our trend measure.

146

7

147   *Traits*

148   We included data on seven traits extracted from Powney *et al.* (2014) (Table 1). Two traits were

149   based on characteristics of a species' distribution pattern, the first, species status, was measured as

150   an ordinal variable based on distribution size, moving from very rare through to very widespread.

151   Secondly, distribution type was a categorical variable that defined a species broad climatic

152   restriction. Species were classified into one of four levels, northern, southern, oceanic or

153   widespread based on their distribution pattern. We included a single morphological trait, thorax

154   length (mm), which was taken as the mean of multiple measurements from museum specimens.

155   Flight period duration was measured as the number of months during which adults are typically

156   recorded in flight. We included two habitat based traits, habitat breadth measured the number of

157   broad habitats a species can utilise, while breeding habitat classified species based on breeding

158   habitat preference, lentic, lotic or both. Finally, we classified species based on their overwintering

159   stage, either eggs, larvae or both. Overwintering stage, breeding habitat and distribution type were

160   coded as continuous variables: Overwintering stage (eggs = -1, both = 0, larvae = 1), breeding habitat

161   (lentic = -1, both = 0, lotic = 1), distribution type (very rare = -1.5, rare = -1, scarce = -0.5, local = 0.5,

162   widespread = 1, very widespread = 1.5). All continuous traits were centred on zero prior to the

163   analysis and ordinal variables were treated as continuous. Following the various exclusion criteria

164   and the coverage of trait data, the final dataset used in this study covered 36 species.

165

166   *Trait analysis*

167   We used the *pgls* function from the R package *caper* (Orme, 2012) to run phylogenetically informed

168   linear models to examine trait-trend relationships while accounting for phylogenetic non-

169   independence (Freckleton *et al.*, 2002). In all phylogenetically informed models, the level of

170   phylogenetic correction (Pagel's λ) was estimated via maximum likelihood (Pagel, 1999; Freckleton

171 *et al.*, 2002). Due to data limitations we used a phylogeny based on taxonomy for the analyses. The

172 phylogeny was built using the *as.phylo* function from the R package *ape* (Paradis *et al.*, 2005) with

173 nodes based on Suborder, Family, Genus and Species, and all branch lengths were set to one.

174

175 The trend measures extracted from each species model formed the response variable for the trait-

176 trend analysis. While this year slope estimate is a useful measure of the direction and intensity of

177 the temporal trend in occupancy in an average site, it does not account for uncertainty in its

178 estimation. We therefore repeated all trait analyses using the year slope estimate weighted by the

179 inverse of its standard error and also the z-score of the fixed effect of year as the response variables.

180 These additional analyses enabled us to examine how robust our results were in relation to

181 uncertainty in our trend estimates.

182

183 To determine the main trait correlates of our species trends we utilised a multi-model inference

184 approach. We applied the *dredge* function of the R package *MuMIn* (Barton, 2013) to fit models for

185 all possible combinations of explanatory trait variables and then ranked them based on AICc. We

186 then extracted the model averaged coefficient for each trait that was present in at least one

187 candidate model from the subset of top models. In addition, we identified the importance of each

188 trait based on its frequency in the subset of top models. The importance scores and the model

189 averaged coefficients were used to determine the main traits for explaining species trends. The set

190 of candidate models was defined as models with ΔAIC ≤ 2. Burnham *et al.* (2010) suggest there is

191 often support for models where ΔAIC is < 7, however, we chose to use ΔAIC < 2 as the null model

192 was the 3rd best model with a ΔAIC of 1.12 and therefore increasing the ΔAIC threshold was simply

193 adding noise (models with little evidence to support them) to the key result.

194

195 A multi-model inference approach while accounting for phylogeny is not straight-forward. In our

196 PGLS models, λ was estimated independently for each model and can therefore be different

197 between the candidate models. Using AIC to compare between these models could be misleading as

198 we could not disentangle the influence of a difference in the evolutionary model (λ) from the

199 influence caused by changing which traits were included in the model on AIC scores. However, all of

200 the models in the top subset had an estimated λ value of 0, implying that species trend in the UK is

201 not phylogenetically-patterned. Therefore ΔAIC was measuring the effect of the trait differences

202 rather than any potential difference in the evolutionary model in this case. All analyses were carried

203 out using R 3.0.2 (R Core Team, 2013).

204

205 **Results**

206 We found significant trends for 72% of the species in this study: of these, 12 were decreasing and 14

207 species were increasing. Species included that showed the greatest declines included: *Ischnura*

208 *pumilio*, *Leucorrhinia dubia* and *Sympetrum danae*, while *Libellula fulva*, *Erythromma najas* and

209 *Brachytron pratense* showed the greatest increases. Using the fitted values from the species trend

210 models we estimated the change in probability of observation over a ten year period for each

211 species. Each species was then categorised using these ten year changes (Figure 2). This figure

212 illustrates the substantial variation in the trend estimates between species, and again highlights the

213 large proportion declining species which is a cause for concern.

214

215 Six models containing various combinations of three traits (distribution type, flight period and thorax

216 length) formed the top subset of models for explaining Odonata distribution trends (Table 2). Of

217 these three traits, distribution type was the most important (importance score = 0.6), and was

218 present in three of the top models. The model averaged coefficients for distribution type reveal that

219 southern species tend to have increased relative to the other categories and northern species have

220 declined on average, with the other two categories (oceanic and widespread) intermediate (Figure

221 3). Notable exceptions to this trend include the strong declines in *Ischnura pumilio* and *Gomphus*

222 *vulgatissimus* both of which were classified as southern species. Flight period was present in two of

223 the top models and had an importance score of 0.34. The coefficient was negative, suggesting that

224 species with longer flight periods had a lower trend estimates (i.e. they declined relative to species

225 with short flight periods). Thorax length was also present in two of the top models but had the

226 lowest importance score (0.24) of all traits present in the top model subset. The model averaged

227 slope for the relationship between thorax length and trend estimate was marginally positive, which

228 suggests that larger species were faring better than smaller species. We note that the 95%

229 confidence intervals of both flight period and thorax length spanned zero, and that the null model

230 was the third best model based on AICc. The top two models explained a modest 13 and 16% of the

231 variation in species trend.

232

233 In general, the key trait-trend relationships and importance scores were robust across the different

234 response variables and modelling approaches (Appendix 1 & 2). Distribution type was the most

235 important trait for four of the five response/modelling approach combinations, while flight period

236 and thorax length were consistently important (Appendix 3). The model averaged coefficients for

237 these three traits were similar across approaches. Other traits including habitat breadth,

238 overwintering stage, breeding habitat and status, were retained in the top model subset for some of

239 the other approaches. However, the model averaged 95% confidence intervals spanned zero in the

240 vast majority of cases for these additional traits (Appendix 2).

241

242 **Discussion**

243   We found that the dragonfly fauna in Britain and Ireland has undergone considerable change during

244   recent decades, with high levels of inter-specific variation in occurrence trends (Figure 2). We found

245   twelve species (33%) had significant negative trends, while 14 species (39%) showed significant

246   increases. Although more species increasing than decreasing is good news for conservation, this

247   could be interpreted as a signal of biotic homogenization, i.e. the fauna becomes dominated by a

248   small number of species, and local and regional difference between communities are eroded (Keith

249   *et al.*, 2009).

250

251   We found distribution type was the key correlate of Odonata trends, with southern species tending

252   to have higher trend estimates than the all other distribution types (Figure 3). This result is in line

253   with our hypothesis that increased temperatures has increased the climate suitability of Britain and

254   Ireland for southerly distributed species. A variety of studies have provided evidence of this

255   relationship, i.e. Devictor *et al.* (2008) found bird communities in France between 1989 and 2006

256   were increasingly dominated by species that prefer warmer conditions, while Lima *et al.* (2007)

257   found evidence of northward range expansions in warm-water adapted Portuguese algae. Hickling

258   *et al.* (2005) used distribution type to explain variation in range shift and expansion in British

259   Odonata, finding that southern species showed greater poleward shifts and expansions compared to

260   northern species. By contrast, Angert *et al.* (2011) found no correlation between range shift and

261   position of the northern range limit (which is related to our measure of distribution type). Despite

262   the wealth of evidence that points to climate change as the likely driver of increases in southern

263   species, we cannot ignore the role of improved water quality and standing water availability in

264   southern Britain (Hickling *et al.*, 2005; Cham *et al.*, 2014). Not all southern species showed positive

265   trend (notably *Ischnura pumilio* and *Gomphus vulgatissimus*), this limited expansion in response to

266   climate warming is likely due to availability of suitable habitat.

267

268   The lower trend estimates for northern species is likely to be the result of the combined pressures of

269   a decline in climate suitability and competition from species that were previously limited by lower

270   thermal tolerance (Myers *et al.*, 2009; Thomas, 2010). Evidence of the loss of northern species has

271   been seen in a variety of taxonomic groups across a variety of geographic regions (Hill *et al.*, 2002;

272   Devictor *et al.*, 2008; Myers *et al.*, 2009; Foufopoulos *et al.*, 2011), and with the persistent and

273   increasing threat of anthropogenically induced climate change, northern species and those reliant

274   upon them are likely to become increasingly threatened.

275

276   We found no evidence for six other hypotheses about the drivers of species trends. Flight period and

277   thorax length appeared marginally important but evidence for this was weak as the 95% CI of these

278   traits spanned zero. Additionally when these two traits were modelled against species trend

279   individually they performed no better than the null model. Body size and flight period were used as

280   surrogates for competitive ability and dispersal ability: it is plausible that more direct measures of

281   these traits do predict the species in decline. The reliability of the trait-trend results depend on the

282   accuracy of the underlying trait data. We note that within a given species, traits can vary spatially

283   (i.e. habitat specificity can vary across a species range – Oliver *et al.*, 2009), however here we use a

284   single value per trait per species. This is a common approach within the comparative analysis

285   literature but is a potential source of noise in the results. One problem with "well-sampled sites"

286   approach is that it amplifies the spatial gradient in recording intensity, such that trends for northern

287   species are estimated from a relatively small number of sites. This has implications for the precision

288   of trend estimates for northern vs southern species, which is accounted-for in the weighted trait

289   models (Appendix 1b). Basing the trend on a small number of sites is unlikely, on its own, to bias the

290   estimate (Isaac *et al.*, 2014b), although we don't know the degree to which trends on these sites

291   (and others considered well-sampled) reflect changes in the wider countryside. We found no

292   evidence of phylogenetic signal in our models, although our phylogeny was based on taxonomy.

293 Using a phylogeny constructed from sequence data would be more rigorous, but such genetic data

294 are currently limited.

295

296 In conclusion, we found variation in species distribution trends was best explained by distribution

297 type, with southern species showing significantly higher trends than widespread and northern

298 species. We believe this reflects the impact of climate change as the increased ambient

299 temperature in Britain and Ireland better suits species that are adapted to warmer conditions. The

300 lower trend estimates for northern species is a cause of conservation concern as this result

301 combined with evidence in previous studies shows that northern species are shifting to higher

302 latitudes and altitudes, are declining in range size and abundance, and are therefore particularly

303 vulnerable to the ever increasing threat of climate change.

304

309

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474 **Tables**

475 **Table 1.** An overview of the Odonata traits included in the comparative analysis.

| Trait	Description
Species status	Species categorised on distribution size: very widespread, widespread, local, scarce, rare, very rare.
Distribution type	Broad climatic categorisation of species: widespread, southern, northern or oceanic.
Thorax length	Mean thorax length based on 10 museum specimens (mm).
Flight period	The duration of the flight period in months.
Habitat breadth	A count of the number of habitat types utilised by the species.
Breeding habitat	Species were classified on their preferred breeding habitat, either lentic, lotic or both.
Overwint. stage	Species categorised as overwintering as larvae, eggs, or both.

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479 **Table 2** Parameter estimates for the subset of best models. For the categorical variable (distribution

480 type) ● denotes that it was present in the selected model, while the slope is displayed for the

481 continuous traits present in the selected model. The final column expresses the importance value

482 for each trait included in the subset of best models.

	Model rank						
	1	2	3	4	5	6	Importance
Distribution	●	●			●		0.60
Flight period		-0.022		-0.023			0.34
Thorax length					0.002	0.002	0.24
AICc	-154.3	-153.7	-153.2	-153.1	-153.0	-152.5	
ΔAIC	0	0.58	1.12	1.17	1.29	1.85	
weight	0.263	0.197	0.150	0.147	0.138	0.104	
Adjusted R^2	0.131	0.155	-	0.032	0.138	0.013	

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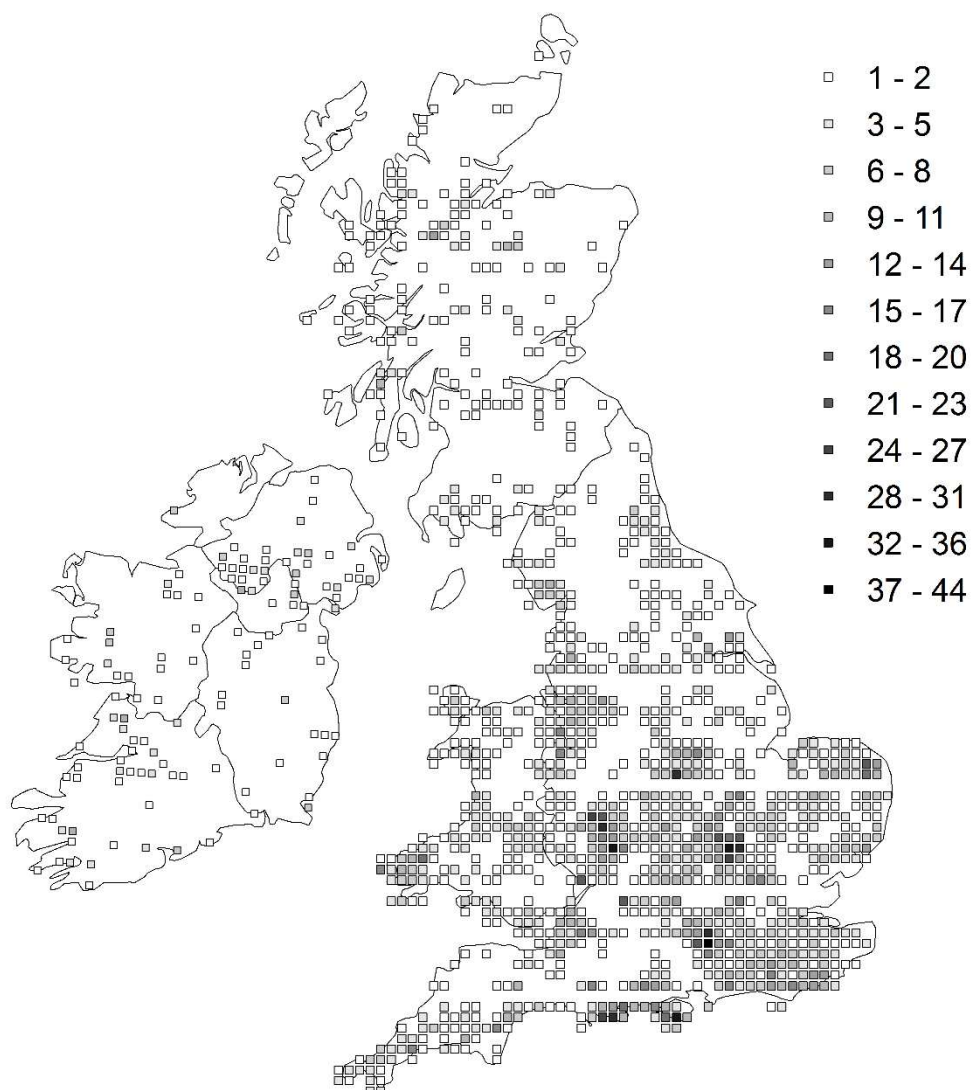
490   **Figure 2** The proportion of species in each trend category. Using the fitted values from the species
491   models, trends were estimated as the percentage change in probability of observation over a ten
492   year period. Shades of red symbolises declines while shades of green are used for increases, the
493   intensity of colour reflects the strength of the trend.

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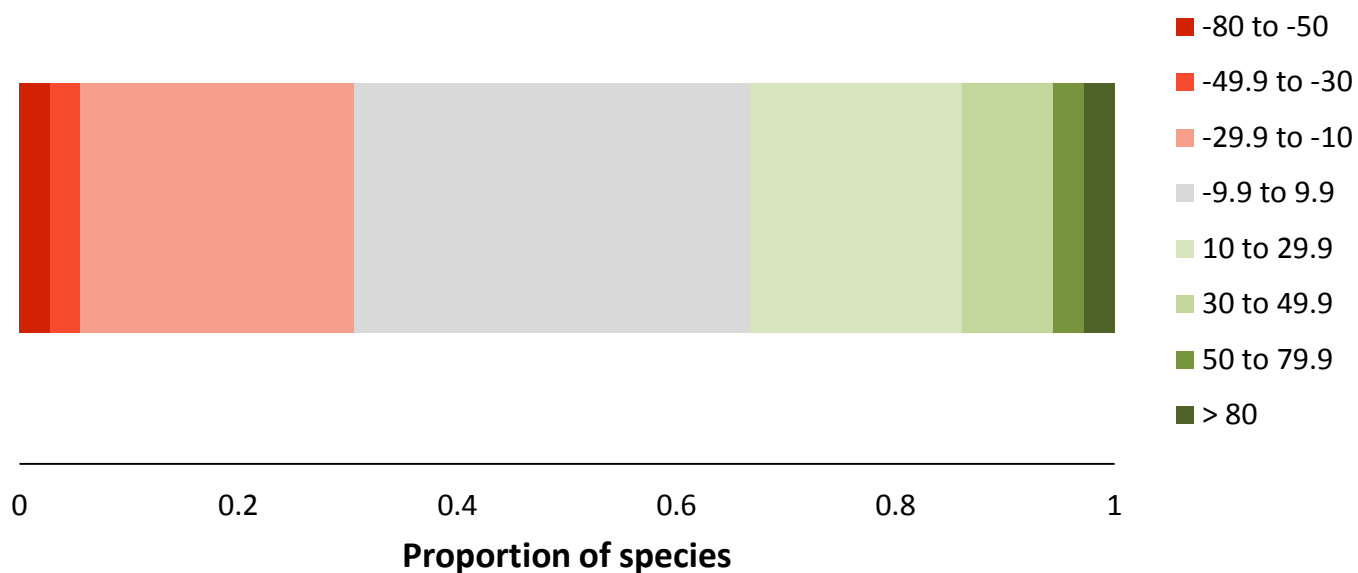
495 **Figure 3** The model averaged coefficients for traits that were retained in the subset of best models.

496 The reference distribution type was "*southern*", which has a parameter estimate set to 0.

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