# Trait correlates of distribution trends in the Odonata of Britain and Ireland

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A major challenge in ecology is understanding why certain species persist, while others decline, in response to environmental change. Trait-based comparative analyses are useful in this regard as they can help identify the key drivers of decline, and highlight traits that promote resistance to change. Despite their popularity trait-based comparative analyses tend to focus on explaining variation in range shift and extinction risk, seldom being applied to actual measures of species decline. Furthermore they have tended to be taxonomically restricted to birds, mammals, plants and butterflies. Here we utilise a novel approach to estimate occurrence trends for the Odonata in Britain and Ireland, and examine trait correlates of these trends using a recently available trait dataset. We found the dragonfly fauna in Britain and Ireland has undergone considerable change between 1980 and 2012, with 22 and 53% of species declining and increasing respectively. Distribution region, habitat specialism and range size were the key traits associated with these trends, where habitat generalists that occupy southern Britain tend to have increased in comparison to the declining narrow-ranged specialist species. In combination with previous evidence, we conclude that the lower trend estimates for the narrow-ranged specialists could be a sign of biotic homogenization with ecological specialists being replaced by warm-adapted generalists.

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

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11

12    **Abstract**

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

14    decline in response to environmental change.  Trait-based comparative analyses are useful in this regard

15    as they can help identify the key drivers of decline, and highlight traits that promote resistance to

16    change.  Despite their popularity trait-based comparative analyses tend to focus on explaining variation

17    in range shift and extinction risk, seldom being applied to actual measures of species decline.

18    Furthermore they have tended to be taxonomically restricted to birds, mammals, plants and butterflies.

19    Here we utilise a novel approach to estimate occurrence trends for the Odonata in Britain and Ireland,

20    and examine trait correlates of these trends using a recently available trait dataset.  We found the

21    dragonfly fauna in Britain and Ireland has undergone considerable change between 1980 and 2012, with

22    22 and 53% of species declining and increasing respectively.  Distribution region, habitat specialism and

23    range size were the key traits associated with these trends, where habitat generalists that occupy

24   southern Britain tend to have increased in comparison to the declining narrow-ranged specialist species.

25   In combination with previous evidence, we conclude that the lower trend estimates for the narrow-

26   ranged specialists could be a sign of biotic homogenization with ecological specialists being replaced by

27   warm-adapted generalists.

28

29   **Introduction**

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

31   recent estimates suggesting that the current extinction rate is 1000 times that of the historical natural

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

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

34   and abundance (Thomas *et al.*, 2004; Biesmeijer *et al.*, 2006; Butchart *et al.*, 2010; Chen *et al.*, 2011).

35   Variation in species responses to environmental change has been found across broad taxonomic groups

36   (Hickling *et al.*, 2006; Angert *et al.*, 2011) but also within taxonomic groups, i.e. between species within

37   an order (Hickling *et al.*, 2005).  A major challenge in conservation ecology is to gain a better

38   understanding of this interspecific variation in response to environmental change, i.e. what enables

39   certain species to persist while others decline?

40

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

42   example, several studies have shown that ecological generalists out-perform specialists in times of

43   environmental change (Walker & Preston, 2006; Ozinga *et al.*, 2012; Newbold *et al.*, 2013).  Such

44   comparative trait-based analyses are popular, as the models help to identify the main drivers of change

45   and allow the prediction of future biodiversity changes based on environmental forecasts (Fisher &

46    Owens, 2004; Cardillo *et al.*, 2006).  Previous comparative trait analyses have tended to focus on

47    explaining variation in range shift (Angert *et al.*, 2011; Mattila *et al.*, 2011; Grewe *et al.*, 2012) and

48    extinction risk (Purvis *et al.*, 2000; Koh *et al.*, 2004; Cardillo *et al.*, 2008; Cooper *et al.*, 2008; Fritz *et al.*,

49    2009).  Despite its popularity, the comparative trait-based approach has seldom been applied to direct

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

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

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

53    has increased (Silvertown, 2009).  Such data tend to be collected without systematic protocols and thus

54    contain many forms of sampling bias and noise, making it hard to detect genuine signals of change

55    (Tingley & Beissinger, 2009; Hassall & Thompson, 2010; Isaac *et al.*, 2014b).  However, recent advances

56    in analytical approaches have improved our ability to estimate reliable trends from these unstructured

57    biological records (Isaac *et al.*, 2014).  In this study we utilise these novel approaches to estimate trends

58    in occurrence for the Odonata in Britain and Ireland, and use species traits to test hypotheses for the

59    interspecific variation in trends.

60

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

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

63    rich and their crucial role across ecosystems, the non-butterfly invertebrate fauna are comparatively

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

65    bioindicators as they are sensitive to degradation of water ecosystems (Samways & Steytler, 1996;

66    Sahlén & Ekestubbe, 2001; Lee Foote & Rice Hornung, 2005).  Thirdly, they provide a valuable ecosystem

67    service as they feed on many insect pests (Brooks & Lewington, 2007).  Finally, the publication of a new

68    atlas (Cham *et al.*, 2014) and trait datasets (Powney *et al.*, 2014) for British Odonata together constitute

69    some of the best quality data of any non-butterfly invertebrate group.  Previous research based on

70    Odonata occurrence data has focussed on the impact of climate change on phenology and distribution.

71    For example Hassall *et al.* (2007) discovered that emergence from overwintering had significantly

72    advanced over the past 50 years, while Hickling *et al.* (2005) showed that the upper latitudinal margin

73    shifted north between 1960 and 1995.  Outside Britain, Bush *et al.* (2014) used species distribution

74    models (SDMs) to predict which Australian odonates were under threat from climate change.

75

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

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

78    advancement, Hassall *et al.* (2007) noted that spring species and those without egg diapause exhibited

79    increased phenological shifts.  Angert *et al.* (2011) examined trait correlates of range shift across

80    multiple taxonomic groups, finding that exophytic Odonata species in Britain shifted further north, on

81    average, than endophytic species.  These insights, combined with extensive knowledge about their

82    natural history (Brooks & Lewington, 2007), form the basis of seven competing hypotheses (outlined

83    below) that aim to explain the interspecific variation in the distribution trends among British Odonata.

84

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

86    change.  Habitat breadth is frequently related to species trends, where habitat generalists outperform

87    specialists due to their greater ability to adapt to novel environmental conditions (Fisher & Owens,

88    2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012).  Ball-Damerow *et al.*, (2014) found evidence of the

89    widespread expansion of habitat generalists which has led to biotic homogenization in the dragonfly

90    fauna of California and Nevada over the last century.  We test the hypothesis that Odonata in Britain

91    and Ireland follow the patterns outlined above, with generalists out-performing specialists.  Dispersal

92    ability affects species' ability to respond to environmental pressures, with higher dispersal ability linked

93    to an enhanced ability to respond (Thomas *et al.*, 2001; Pöyry *et al.*, 2011; Grewe *et al.*, 2012).  Using

94    SDMs, Hof *et al.* (2012) found lentic (i.e. pond and lake dwelling) species had a greater ability to track

95    changes in their climatic niche.  This was linked to greater dispersal ability, which is essential given the

96    ephemeral nature of their breeding sites (Hof *et al.*, 2006).  We predict lentic species will have higher

97    (more positive) trend estimates than lotic species as their increased dispersal ability enables them to

98    persist during times of environmental change through the efficient relocation to newly suitable areas.

99    Geographic range size and body size are both frequently used as surrogates for a whole host of traits

100    associated with ecological specialism and competitive ability (Gittleman, 1985; Gaston, 2003; Angert *et*

101    *al.*, 2011).  We predict that widespread species and the larger, therefore more competitive species, are

102    likely to show positive trends.  Climate warming has increased the suitability of the landscape to those

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

104    Dingemanse & Kalkman, 2008; Bellard *et al.*, 2012), and evidence of the loss of northern species has

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

106    Devictor *et al.*, 2008; Myers *et al.*, 2009; Foufopoulos *et al.*, 2011).  We therefore predict that southerly

107    distributed species will show the most positive trend estimates.  An additional aspect of climate change

108    that has been linked with trends in Odonata is the increase in flood events in Britain.  Species which

109    overwinter as larvae are particularly vulnerable to flooding as they can be swept away from ideal habitat

110    areas to unsuitable regions in which they cannot persist (Cham *et al.*, 2014).  As a result we predict

111    species that overwinter as larvae will have undergone the greatest declines.  Finally we test the

112    hypothesis that flight period will be positively related with species' trend.  Grewe *et al.*, (2012) argued

113    that species with longer flight periods have increased dispersal ability, and therefore have a greater

114    capacity to adapt in response to environmental change.

115

116    **Materials & Methods**

117    *Occurrence trends*

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

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

120    on 588,480 records of 36 native species collected between 1980 and 2012 where the recording date is

121    known and the location was recorded to 1 km² precision or better.  As these occurrence records were

122    collected without a specific sampling design they contain a variety of bias which inhibit their use in

123    estimating reliable trends.  For example, the number of records collected each year has increased

124    dramatically over time (Cham *et al.*, 2014), such that simply counting the number of  occupied sites

125    would produce biased trend estimates (Prendergast *et al.*, 1993; Isaac *et al.*, 2014).  To account for these

126    biases we estimated species trends using an approach based on Bayesian occupancy modelling (van

127    Strien *et al.*, 2013; Isaac *et al.*, 2014).  We first arranged the records into 212,574 visits, which were

128    defined as unique combinations of date and 1 km² grid cell (site).  For each visit, each of the 36 species

129    was coded as either recorded (1) or not-recorded (0).  We then selected sites with at least three years of

130    data, ensuring we retained only the well-sampled sites (Figure 1).  Our final dataset contains 467,899

131    records from 157,507 visits to 11,435 sites (64,005 site-year combinations).  We ran occupancy models

132    for each species based on the methodology of Van Strien *et al*. (2013) and Isaac *et al.* (2014).  The

133    approach uses two hierarchically coupled sub-models, one, the state model, governs the true

134    presence/absence of a species at a site in a given year, the second, the observation model, governs the

135    probably of detecting that species given its presence or absence, and is therefore conditional on the

136    state model.  The detection probability per visit is a function of the number of species recorded on that

137    visit (the 'list length': see appendix 1 for detailed model description).  For each site-year combination

138    the model estimates presence or absence for the species in question given variation in detection

139    probability: from this the proportion of occupied sites ('occupancy') was estimated for each year.

140    Finally, within the Bayesian framework, a linear trend was fitted to these annual proportions to identify

141    a temporal trend in species occupancy.  The slope of this regression of occupancy against year was used

142    as the species-specific trend measure in the cross-species comparative analysis.

143

144    *Species' trait data*

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

146    on characteristics of a species' distribution pattern, the first, species status, was measured as an ordinal

147    variable based on distribution size, moving from very rare through to very widespread.  Secondly,

148    distribution region was a categorical variable that defined a species broad climatic restriction, with

149    species classified into one of four levels, northern, southern (which included continental species from

150    the original classification), oceanic or widespread based on their distribution pattern.  We included a

151    single morphological trait, thorax length (mm), which was taken as the mean of multiple measurements

152    from museum specimens.  Flight period duration was measured as the number of months during which

153    adults are typically recorded in flight.  We included two habitat based traits, habitat breadth measured

154    the number of broad habitats a species can utilise (maximum of 6), while breeding habitat classified

155    species based on breeding habitat preference, lentic, lotic or both.  Finally, we classified species based

156    on their overwintering stage, either eggs, larvae or both.  Distribution status was coded as an ordinal

157    variable: very rare = -1.5, rare = -1, scarce = -0.5, local = 0.5, widespread = 1, very widespread = 1.5, and

158    modelled as a continuous term in the analysis (as opposed to a factor).  All continuous traits were

159    centred on zero prior to the analysis.

160

161    *Comparative analysis*

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

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

164    (Freckleton *et al.*, 2002).  In all phylogenetically informed models, the level of phylogenetic correction

165    (Pagel's λ) was estimated via maximum likelihood (Pagel, 1999; Freckleton *et al.*, 2002).  Due to data

166    limitations we used a phylogeny based on taxonomy for the analyses.  The phylogeny was built using the

167    *as.phylo* function from the R package *ape* (Paradis *et al.*, 2005) with nodes based on Suborder, Family,

168    Genus and Species, and all branch lengths were set to one.

169

170    We tested seven hypotheses about the drivers of species' trends whilst incorporating uncertainty in the

171    trend estimates of each species. To do this, we fitted 10,000 trait-trend models: in each model we

172    selected, at random, one value from the posterior distribution of trend estimates for each species. In all

173    10,000 models we estimated the coefficients for each of the seven traits (described above) as fixed

174    effects.  From these models, we then calculated the mean and 95% confidence intervals for the trait-

175    trend parameter estimates across all iterations.

176

177    **Results**

178    We found substantial variation in the trend estimates between species.  Of 36 species included in the

179    analysis, 8 had negative trends and 19 had positive trends where the 95 percentiles (2.5 and 97.5

180    percentiles) did not bridge zero (Appendix 2).  Species that showed the greatest declines included:

181    *Aeshna juncea* and *Sympetrum danae*, while *Anax imperator* and *Aeshna mixta* showed the greatest

182    increases.

183

184    Key results from the comparative trait-analysis (Table 2 and Figure 2) showed distribution status, habitat

185    breadth and thorax length were positively associated with species trend, while species with longer flight

186    periods tended to have lower trend estimates (i.e. they declined relative to species with short flight

187    periods).  Distribution region was an important predictor of species trend, where southern species

188    increased relative to oceanic and widespread species.  Notable exceptions to this trend include the

189    declines in *Ischnura pumilio* and *Gomphus vulgatissimus* both of which were classified as southern

190    species.  Northern species showed the largest increases, although this result is highly uncertain

191    (reflected in the wide 95% CI across the 10,000 iterations).  Lentic species tended to have lower trend

192    estimates than lotic species and those species that utilise both breeding habitat strategies.  Finally, there

193    appeared to be little evidence of an influence of overwintering stage on species trend.  Trends tended to

194    be similar between species that overwinter as eggs and those that overwinter as larvae.  Species that

195    can overwinter as both eggs and larvae had the lowest average trend estimates, however this category

196    was comprised of four species only.  In general, the phylogenetic signal across the model iterations was

197    low, with a mean of 0.035 (0.0 – 0.36).

198

199    **Discussion**

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

201    recent decades, with high levels of interspecific variation in occurrence trends.  We found 8 species

202    (22%) had declined, whereas 19 species (53%) showed increasing trends.  The large number of species

203    with positive trends is likely to reflect the recovery of dragonfly populations in response to increased

204    water quality in Britain since the mid-20th Century.  Although a greater number of species increasing

205    than declining is good news for conservation, this could reflect biotic homogenization, i.e. the fauna

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206   becoming dominated by a certain group of species, leading to the erosion of local and regional

207   difference between communities (Keith *et al.*, 2009).

208

209   We found distribution region was a key correlate of Odonata occurrence trends, with southern species

210   tending to have higher trend estimates than the oceanic and widespread species (Figure 2).  This result

211   is in line with our hypothesis that increased temperatures has increased the climate suitability of Britain

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

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

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

215   evidence of northward range expansions in warm-water adapted Portuguese algae.  Hickling *et al.*

216   (2005) used distribution region to explain variation in range shift and expansion in British Odonata,

217   finding that southern species showed greater poleward shifts and expansions compared to northern

218   species.  We found little evidence of a difference between northern and southern species, however this

219   is likely due the low number of northern species (n = 4) included in our dataset.  Interestingly, Angert *et*

220   *al.* (2011)  found no correlation between range shift and position of the northern range limit (which is

221   related to our measure of distribution region).  Despite the wealth of evidence that points to climate

222   change as the likely driver of increases in southern species, we cannot ignore the role of improved water

223   quality and standing water availability in southern Britain (Hickling *et al.*, 2005; Vaughan & Ormerod,

224   2012; Cham *et al.*, 2014).  Durance & Ormerod (2009) noted that improved water quality can confound

225   attempts to detect the impact of climate change on freshwater macroinvertebrates.  Southern species

226   are likely to have benefitted from both the increased water quality in southern Britain and improved

227   climate suitability, while the former was the main positive driver for widespread species, this could

228   explain the greater increases in southern compared to widespread species.  Not all southern species

229    showed positive trends (notably *Ischnura pumilio* and *Gomphus vulgatissimus*), here the limited

230    expansion is likely due to a lack of suitable habitat.

231

232    Numerous studies have related habitat breadth to species trends and tend to find that habitat

233    generalists outperform specialists (Fisher & Owens, 2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012).

234    Much of the evidence of this relationship is based on studies of terrestrial organisms (Biesmeijer *et al.*,

235    2006; Ozinga *et al.*, 2012; Newbold *et al.*, 2013), with a notable exception from Ball-Damerow *et al.*,

236    (2014).  Here, we found that the relationship holds in the Odonata fauna of the UK as habitat breadth

237    was positively correlated with occurrence trend.  The likely cause of this relationship is that habitat

238    generalists have a greater ability to adapt to novel environmental conditions, which is particularly

239    important in our current climate of anthropogenically driven environmental change (Travis, 2003;

240    Newbold *et al.*, 2013).  Thorax length and distribution status (used here as a measure of range size) were

241    positively related to occurrence trends, i.e. narrow ranged, "rare", small sized species tended to have

242    lower trend estimates than wider ranging, larger species.  Geographic range size and thorax length are

243    often used as surrogates for traits associated with ecological specialism and competitive ability

244    (Gittleman, 1985; Gaston, 2003; Angert *et al.*, 2011).  Therefore, as with habitat specialism above, we

245    believe this result is driven by the greater ability of competitive ecological generalists to adapt to

246    environmental change than specialists.

247

248    Hof *et al.* (2012) found lentic (i.e. pond and lake dwelling) species had a greater ability to track changes

249    in their climatic niche due to their greater dispersal ability, essential given the ephemeral nature of their

250    breeding sites.  We hypothesised that the greater dispersal ability of lentic species would promote their

251    resilience to environmental change leading to a higher average trend estimate than lotic species.  The

252    results in this study do not support our hypothesis as lentic species tended to have lower trend

253    estimates than lotic species.  Differences in mean trend between lentic and lotic species are likely due to

254    differences in the impact environmental stressors (e.g. climate change, eutrophication and other forms

255    of habitat degradation), interactions between them and subsequent restoration between rivers and

256    lakes (Vaughan & Ormerod, 2012).  A study aimed at improving our understanding of the variation

257    between lentic and lotic species is a prime candidate for future work.

258

259    Finally we found that flight period was negatively related to occurrence trend, a result contrary to

260    expectations.  As with the lentic/lotic hypothesis, initially we suspected that species with greater

261    dispersal ability would show higher trends as increased dispersal capacity increases the ability to

262    mitigate the negative effects of environmental.  We used flight period as a surrogate of dispersal ability

263    on the premise that the longer the flight season the more time a species has to disperse (Grewe *et al.*,

264    2012).  It is plausible that the use of a more direct measure of dispersal ability would have produced a

265    result that is consistent with the literature on dispersal ability and species trends.  It is worth noting that

266    the reliability of the trait-trend results depend on the accuracy of the underlying trait and trend data,

267    and we note that within a given species, traits can vary spatially.  One such plastic trait includes flight

268    period that has been shown to vary with latitude (Corbet, 2004). Summarising this variation into a single

269    value per trait per species is a common approach but can create noise in model results.

270

271    In conclusion, we found that a large number of dragonfly species have increased in the UK between

272    1980 and 2012, and is likely a response to increased water quality.  We found that habitat generalists

273    that occupy southern Britain tend to have increased in comparison to the narrow-ranged specialist

274    species of dragonfly.  We believe this reflects the impact of environmental change, particularly climate

275   change, as the increased ambient temperature in Britain and Ireland better suits species that are

276   adapted to warmer conditions.  The lower trend estimates for specialist species is a cause of

277   conservation concern as this result combined with evidence in previous studies could be a sign of biotic

278   homogenization with ecological specialists being replaced by warm-adapted generalists.

279

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285

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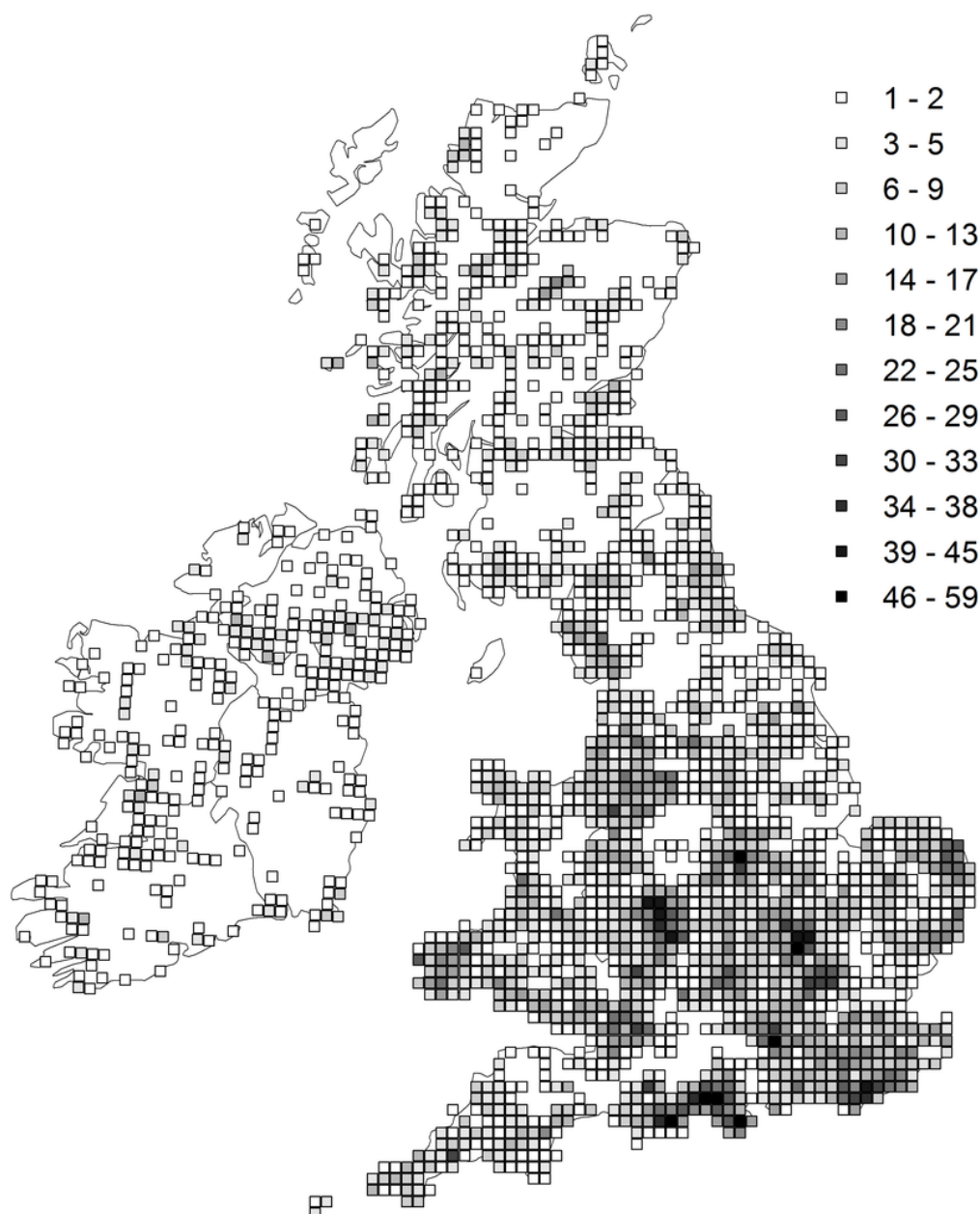397    effort in analyses of diversity hotspots. Biodiversity Letters, 1, 39–53.

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423

# 1

Figure 1 The distribution and density of sites (monads) from which the trend estimates were derived.

The shading represents the number of unique sites within the hectad that were included in the analysis.

| | |
|---|---|
| □ | 1 - 2 |
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| ■ | 46 - 59 |

# 2

Figure 2 The mean and 95 percentiles of the trait coefficients across 10,000 model iterations.

Each categorical variable had a reference category which had a parameter estimate set to 0. The reference categories were as follows: region = "southern", breeding habitat = "lentic", and for overwintering stage = "eggs".
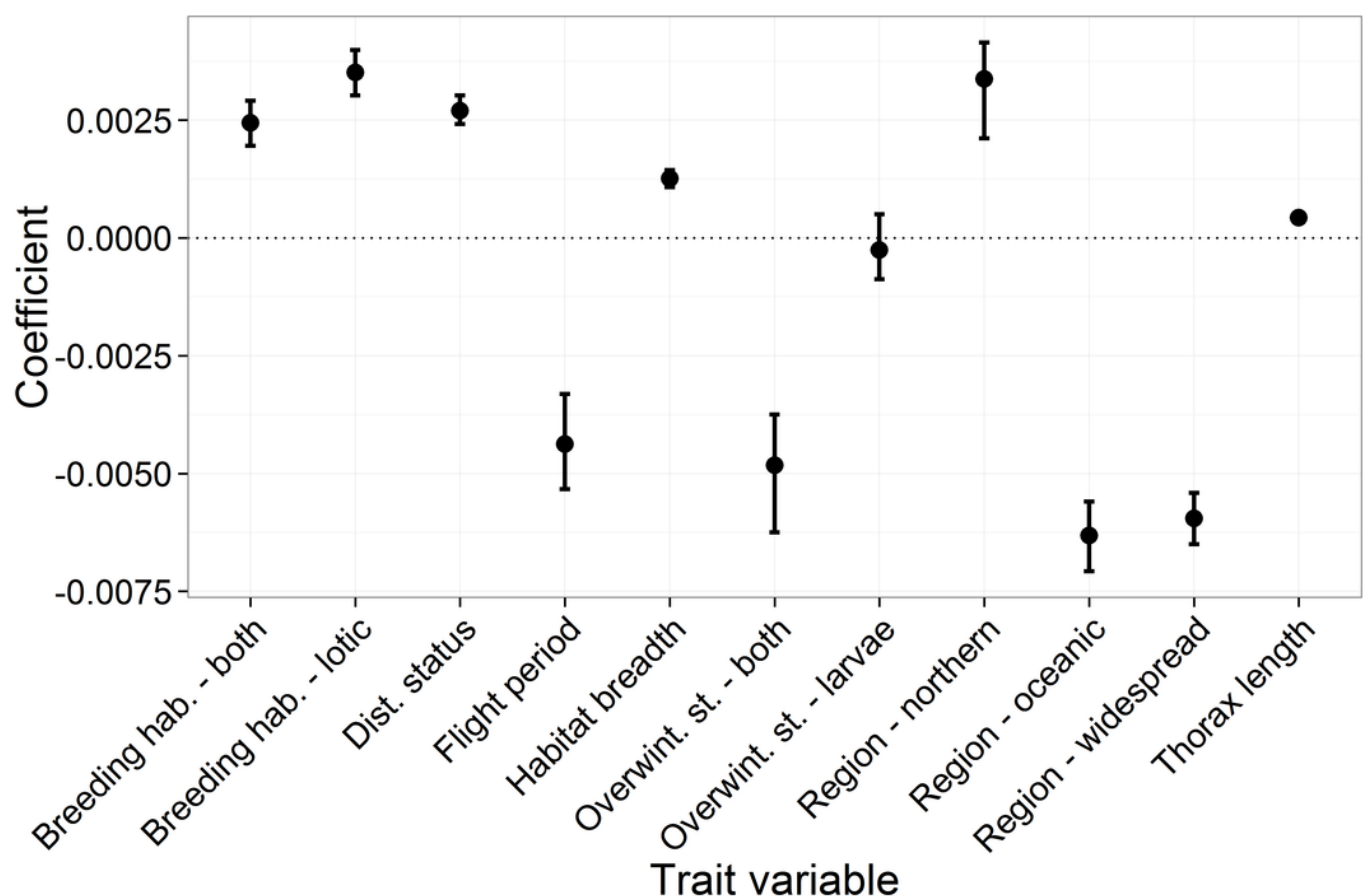
**Table 1**(on next page)

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

| Trait | Description | Class |
|---|---|---|
| Species status | Species categorised on distribution size: very widespread, widespread, local, scarce, rare, and very rare. | Ordinal |
| Distribution region | Broad climatic categorisation of species: widespread, southern, northern or oceanic. | Categorical |
| Thorax length | Mean thorax length based on 10 adult (5 male and 5 female) museum specimens (mm). | Continuous |
| Flight period | The duration of the flight period in months. | Continuous |
| 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. | Categorical |
| Overwint. stage | Species categorised as overwintering as larvae, eggs, or both. | Categorical |

1

2

# Table 2(on next page)

Table 2 The mean and 95 percentiles of the trait coefficients estimated from 10,000 model iterations.

The coefficients for the categorical variables (overwintering stage, region and breeding habitat) are shown as contrasts to the reference category (eggs, southern and lentic, respectively). The mean level of phylogenetic signal ($\lambda$) across the 10,000 iterations is presented alongside its 95 percentiles.

1

| Parameter | Mean coef. | 95 Percentile | |
|---|---|---|---|
| | | 0.025 | 0.975 |
| Thorax length | $4.87 \times 10^{-4}$ | $4.15 \times 10^{-4}$ | $5.65 \times 10^{-4}$ |
| Overwintering stage - both | -0.005 | -0.006 | -0.004 |
| Overwintering stage - larvae | $-2.82 \times 10^{-4}$ | $-9.58 \times 10^{-4}$ | $6.78 \times 10^{-4}$ |
| Flight period duration | -0.004 | -0.005 | -0.002 |
| Distribution status | 0.003 | 0.002 | 0.003 |
| Region - Northern | 0.003 | 0.001 | 0.004 |
| Region - Oceanic | -0.007 | -0.007 | -0.006 |
| Region - Widespread | -0.005 | -0.007 | -0.005 |
| Habitat breadth | 0.001 | 0.001 | 0.001 |
| Breeding habitat - both | 0.003 | 0.002 | 0.003 |
| Breeding habitat - lotic | 0.004 | 0.003 | 0.004 |
| $\lambda$ (phylo. signal) | 0.035 | <0.001 | 0.36 |

2