Trait correlates of distribution trends in the Odonata of Britain and Ireland: Southern species benefit from climate warming

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A major challenge in ecology is understanding what enables certain species to 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 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 33 and 39% of species showing significant declines and increases respectively. Distribution type was the key trait associated with these trends, where southern species showed significantly higher trends than widespread and northern species. We believe this reflects the impact of climate change as the increased ambient temperature in Britain and Ireland better suits species that are adapted to warmer conditions. We conclude that northern species are particularly vulnerable to climate change due to the combined pressures of a decline in climate suitability, and competition from species that were previously limited by lower thermal tolerance.

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Abstract

A major challenge in ecology is understanding what enables certain species to 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 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

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Introduction

Defaunation, the loss of species and populations (Dirzo *et al.*, 2014), is occurring at an alarming rate with recent estimates suggesting that the current extinction rate is 1000 times that of the historical natural background rate (De Vos *et al.*, 2014). These declines are driven by environmental change, particularly habitat loss and climate change, and can be measured in a number of ways, e.g. changes in distribution and abundance (Thomas *et al.*, 2004; Biesmeijer *et al.*, 2006; Butchart *et al.*, 2010; Chen *et al.*, 2011). Variation in species responses to environmental change has been found across broad taxonomic groups (Hickling *et al.*, 2006; Angert *et al.*, 2011) but also within taxonomic groups, i.e. between species within an order (Hickling *et al.*, 2005). A major challenge in conservation ecology is to gain a better understanding of this interspecific variation in response to environmental change, i.e. what enables certain species to persist while others decline?

Species traits play an important role in determining species' ability to resist environmental change. For example, several studies have shown that ecological generalists out-perform specialists (Walker & Preston, 2006; Ozinga *et al.*, 2012; Newbold *et al.*, 2013). Such comparative trait-based analyses are popular, as the models help to identify the main drivers of change and allow the prediction of future biodiversity changes based on environmental forecasts (Fisher & Owens, 2004; Cardillo *et al.*, 2006). Previous comparative trait analyses have tended to focus on explaining variation in range shift (Angert *et al.*, 2011; Mattila *et al.*, 2011; Grewe *et al.*, 2012) and extinction risk (Purvis *et al.*, 2000; Koh *et al.*, 2004; Cardillo *et al.*, 2008; Cooper *et al.*, 2008; Fritz *et al.*, 2009). Despite its popularity, the comparative trait-based approach has seldom been applied to direct measures of species' changing status (i.e. rates of decline or increase). Currently data on such measures of decline are rare, particularly at large (e.g. national) scales and across multiple species. With the increase in public participation in biological recording, the availability of large-scale distribution datasets has increased (Silvertown, 2009). Such data tend to be collected without systematic protocols and thus contain many forms of sampling bias and noise, making it hard to detect genuine signals of change (Tingley & Beissinger, 2009; Hassall & Thompson, 2010; Isaac *et al.*, 2014b). However, recent advances in analytical approaches have improved our ability to estimate reliable trends from these unstructured biological records (Isaac *et al.*, 2014b). In this study we utilise these novel approaches to estimate trends for the Odonata in Britain and Ireland, and use species traits to test hypotheses for the interspecific variation in trends.

We chose to examine Odonata for a number of reasons. Firstly, previous trait-based comparative analyses have tended to focus on birds, mammals, plants and butterflies. Despite being highly species rich and their crucial role across ecosystems, the non-butterfly invertebrate fauna are comparatively poorly studied

(IUCN, 2001; Dirzo *et al.*, 2014). Secondly, Odonata are thought to be excellent bioindicators as they are sensitive to degradation of water ecosystems (Samways & Steytler, 1996; Sahlén & Ekestubbe, 2001; Lee Foote & Rice Hornung, 2005). Thirdly, they provide a valuable ecosystem service as they feed on many insect pests (Brooks & Lewington, 2007). Finally, the publication of a new atlas (Cham *et al.*, 2014) and trait datasets (Powney *et al.*, 2014) for British Odonata together constitute some of the best quality data of any non-butterfly invertebrate group.

Previous research based on Odonata occurrence data has focussed on the impact of climate change on phenology and distribution. For example Hassall *et al.*, (2007) discovered that emergence from overwintering had significantly advanced over the past 50 years, while Hickling *et al.*, (2005) showed that the upper latitudinal margin shifted north between 1960 and 1995. Outside Britain, Bush *et al.*, (2014) used species distribution models (SDMs) to predict which Australian odonates were under threat from climate change.

Several studies have utilised traits to explain variation in several aspects of Odonata ecology, but typically focus on explaining variation in species response to climate change. In terms of phenological advancement, Hassall *et al.*, (2007) noted that spring species and those without egg diapause exhibited increased phenological shifts. Angert et al (2011) examined trait correlates of range shift across multiple taxonomic groups, finding that exophytic Odonata species in Britain shifted further north, on average, than endophytic species. These insights, combined with extensive knowledge about their natural history (Brooks & Lewington, 2007), form the basis of seven competing hypotheses (outlined below) that aim at explain the interspecific variation in the distribution trends among British Odonata.

All traits included in the analysis have been shown to affect species' ability to respond to environmental change. Habitat breadth is frequently related to species trends, where habitat generalists outperform specialists due to their greater ability to adapt to novel environmental conditions (Fisher & Owens, 2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012). Ball-Damerow *et al.*, (2014) found evidence of the widespread expansion of habitat generalists which has led to biotic homogenization in the dragonfly fauna of California and Nevada over the last century. We test the hypothesis that Odonata in Britain and Ireland follow the patterns outlined above, with generalists out-performing specialists. Dispersal ability affects species' ability to respond to environmental pressures, with higher dispersal ability linked to an enhanced ability to respond (Thomas *et al.*, 2001; Pöyry *et al.*, 2011; Grewe *et al.*, 2012). Using SDMs, Hof *et al.*, (2012) found lentic (i.e. pond and lake dwelling) species had a greater ability to track changes in their climatic niche. This was linked to greater dispersal ability, which is essential given the ephemeral nature of their breeding sites (Hof *et al.*, 2006). We predict lentic species will have higher (more positive) trend estimates than lotic species as their increased dispersal ability enables them to persist during times of environmental change through the efficient relocation to newly suitable areas. Geographic range size and body size are both frequently used as surrogates for a whole host of traits associated with ecological specialism and competitive ability (Gittleman, 1985; Gaston, 2003; Angert *et al.*, 2011). We predict that widespread species and the larger, therefore more competitive species, are likely to show positive trends. Climate warming has increased the suitability of the landscape to those species that were previously limited by their lower thermal tolerance threshold (Devictor *et al.*, 2008; Dingemanse & Kalkman, 2008; Bellard *et al.*, 2012), therefore we predict that southerly distributed species will show the highest trend estimates. An additional aspect of climate change that has been linked with trends in Odonata is the increase in flood events in Britain. Species which overwinter as larvae are particularly vulnerable to flooding as they can be swept away from ideal habitat areas to unsuitable regions in which they cannot persist (Cham *et al.*, 2014). Alternatively, floods may aid the dispersal of such species that overwinter as larvae and therefore we may expect to see positive trends for such species. Finally we test the hypothesis that flight period will be positively related with species' trend. Grewe *et al.*, (2012) argued that species with longer flight periods have increased dispersal ability, and therefore have a greater capacity to adapt in response to environmental change.

Materials & Methods

Occurrence trends

Trends were estimated from Odonata distribution records in Britain and Ireland collected by the Dragonfly Recording Network and coordinated by the British Dragonfly Society. Our analyses are based on 895,022 records of 38 native species collected between 1980 and 2012 where the recording date is known and the location was recorded to 1 km^2 precision or better. As these occurrence records were collected without a specific sampling design they contain a variety of bias which inhibit their use in estimating reliable trends. For example, the number of records collected each year has increased dramatically over time (Cham *et al.*, 2014), such that simply counting the number of occupied sites would produce biased trend estimates (Prendergast *et al.*, 1993; Isaac *et al.*, 2014b). To account for these biases we estimated species trends using a method known elsewhere as the ‘well-sampled sites’ (Isaac *et al.*, 2014a), which aims to remove the noise and bases the statistical inference on a ‘well-sampled’ subset of the data. We first arranged the records into 239,392 visits, which are defined as unique combinations of date and 1 km^2 grid cell (site). For each visit, each of the 38 species was coded as either recorded (1) or not-recorded (0). We then removed all visits where ~~less~~ than three species were recorded, since these short lists probably represent incomplete sampling (van Strien *et al.*, 2010). We then selected sites with at least three years of data, ensuring we retained only the ‘well-sampled’ sites (Figure 1). Our final dataset contains 357,654 records from 67,382 visits to 5,352 sites (30,481 site-year combinations). Different thresholds for defining the well-sampled set (two species recorded and two years of data) produced qualitatively identical results (not shown). For each species, we estimated a linear trend in the probability of being recorded on an average site visit. This was achieved using binomial generalised linear mixed-effects models (GLMMs), implemented by the R package *lme4* (Bates *et al.*, 2011), with the log odds of being recorded modelled as a linear function of a fixed effect for year, and a random intercept for site. We used the slope estimate for the fixed effect of year as our trend measure.

Traits

We included data on seven traits extracted from Powney *et al.* (2014) (Table 1). Two traits were based on characteristics of a species’ distribution pattern, the first, species status, was measured as an ordinal variable based on distribution size, moving from very rare through to very widespread. Secondly, distribution type was a categorical variable that defined a species broad climatic restriction. Species were classified into one of four levels, northern, southern, oceanic or widespread based on their distribution pattern. We included a single morphological trait, thorax length (mm), which was taken as the mean of multiple measurements from museum specimens. Flight period duration was measured as the number of months during which adults are typically recorded in flight. We included two habitat based traits, habitat breadth measured the number of broad habitats a species can utilise, while breeding habitat classified species based on breeding habitat preference, lentic, lotic or both. Finally, we classified species based on their overwintering stage, either eggs, larvae or both. Overwintering stage, breeding habitat and distribution type were coded as continuous variables: Overwintering stage (eggs = -1, both = 0, larvae = 1), breeding habitat (lentic = -1, both = 0, lotic = 1), distribution type (very rare = -1.5, rare = -1, scarce = -0.5, local = 0.5, widespread = 1, very widespread = 1.5). All continuous traits were centred on zero prior to the analysis and ordinal variables were treated as continuous. Following the various exclusion criteria and the coverage of trait data, the final dataset used in this study covered 36 species.

Trait analysis

We used the *pgls* function from the R package *caper* (Orme, 2012) to run phylogenetically informed linear models to examine trait-trend relationships while accounting for phylogenetic non-independence (Freckleton *et al.*, 2002). In all phylogenetically informed models, the level of phylogenetic correction (Pagel's λ) was estimated via maximum likelihood (Pagel, 1999; Freckleton *et al.*, 2002). Due to data limitations we used a phylogeny based on taxonomy for the analyses. The phylogeny was built using the *as.phylo* function from the R package *ape* (Paradis *et al.*, 2005) with nodes based on Suborder, Family, Genus and Species, and all branch lengths were set to one.

The trend measures extracted from each species model formed the response variable for the trait-trend analysis. While this year slope estimate is a useful measure of the direction and intensity of the temporal trend in occupancy in an average site, it does not account for uncertainty in its estimation. We therefore repeated all trait analyses using the year slope estimate weighted by the inverse of its standard error and also the z-score of the fixed effect of year as the response variables. These additional analyses enabled us to examine how robust our results were in relation to uncertainty in our trend estimates.

To determine the main trait correlates of our species trends we utilised a multi-model inference approach. We applied the *dredge* function of the R package *MuMIn* (Barton, 2013) to fit models for all possible combinations of explanatory trait variables and then ranked them based on AICc. We then extracted the model averaged coefficient for each trait that was present in at least one candidate model from the subset of top models. In addition, we identified the importance of each trait based on its frequency in the subset of top models. The importance scores and the model averaged coefficients were used to determine the main traits for explaining species trends. The set of candidate models was defined as models with $\Delta AIC \leq 2$. Burnham *et al.* (2010) suggest there is often support for models where ΔAIC is < 7, however, we chose to use $\Delta AIC < 2$ as the null model was the 3rd best model with a ΔAIC of 1.12 and therefore increasing the ΔAIC threshold was simply adding noise (models with little evidence to support them) to the key result.

A multi-model inference approach while accounting for phylogeny is not straight-forward. In our PGLS models, λ was estimated independently for each model and can therefore be different between the candidate models. Using AIC to compare between these models could be misleading as we could not disentangle the influence of a difference in the evolutionary model (λ) from the influence caused by changing which traits were included in the model on AIC scores. However, all of the models in the top subset had an estimated λ value of 0, implying that species trend in the UK is not phylogenetically-patterned. Therefore ΔAIC was measuring the effect of the trait differences rather than any potential difference in the evolutionary model in this case. All analyses were carried out using R 3.0.2 (R Core Team, 2013).

Results

We found significant trends for 72% of the species in this study: of these, 12 were decreasing and 14 species were increasing. Species included that showed the greatest declines included: *Ischnura pumilio*, *Leucorrhinia dubia* and *Sympetrum danae*, while *Libellula fulva*, *Erythromma najas* and *Brachytron pratense* showed the greatest increases. Using the fitted values from the species trend models we estimated the change in probability of observation over a ten year period for each species. Each species was then categorised using these ~~ten~~ year changes (Figure 2). This figure illustrates the substantial variation in the trend estimates between species, and again highlights the large proportion declining species which is a cause for concern.

Six models containing various combinations of three traits (distribution type, flight period and thorax length) formed the top subset of models for explaining Odonata distribution trends (Table 2). Of these three traits, distribution type was the most important (importance score = 0.6), and was present in three of the top models. The model averaged coefficients for distribution type reveal that southern species tend to have increased relative to the other categories and northern species have declined on average, with the other two categories (oceanic and widespread) intermediate (Figure 3). Notable exceptions to this trend include the strong declines in *Ischnura pumilio* and *Gomphus vulgatissimus* both of which were classified as southern species. Flight period was present in two of the top models and had an importance score of 0.34. The coefficient was negative, suggesting that species with longer flight periods had ~~a~~ lower trend estimates (i.e. they declined relative to species with short flight periods). Thorax length was also present in two of the top models but had the lowest importance score (0.24) of all traits present in the top model subset. The model averaged slope for the relationship between thorax length and trend estimate was marginally positive, which suggests that larger species were faring better than smaller species. We note that the 95% confidence intervals of both flight period and thorax length spanned zero, and that the null model was the third best model based on AICc. The top two models explained a modest 13 and 16% of the variation in species trend.

In general, the key trait-trend relationships and importance scores were robust across the different response variables and modelling approaches (Appendix 1 & 2). Distribution type was the most important trait for four of the five response/modelling approach combinations, while flight period and thorax length were consistently important (Appendix 3). The model averaged coefficients for these three traits were similar across approaches. Other traits including habitat breadth, overwintering stage, breeding habitat and status, were retained in the top model subset for some of the other approaches. However, the model averaged 95% confidence intervals spanned zero in the vast majority of cases for these additional traits (Appendix 2).

Discussion

We found that the dragonfly fauna in Britain and Ireland has undergone considerable change during recent decades, with high levels of inter-specific variation in occurrence trends (Figure 2). We found twelve species (33%) had significant negative trends, while 14 species (39%) showed significant increases. Although more species increasing than decreasing is good news for conservation, this could be interpreted as a signal of biotic homogenization, i.e. the fauna becomes dominated by a small number of species, and local and regional difference between communities are eroded (Keith *et al.*, 2009).

We found distribution type was the key correlate of Odonata trends, with southern species tending to have higher trend estimates than the all other distribution types (Figure 3). This result is in line with our hypothesis that increased temperatures has increased the climate suitability of Britain and Ireland for southerly distributed species. A variety of studies have provided evidence of this relationship, i.e. Devictor *et al.* (2008) found bird communities in France between 1989 and 2006 were increasingly dominated by species that prefer warmer conditions, while Lima *et al.* (2007) found evidence of northward range expansions in warm-water adapted

Portuguese algae. Hickling *et al.* (2005) used distribution type to explain variation in range shift and expansion in British Odonata, finding that southern species showed greater poleward shifts and expansions compared to northern species. By contrast, Angert *et al.* (2011) found no correlation between range shift and position of the northern range limit (which is related to our measure of distribution type). Despite the wealth of evidence that points to climate change as the likely driver of increases in southern species, we cannot ignore the role of improved water quality and standing water availability in southern Britain (Hickling *et al.*, 2005; Cham *et al.*, 2014). Not all southern species showed positive ~~trend~~ (notably *Ischnura pumilio* and *Gomphus vulgatissimus*), this limited expansion in response to climate warming is likely due to availability of suitable habitat.

The lower trend estimates for northern species is likely to be the result of the combined pressures of a decline in climate suitability and competition from species that were previously limited by lower thermal tolerance (Myers *et al.*, 2009; Thomas, 2010). Evidence of the loss of northern species has been seen in a variety of taxonomic groups across a variety of geographic regions (Hill *et al.*, 2002; Devictor *et al.*, 2008; Myers *et al.*, 2009; Foufopoulos *et al.*, 2011), and with the persistent and increasing threat of anthropogenically induced climate change, northern species and those reliant upon them are likely to become increasingly threatened.

We found no evidence for six other hypotheses about the drivers of species trends. Flight period and thorax length appeared marginally important but evidence for this was weak as the 95% CI of these traits spanned zero. Additionally when these two traits were modelled against species trend individually they performed no better than the null model. Body size and flight period were used as surrogates for competitive ability and dispersal ability: it is plausible that more direct measures of these traits do predict the species in decline. The reliability of the trait-trend results depend on the accuracy of the underlying trait data. We note that within a given species, traits can vary spatially (i.e. habitat specificity can vary across a species range – Oliver *et al.*, 2009), however here we use a single value per trait per species. This is a common approach within the comparative analysis literature but is a potential source of noise in the results. One problem with “well-sampled sites” approach is that it amplifies the spatial gradient in recording intensity, such that trends for northern species are estimated from a relatively small number of sites. This has implications for the precision of trend estimates for northern vs southern species, which is accounted-for in the weighted trait models (Appendix 1b). Basing the trend on a small number of sites is unlikely, on its own, to bias the estimate (Isaac *et al.*, 2014b), although we don’t know the degree to which trends on these sites (and others considered well-sampled) reflect changes in the wider countryside. We found no evidence of phylogenetic signal in our models, although our phylogeny was based on taxonomy. Using a phylogeny constructed from sequence data would be more rigorous, but such genetic data are currently limited.

In conclusion, we found variation in species distribution trends was best explained by distribution type, with southern species showing significantly higher trends than widespread and northern species. We believe this reflects the impact of climate change as the increased ambient temperature in Britain and Ireland better suits species that are adapted to warmer conditions. The lower trend estimates for northern species is a cause of conservation concern as this result combined with evidence in previous studies shows that northern species are shifting to higher latitudes and altitudes, are declining in range size and abundance, and are therefore particularly vulnerable to the ever increasing threat of climate change.

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Table 1(on next page)

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.

Table 2(on next page)

Table 2 Parameter estimates for the subset of best models.

For the categorical variable (distribution type) ● denotes that it was present in the selected model, while the slope is displayed for the continuous traits present in the selected model. The final column expresses the importance value 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	

Figure 1(on next page)

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

The shading represents the number of unique monads within the hectad that were included in the analysis, the “well-sampled sites”.

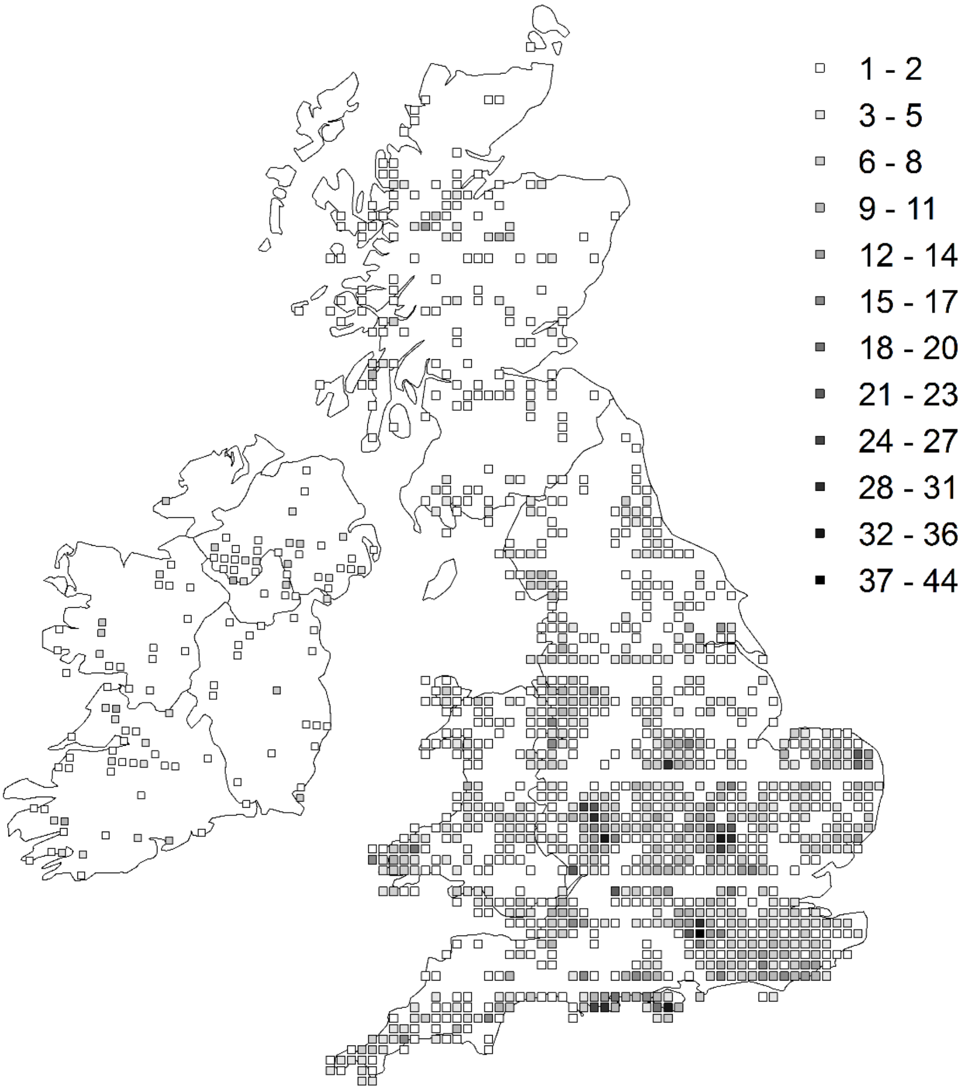

1 - 2
3 - 5
6 - 8
9 - 11
12 - 14
15 - 17
18 - 20
21 - 23
24 - 27
28 - 31
32 - 36
37 - 44

Figure 2(on next page)

Figure 2 The proportion of species in each trend category.

Using the fitted values from the species models, trends were estimated as the percentage change in probability of observation over a ten year period. Shades of red symbolises declines while shades of green are used for increases, the intensity of colour reflects the strength of the trend.

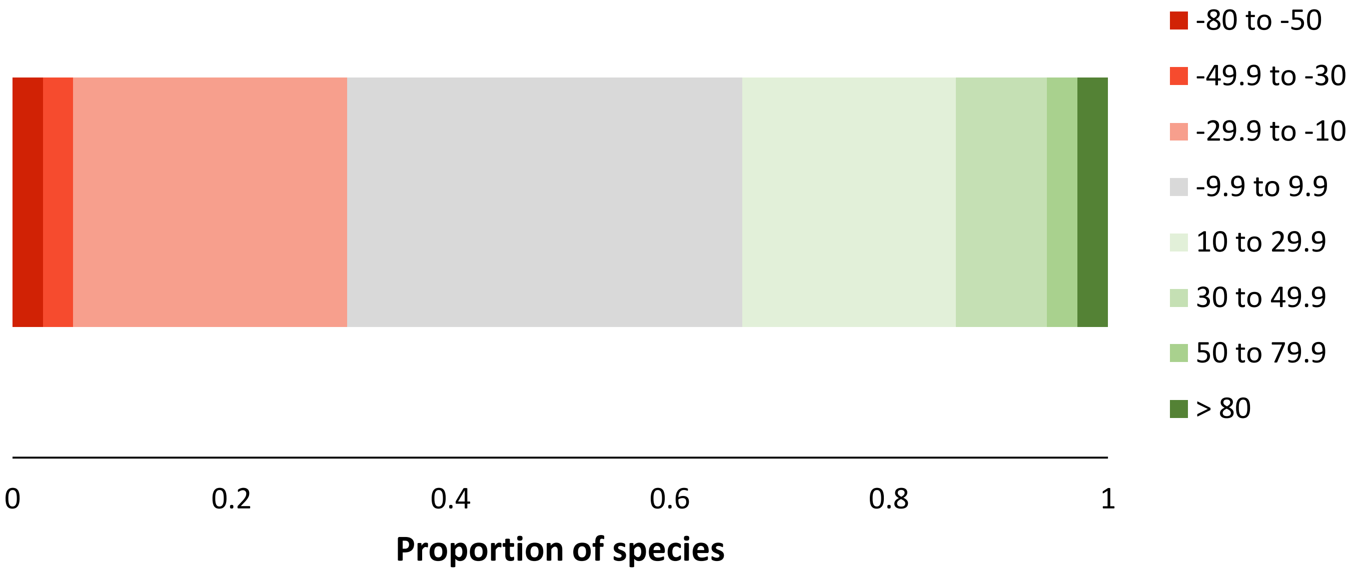
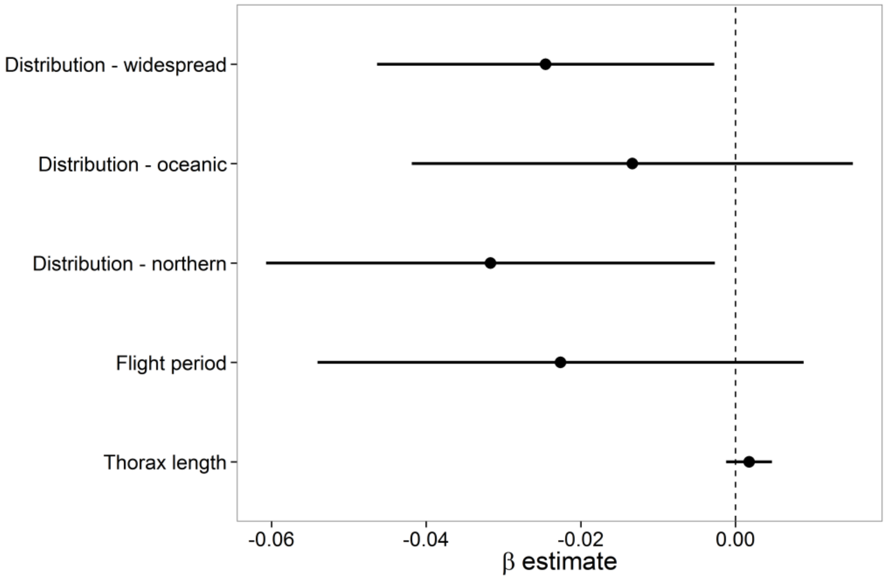

-80 to -50
-49.9 to -30
-29.9 to -10
-9.9 to 9.9
10 to 29.9
30 to 49.9
50 to 79.9
> 80
0
0.2
0.4
0.6
0.8
1
Proportion of species

Figure 3(on next page)

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

The reference distribution type was “southern”, which has a parameter estimate set to 0.


Distribution - widespread
Distribution - oceanic
Distribution - northern
Flight period
Thorax length
-0.06
-0.04
-0.02
0.00
β estimate