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1 **A new approach to modelling the relationship between annual population**  
2 **abundance indices and weather data**

3 **Running title:** Modelling annual population abundance indices

4

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6 Harrington, R.<sup>4</sup>, Monteith, D.<sup>3</sup>, Brereton, T.M.<sup>5</sup>, Boughey, K.L.<sup>6</sup> & Pearce-Higgins, J.W.<sup>2</sup>

7

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18

19 **Abstract (231 words)**

20 Weather has often been associated with fluctuations in population sizes of species, however, it  
21 can be difficult to estimate the effects satisfactorily because population size is naturally  
22 measured by annual abundance indices whilst weather varies on much shorter timescales. We  
23 describe a novel method for estimating the effects of a temporal sequence of a weather variable  
24 (such as mean temperatures from successive months) on annual species abundance indices.  
25 The model we use has a separate regression coefficient for each covariate in the temporal  
26 sequence and over-fitting is avoided by constraining the regression coefficients to lie on a curve  
27 defined by a small number of parameters. The constrained curve is the product of a periodic  
28 function, reflecting assumptions that associations with weather will vary smoothly throughout  
29 the year and tend to be repetitive across years, and an exponentially decaying term, reflecting  
30 an assumption that the weather from the most recent year will tend to have the greatest effect  
31 on the current population and that the effect of weather in previous years tends to diminish as  
32 the time lag increases. We have used this approach to model 501 species abundance indices  
33 from Great Britain, and present detailed results for two contrasting species alongside an overall  
34 impression of the results across all species. We believe this approach provides an important  
35 advance to the challenge of robustly modelling relationships between weather and species  
36 population size.

37

38 **Key-words:** Abundance index; climate change impacts; distributed lag models; population  
39 abundance models; population change, weather variables.

40

41 **1. Introduction**

42 It is important for ecologists to understand the relationships between species abundance and  
43 weather. These relationships matter in many applied situations, when knowledge is required of

44 the determinants of species distributions, changes to population sizes and distributions, and  
45 more recently the likely effects of climate change, particularly for those species identified as  
46 requiring protection at global (UN convention) and continental (e.g. EU directive) scales. In  
47 many studies, spatial relationships between species abundance and weather are analysed by  
48 modelling species data from a large number of contrasting locations as a function of a few  
49 bioclimatic variables (e.g. Chen et al 2011, Bellard et al 2012, Warren et al 2013). These  
50 approaches require extensive distributional data. For many species there are not data from a  
51 enough sites across a sufficiently broad spatial extent and in such cases, longitudinal studies of  
52 population change in confined geographical areas may be used to infer potential sensitivities  
53 and responses to climate change (e.g. Martay *et al.* 2016). However, these studies present  
54 challenges to inferring impacts of weather, due to population data that are at a coarse spatial  
55 extent, often aggregated to an annual estimate of the population index. We demonstrate a novel  
56 modelling approach that can extract more information from such longitudinal population  
57 change data than previous analytical methods.

58

59 Estimation of the relationship between weather and annual species abundance indices is less  
60 straightforward than it might at first seem. Sometimes there is a clear causal link between  
61 particular weather variables and species' abundance (e.g. Pollard 1988; Roy *et al.* 2001;  
62 Pearce-Higgins *et al.* 2010), but often the nature and timing of the relationships are not known  
63 *a priori*. This means that the weather from many different seasons may affect populations,  
64 leading to the number of potential explanatory variables being large relative to the number of  
65 years for which abundance indices are available. Even if each weather variable to be  
66 considered is summarised across a time period of some suitable duration (which we take  
67 henceforth as being a calendar month), then there are still many potential combinations of types  
68 of weather variable (e.g. monthly minimum, mean and maximum temperature, frost days,

69 precipitation) and months in the years leading up to each abundance index record.  
70 Furthermore, a species abundance index may respond differently to the same weather variable  
71 (e.g. temperature) in different months (e.g. Pollard 1988, Pearce-Higgins *et al.* 2015), creating  
72 a tension between model flexibility and the avoidance of over-specification.

73

74 The principal assumption underlying traditional approaches to modelling annual abundance  
75 index data is that any individual model can contain only a small number of covariates relative  
76 to the number of observations, often leading to construction and use of covariates at a seasonal  
77 (quarterly) level summarising individual weather variables (e.g. mean temperature) or weather  
78 patterns (e.g. winter North Atlantic Oscillation). Whilst this assumption may hold when each  
79 covariate has its own regression coefficient whose value is free to vary independently of all  
80 other regression coefficients, it does not hold if the regression coefficients can be constrained  
81 in some manner. A natural way of thinking about the problem is to consider that each index  
82 value  $y_t$  for years  $t=1\dots T$  contained in the vector  $\mathbf{y}$ , depends on the weather records  $x_{t1}, x_{t2}, x_{tM}$ ,  
83 from  $M$  successive past months, specified as the entries in the corresponding rows of monthly  
84 weather covariates,  $\mathbf{x}_1, \mathbf{x}_2$  up to  $\mathbf{x}_M$ , each of length  $T$ . Associated with each of these  $M$   
85 covariates is a single covariate regression coefficient,  $b_m$ , for  $m=1\dots M$ . As successive  
86 covariates correspond to the weather in consecutive months, we may expect neighbouring  
87 covariate regression coefficients to be related, and we use these relationships to reduce the  
88 number of free parameters associated with the sequence of covariate regression coefficients,  
89  $b_1\dots b_M$ . The approach we have taken is to specify a parametric function,  $b_m=f(m,\boldsymbol{\theta})$ , for the  
90 monthly covariate regression coefficients, in which the function  $f(m,\boldsymbol{\theta})$  was selected to enforce  
91 what we considered to be ecologically reasonable constraints on the sequence of covariate  
92 regression coefficients through a low-dimensional vector,  $\boldsymbol{\theta}$ , of underlying parameters to be  
93 estimated.

94

95 Modern statistics offers a selection of alternative approaches to imposing the belief of similarity  
96 in successive values of the sequence of covariate regression coefficients,  $b_1 \dots b_M$ . Forms of  
97 penalised signal regression using as roughness penalty the squares of the first, second or third  
98 differences of the sequence  $b_1 \dots b_M$  (Marx & Eilers 1999) have been used to model the effect of  
99 long sequences of weather variables on species traits other than population size (Sims *et al.*  
100 2007; Roberts 2008; Roberts 2012). Alternatively, the problem can be treated as a particular  
101 case of a distributed lag model (e.g. Baltagi, 2008) in which the  $b_1 \dots b_M$  are derived from a  
102 suitably flexible series of basis functions. We shall use this latter formulation to compare our  
103 parametric specifications with a more flexible alternative.

104

105 In this paper, we begin by describing the data sets available, including how these have been  
106 used to construct national species abundance indices and associated sequences of weather  
107 covariates. We then define a parametric form  $f(m, \theta)$  for the model of monthly covariate  
108 regression coefficients with what we consider to be the relevant desirable properties, presenting  
109 an approach to estimating the underlying parameters and constructing confidence intervals for  
110 both the monthly covariate regression coefficients and fitted values for the model of the  
111 abundance indices. The final methodological element considered is how to summarise the  
112 model fits across a large number of species. The methods, and their comparison with fitting a  
113 distributed lag model without such strong functional constraints, are illustrated using two  
114 contrasting species. We conclude by discussing the merits of our approach, what has been  
115 learned and how it may be improved. Throughout, the notation used omits reference to  
116 particular weather variables or species except where this is essential.

117

118 **2. Materials and methods**

## 119 2.1 Derivation of annual abundance indices for each species

120 We extracted site- and year-specific records of abundance for 501 species of butterflies, moths,  
121 aphids, birds, and mammals from the databases of various long-term monitoring schemes  
122 within Great Britain (see Martay *et al.* 2016 for details of all data sources). For each species,  
123 these data comprised estimates of abundance from individual site by year combinations, using  
124 available years between 1966 and 2011. Generalised linear models with Poisson errors and a  
125 log link function, including categorical variables for site and year, were fitted to the site-by-  
126 year abundance data for each species. The estimated year effects,  $y_t$ , from these log-linear  
127 models for  $t$  ranging from 1 (the oldest value) to  $T$  (the most recent), were taken as the annual  
128 population indices to be modelled, adopting the convention that  $y_t=0$  to resolve the aliasing in  
129 the full set of year-specific and site-specific parameters. These estimated annual species  
130 abundance indices are therefore on a logarithmic scale, and their construction makes best use  
131 of the available data, in particular allowing for the fact that not all sites provide records for all  
132 years (Freeman & Newson, 2008). Following existing protocols for bats (Barlow *et al.*, 2015),  
133 survey-specific methodological and effort covariates known to strongly influence each  
134 abundance record (survey weather, type of bat detector, timing of survey) were included in the  
135 log-linear models leading to the derivation of the annual abundance indices adjusted for these  
136 survey-specific covariates.

137

## 138 2.2 Weather data

139 We chose to examine the effect of two key weather variables, precipitation and temperature,  
140 on the annual abundance indices, both having been found previously to affect population sizes  
141 of the species groups of interest (see, e.g., Huntley *et al.*, 2007, or Johnston *et al.*, 2013). Data  
142 values for these weather variables were downloaded from the UK Met Office as national-level  
143 summaries for each month of all calendar years from 1910 to 2011 (Perry & Hollis, 2005). A

144 comparison of mean, minimum and maximum temperature values indicated that these were  
145 highly correlated: consequently the corresponding fitted models in test runs were similar and a  
146 decision was taken to use only the mean temperature. Thus models were fitted based on either  
147 precipitation or mean temperature data, using monthly total precipitation and the product of  
148 monthly mean temperature and number of days in the each month to equalise the influence of  
149 weather from individual days on the annual abundance indices. Either UK or English weather  
150 data were used as appropriate for each species, given the geographical coverage of sampling  
151 locations.

152

153 For each species, some care was needed to define the weather covariates to ensure the analyses  
154 were based only on months that could have influenced the response variable. This required the  
155 identification of a reference month,  $r$  ranging in value from  $r=1$  for January to  $r=12$  for  
156 December, based on knowledge of the ecology and survey protocols for the species in question,  
157 such that only the weather up to and including month  $r$ , in year  $t$  could influence the  
158 corresponding index value  $y_t$ . The weather data  $w_{rt}$  on either mean temperature or precipitation  
159 from month  $r$  in each of years  $t=1 \dots T$  were used to construct the first monthly weather covariate,  
160  $\mathbf{x}_1$ : thus  $x_{1t} = w_{rt}$ . Successive weather covariates  $\mathbf{x}_2$  up to  $\mathbf{x}_M$  were created by working backwards  
161 through the monthly weather data, one month a time: thus  $x_{2t} = w_{r-1,t}$  unless  $r=1$  in which case  
162  $x_{2t} = w_{12,t-1}$ . Since the entries in successive rows of  $\mathbf{x}_1$  are separated by 12 months, the values in  
163  $\mathbf{x}_1$ ,  $\mathbf{x}_2$  up to  $\mathbf{x}_M$  have a repeating structure in the sense that  $x_{m+12,t} = x_{m,t-1}$ . For simplicity,  
164 however, in the following sections we describe the models in terms of these derived covariates  
165 rather than the original sequence of weather data.

166

167 2.3 Relating annual species abundance indices to weather



168 The general approach that we have taken allows data on a single weather variable from a large  
 169 number of past months to be included in the model for the abundance index of some particular  
 170 species, and is as follows. Let  $y_t$  be the national index of abundance on a natural logarithmic  
 171 scale from year  $t$  for  $t=1\dots T$ . In the absence of any weather effect, a simple model for  $y_t$  showing  
 172 a general trend with errors  $e_t$  would be defined mathematically as:

$$173 \quad y_t = a + ct + e_t, e_{1\dots T} \sim \text{Gaussian AR}(1). \quad (1)$$

174 In Equation 1, which defines our null model (denoted  $E_0$ ) for variation in the absence of any  
 175 weather effect,  $(\theta_1, \theta_2)=(a, c)$  where  $a$  is some overall intercept,  $c$  is the regression coefficient  
 176 of a year of survey covariate included to remove any linear trend, whether intrinsic to the  
 177 population or arising from excluded effects. The error terms  $e_t$  are assumed to come from  
 178 normal (Gaussian) distributions through which both here and elsewhere we allow for temporal  
 179 correlation by assuming the sequence of error terms  $e_1 \dots e_T$  follows a first order auto-  
 180 regressive, AR(1), process.

181

182 We extend the null model by inclusion of a sequence of monthly covariates,  $x_{m,t}$ , as defined in  
 183 Section 2.2, each with an associated covariate regression coefficient  $b_m$ , giving rise to the  
 184 expression:

$$185 \quad y_t = a + ct + \sum_{m=1}^M b_m x_{m,t} + e_t, e_{1\dots T} \sim \text{Gaussian AR}(1). \quad (2)$$

186 Rather than estimating each covariate regression coefficient  $b_m$  independently, which in general  
 187 is not possible since for large  $M$  the number of covariates exceeds  $T$ , the number of observations  
 188 of the response variable, we specify a functional relationship  $b_m=f(m,\boldsymbol{\theta})$  for which the number  
 189 of elements,  $P$ , of the underlying parameter vector  $\boldsymbol{\theta}$  of length is sufficiently small to be well  
 190 estimated. The function  $f(m,\boldsymbol{\theta})$  itself is selected to impose two beliefs in addition to smoothness  
 191 about the sequence of regression coefficients. First, the covariate regression coefficients  $b_m$  will

192 decay towards zero as  $m$  increases due to the declining influence of weather many years prior  
 193 to any given abundance estimate. Second, the covariate regression coefficients  $b_m$  will show  
 194 some periodicity with respect to  $m$ , in the sense that we might expect covariate regression  
 195 coefficients lagged by whole calendar years ( $b_m$  and  $b_{m+12}$ ) to take the same sign, whilst  
 196 allowing for potential opposing effects within a year. We enforce these two beliefs by writing  
 197  $f(m, \theta)$  as the product of a decaying term, defined by a single underlying non-linear parameter,  
 198  $\kappa$ , which for purposes of exposition we replace by  $\lambda = \exp(\kappa)/(1 + \exp(\kappa))$  with  $0 < \lambda < 1$ , and a  
 199 periodic term defined by multiple underlying linear parameters. By expressing the periodic  
 200 term as a first-order Fourier series, we obtain:

$$201 \quad b_m = \lambda^{m-1} (\beta_1 + \beta_2 \sin(2\pi m/12) + \beta_3 \cos(2\pi m/12)); \quad (3)$$

202 with the combination of (2) and (3) defining our simplest alternative model,  $E_1$ , for the  
 203 covariate regression coefficients ( $b_m$ ) which thus enlarges on the null model  $E_0$  by the inclusion  
 204 of four underlying parameters,  $(\theta_3, \theta_4, \theta_5, \theta_6) = (\beta_1, \beta_2, \beta_3, \lambda)$ . The underlying parameter  $\beta_1$   
 205 describes the average effect of the weather variable under investigation, regardless of time of  
 206 year, and facilitates the possibility that all covariate regression coefficients may take the same  
 207 sign. The pair of underlying parameters  $\beta_2$  and  $\beta_3$  define the phase and amplitude of the sine  
 208 wave, and both are required to ensure that the phase of the underlying sine wave is  
 209 unconstrained by the allocation of calendar months to the integers from 1 to 12. This allows  
 210 the model to account for potentially contrasting positive and negative impacts of temperature  
 211 and precipitation on the same population at different times of the year; for example accounting  
 212 for potentially contrasting effects of summer and winter warmth within the same year upon  
 213 butterfly populations (Long *et al.* 2016). Some examples of the sequences of covariate  
 214 regression coefficients that can be generated from (3) are given as Supplementary Material.

215

216 This alternative model can be elaborated on in a number of ways, of which we consider two.  
 217 The first elaboration, which we shall refer to as model  $E_2$ , introduces a term of period six  
 218 months into the cyclic part of the underlying model, leading to covariate regression coefficients  
 219 defined by the following equation:

$$220 \quad b_m = \lambda^{m-1} [\beta_1 + \beta_2 \sin(2\pi m/12) + \beta_3 \cos(2\pi m/12) + \beta_4 \sin(4\pi m/12) + \beta_5 \cos(4\pi m/12)],$$

221 (4)

222 for which  $P=8$  and  $\theta^T=(a, c, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \lambda)$ . The benefit of this first elaboration can be  
 223 thought of as enabling two peaks per year in the series of covariate regression coefficients, and  
 224 / or removing the constraint under model  $E_1$  of symmetry in the periodic element either side of  
 225 the peaks and troughs. This can be important, for example allowing positive effects of both  
 226 spring and winter temperature upon resident bird species within the same year (Pearce-Higgins  
 227 *et al.* 2015). The second elaboration, which we shall refer to as model  $E_3$ , introduces a term of  
 228 period two years into the cyclic part of the underlying model, leading to covariate regression  
 229 coefficients defined by the following equation:

$$230 \quad b_m = \lambda^{m-1} [\beta_1 + \beta_2 \sin(2\pi m/12) + \beta_3 \cos(2\pi m/12) + \beta_4 \sin(\pi m/12) + \beta_5 \cos(\pi m/12)]. \quad (5)$$

231 The benefit of this second elaboration can be thought of as allowing the sign of covariate  
 232 regression coefficients to alternate between years, introducing the concept of differential  
 233 lagged effects, for example as may occur as a result of contrasting direct effects of spring  
 234 temperature upon chick growth rates, and indirect (lagged) negative effects of temperature  
 235 upon the same species, mediated through reductions in prey populations (Pearce-Higgins *et al.*  
 236 2010).

237

## 238 2.4 Estimation

239 We have fitted the four models described above, ( $E_0$ ,  $E_1$ ,  $E_2$  and  $E_3$ ), to annual abundance index  
 240 data from all 501 available species, using as covariate sequences of either mean temperature or

241 precipitation either over the preceding single year or over the preceding 40 years as covariates,  
 242 giving a total of 12 or 480 weather covariates respectively. Estimation of the parameters in the  
 243 four underlying models which defined the sequences of 480 covariate regression coefficients  
 244 was implemented using the *lme*, *gls* and *nlme* functions in the *nlme* package (Pinheiro *et al.*,  
 245 2014) of the R software (R Core Team, 2015), making use of the fact that each regression  
 246 model for the abundance indices can be expressed directly as a function of the underlying  
 247 parameters, such as

$$\begin{aligned}
 248 \quad y_t = a + ct + \beta_1 \sum_{m=1}^M \lambda^{m-1} x_{m,t} + \beta_2 \sum_{m=1}^M \sin(2\pi m/12) \lambda^{m-1} x_{m,t} + \\
 249 \quad \beta_3 \sum_{m=1}^M \cos(2\pi m/12) \lambda^{m-1} x_{m,t} + e_t, \quad (6)
 \end{aligned}$$

250 for  $E_1$ . Such reformulations demonstrate that, conditional on the value of  $\lambda$  (equivalently  $\kappa$ ),  
 251 the other underlying parameters in the model for the mean value of  $y_t$  appear linearly  
 252 (Ratkowsky 1983). The model for the abundance indices corresponding to  $\lambda=1$  (equivalently  
 253  $\kappa=\infty$ ) was fitted separately if required. Estimation of the underlying parameters for models  $E_1$ ,  
 254  $E_2$  and  $E_3$  began with a grid search on values of  $\kappa$  from -3 to 9 in steps of 0.25, with each value  
 255 of  $\kappa$  treated as fixed and optimising over all other underlying parameters to find the conditional  
 256 maximum likelihood. The resulting profile likelihoods were not necessarily unimodal: we  
 257 present below the results of subsequent optimisations for all model parameters, performed  
 258 starting from the optimum arising from the grid search for  $\kappa$  followed by conditional  
 259 optimisation of remaining parameters. To avoid over-fitting, the underlying models containing  
 260 second-order Fourier terms,  $E_2$  and  $E_3$ , were only fitted when at least 20 abundance index  
 261 values were present. During the implementation of the fitting procedure, we mean-centred  
 262 each covariate  $\mathbf{x}_{1...M}$  before inclusion in the model to aid interpretation and to reduce the  
 263 correlation between underlying parameters describing the periodic cycle and the overall  
 264 intercept  $a$ .

265

## 266 2.5 Calculation of confidence intervals

267 The presence of the non-linear parameter,  $\kappa$ , in the model for the mean value of  $y_i$  not only  
268 complicated the estimation of the vector,  $\theta$ , of underlying model parameters: it also caused  
269 added complications when calculating confidence intervals for the covariate regression  
270 coefficients,  $b_m$ , and the fitted values in the model for the abundance indices, all of which are  
271 non-linear functions of  $\kappa$ . We found the most satisfactory way of calculating confidence  
272 intervals was to use importance sampling, implemented as a two-step procedure: firstly, sample  
273  $\kappa$  according to a quadratic (Gaussian) approximation to the profile log-likelihood; secondly,  
274 conditional on  $\kappa$ , sample the remaining parameters  $\theta_{1\dots P-1}$  according to the quadratic Gaussian  
275 log-likelihood for (6) defined by the conditional estimates of  $\theta_{1\dots P-1}$  and associated covariance  
276 matrix. For each set of parameter values thus derived, the associated likelihood for (6) was  
277 calculated, and the ratios of these actual likelihoods to the product of the two importance  
278 sampling likelihoods (firstly for  $\kappa$ , secondly for  $\theta_{1\dots P-1}$  given  $\kappa$ ) were then used as importance  
279 weights. Confidence intervals for the covariate regression coefficients,  $b_m$ , and prediction  
280 intervals for the fitted values of the model of the abundance indices were formed from  
281 importance-weighted quantiles of the corresponding sets of values calculated from the  
282 underlying parameter values simulated as above. Exact details for how this was done can be  
283 seen from the *R* code provided as Supplementary Material.

284

## 285 2.6 Model summaries and comparisons

286 We assessed the evidence for increasing model complexity by using *F*-tests to examine the  
287 statistical significance of changes in deviance when adding underlying parameters to the model.  
288 For these *F*-tests the numerator degrees of freedom was taken as the number of added  
289 parameters and the denominator degrees of freedom was calculated as the difference between

290 the number of index values and the number of parameters in the model for the mean value.  
291 This evidence is presented across species as histograms of  $p$ -values corresponding to the  
292 transitions between the different models. Histograms of estimates of  $\lambda^{12}$  are shown also, to  
293 indicate the annual decay rate of the covariate regression coefficients determined by the  
294 periodic part of the model.

295

296 For model  $E_1$ , we summarised the covariate regression coefficients across species by presenting  
297 standardised weighted means of the covariate regression coefficients (SWMCRC).

298 Augmenting the above notation so that the covariate regression coefficient for covariate  $x_m$  for  
299 species  $i$  is  $b_{mi}$ , we first normalised the covariate regression coefficients for any given species

300 by dividing by  $\max(|b_{mi}|, m=1\dots 12)$ , then weighted the normalised values by  $1 - p_i$  where  $p_i$

301 indicates the significance of the transition from  $E_0$  to  $E_1$ , giving  $B_{mi} = (1 - p_i)b_{mi} / \max(|b_{mi}|)$ . Our

302 standardised presentation for any group  $S$  of  $N_S$  species all with the reference month, comprises

303 two weighted means,  $A_m^{S+} = \Sigma^{S+} B_{mi} / N_S$  and  $A_m^{S-} = \Sigma^{S-} B_{mi} / N_S$ , in which  $\Sigma^{S+}$  and  $\Sigma^{S-}$  denote

304 summation over species  $i$  in  $S$  for which  $B_{mi}$  is positive or negative respectively. We calculate

305 and present these for covariates  $m=1\dots 12$  only, since values for later months are necessarily

306 smaller. The net result of this combination of covariate regression coefficients is to produce

307  $A_m^{S+}$  and  $A_m^{S-}$ , bounded by 0 and +1 or -1 respectively, the extrema being approached only if

308 the covariate regression coefficients for all species take their maximum absolute value in the

309 same month, have the same sign in that month, and the transitions from model  $E_0$  to  $E_1$  are

310 highly statistically significant for all species. Where species in  $S$  do not all have the same

311 reference month, an additional step is required to align the values of  $B_{mi}$  from different species

312 so that the values of  $A_m^{S+}$  and  $A_m^{S-}$  are formed for each relevant calendar month, rather than

313 according to lags from the differing reference months, the divisor for each month then being

314 the number of contributing species for that month rather than  $N_s$ . Statistical significance of  
315 SWMCRC was assessed using a sign test, considering the sign of each covariate regression  
316 coefficient  $b_{mi}$  to be random under the null hypothesis of no effects of weather.

317

## 318 2.7 Comparison with a less constrained alternative model

319 We compare the sequences of covariate regression coefficients,  $b_1 \dots b_M$ , with their counterparts  
320 estimated assuming linear dependence between the weather covariates and the population  
321 abundance indices by fitting distributed lag models (DLM) using the *dlnm* package (Gasparrini  
322 2011) of *R*. Due to the oscillatory nature of the sequence, with each oscillation having period  
323 one year and so needing to be approximated by a cubic polynomial, we found it necessary to  
324 use a basis function with 3 knots per year. The basis functions were created with the default  
325 knot locations using four years of monthly weather covariates (48 covariates and 12 knots in  
326 total) by the function *crossbasis*. Parameter estimation used *lme* with a linear trend over years  
327 and auto-regressive, AR(1), errors to ensure equivalence to the fitting of models  $E_1$ ,  $E_2$  and  $E_3$ .

328

## 329 3. Results

### 330 3.1 Results for two example species

331 The wren (*Troglodytes troglodytes*) is a small songbird whose population abundance index is  
332 derived from the BTO's Breeding Bird Survey (BBS) and Common Bird Census (CBC) (see  
333 Pearce-Higgins *et al.* 2015). The species is found throughout the UK, but because of the higher  
334 density of sites in England our modelling uses only English abundance data and hence only  
335 English weather data. The abundance index was assigned a reference month of June ( $r=6$ )  
336 since the latest of the two annual BBS site visits takes place then, and the time series used runs  
337 from 1966 to 2011, excepting 2001 when access to sites was restricted due to a national disease  
338 outbreak. We report here the modelled response to mean temperature, the species having been

339 found to be much less responsive to precipitation. The initial grid searches indicated well-  
340 defined optima: the values of the transformed decay parameter  $\kappa$  most strongly supported by  
341 the data lay in the range from 2.5 to 3.5 for the models  $E_1$ ,  $E_2$  and  $E_3$  (Fig. 1, top). Maximised  
342 log-likelihood values for the three models, along with the corresponding value for the null  
343 model  $E_0$ , are given in Table 1. These indicate that the transition from the null model  $E_0$  to the  
344 model in which the covariate regression coefficients are defined by a first order damped Fourier  
345 series  $E_1$  is highly statistically significant ( $F_{4,39}=9.95$ ;  $p < 10^{-4}$ ), whereas the evidence in support  
346 of an elaboration from  $E_1$  to either of the more complex models is much weaker ( $F_{2,37} = 2.12$ ,  
347  $0.97$ ;  $p = 0.13, 0.39$ ; for the transitions from  $E_1$  to  $E_2$  and  $E_1$  to  $E_3$  respectively). Inspection of  
348 the plot of covariate regression coefficients  $b_m$  against  $m$  for underlying model  $E_1$  (Fig. 1,  
349 middle) indicates that the signs of  $b_m$  oscillate approximately about zero, with negative values  
350 in mid-summer (when higher temperatures correlate with lower abundance indices) and  
351 positive values in mid-winter (when higher temperatures correlate with higher abundance  
352 indices). Values of the covariate regression coefficients decay by a factor of about 0.51 (=   
353  $\lambda^{12}$ ) between successive years. Regression coefficients estimated using DLM follow a similar  
354 pattern to those estimated using model  $E_1$ , comparison of the maximised log likelihoods  
355 indicating little evidence to justify the additional parameters required by the DLM (Table 1,  
356 column 1). The time series plot showing abundance indices and fitted values (Fig. 1, bottom)  
357 indicates broad agreement between observed and modelled series, although the sharp drop in  
358 log abundance in 1991 is not picked up well.

359

360 The flounced rustic (*Luperina testacea*) is a univoltine, grass-feeding noctuid moth whose  
361 population abundance index is derived from adults attracted to light traps mostly in August and  
362 September, as recorded by the Rothamsted Insect Survey. Our analyses used abundance and



363 weather data from all of the UK, with response data from 1975 to 2010, with a reference month  
364 of September ( $r=9$ ). We report here the modelled response to precipitation, the species having  
365 been found to be less responsive to temperature. The initial grid searches indicated well-  
366 defined optima for  $\kappa$  in the range from 3.0 to 4.0 for the models  $E_1$ ,  $E_2$  and  $E_3$  (Fig. 2, top).  
367 Maximised likelihood values (Table 1) indicate that the transition from the null model  $E_0$  to the  
368 model  $E_1$  is highly statistically significant ( $F_{4,30} = 8.82$ ;  $p < 10^{-4}$ ), whereas the evidence in  
369 support of either elaboration from  $E_1$  is much weaker ( $F_{2,28} = 1.23, 1.80$ ;  $p = 0.31, 0.18$ ; for the  
370 transitions to  $E_2$  and  $E_3$  respectively). Inspection of the plot of covariate regression coefficients  
371 for model  $E_1$  (Fig. 2, middle) indicates that the  $b_m$  are universally negative (higher than normal  
372 precipitation in any month is associated with lower abundance indices) with the strongest  
373 influence of precipitation in mid-summer. Values of the covariate regression coefficients decay  
374 by a factor of about 0.73 ( $= \lambda^{12}$ ) between successive years. Regression coefficients estimated  
375 using DLM follow a similar pattern to those estimated using model  $E_1$ , with no obvious benefit  
376 indicated by the maximised log likelihood (Table 1, column 2). The time series plot showing  
377 abundance indices and fitted values (Fig. 2, bottom) indicates broad agreement between  
378 observed and modelled series.

379

### 380 3.2 Summaries of model fits across all species in the study

381 The histograms of  $p$ -values for the augmentation from  $E_0$  to  $E_1$  have a more pronounced peak  
382 close to  $p=0$  compared with either of the elaborations from  $E_1$  to  $E_2$  or  $E_1$  to  $E_3$  (Fig. 3). This  
383 is true both when the covariates are based on mean temperatures and on precipitation: thus  
384 although there is certainly evidence to support the more elaborate models for some species (as  
385 evidenced by the non-uniform nature of the histograms), the main gain is to be had in inclusion  
386 of the first order Fourier terms in the underlying model.

387

388 Comparison across species of AIC values obtained from fitting model  $E_1$  with 480 monthly  
389 weather covariates (spanning 40 years) with values obtained from fitting model  $E_1$  with 12  
390 monthly weather covariates (spanning 1 year) strongly indicated support from the likelihoods  
391 for extending the series of weather covariates beyond the twelve most recent months at the cost  
392 of no extra parameters. For mean temperature, the AIC values for using 480 covariates was at  
393 least 2.0 greater than the corresponding value using 12 covariates for 164 species, whereas AIC  
394 differentials exceeded 2.0 in the opposite direction for just 23 species. The corresponding  
395 figures using the precipitation covariate were 176 and 11 respectively (histograms of AIC  
396 values provided as Supplementary Material).

397

398 The histogram of annualised decay parameter values,  $\lambda^{12}$ , has modes close both to 0 (only the  
399 covariates for the 12 months leading up to the abundance index are relevant) and to 1  
400 (covariates for the 12 months leading up to the abundance index are given little more weight  
401 than covariates for earlier years). These modes are present for both temperature and rainfall  
402 covariates, and all three models (Fig. 4). Hence, the observation from the two example species  
403 that the regression coefficients decay steadily towards zero over approximately five years is  
404 not generally followed.

405 The SWMCRC values for temperature demonstrate a peak in positive values ( $A^{S^+}_m$ )  
406 corresponding to July of the year of the abundance index, the values for this and adjacent  
407 months substantially exceeding the critical value of a one-sided test at the 5% significance level  
408 (Fig. 5). There is also some relatively weak evidence of an overall negative effect of  
409 temperature in January and February of the year of the abundance index. Conversely, for  
410 precipitation, the SWMCRC shows a peak in the negative ( $A^{S^-}_m$ ) values, again with a peak  
411 corresponding to July of the year of the abundance index. There are no months in which the

412 positive SWMCRC values ( $A^+_m$ ) even come close to statistical significance for precipitation,  
413 reinforcing the overall negative effect of unusually high precipitation on abundance indices  
414 across species.

415

#### 416 **4. Discussion**

417 The above analyses showed strong evidence for an effect of temperature upon wren abundance.  
418 There was a positive effect of warmer winter temperatures, peaking in January, and a weaker  
419 negative effect of summer temperature. The effects of winter temperature support the results  
420 of previous studies of this species, whose populations are known to decline in response to cold  
421 winters (Greenwood & Baillie 1991, Newton *et al.* 1998, Morrison *et al.* 2016), due to reduced  
422 survival as a consequence of prolonged periods of frost and snow (Peach *et al.* 1995, Robinson  
423 *et al.* 2007). The negative effect of summer temperature upon wren populations has not  
424 previously been reported although there is increasing evidence that hot summer weather can  
425 have a negative impact on bird populations in the UK (Pearce-Higgins *et al.* 2010, Pearce-  
426 Higgins *et al.* 2015).

427

428 Little seems to have been published previously about the sensitivity of flounced rustic  
429 populations to either temperature or rainfall. The negative associations between abundance  
430 and rainfall, including timing of peak and least sensitivity, appear to be well aligned with the  
431 life history of the species: after hatching in early autumn, the larvae descend to the soil where  
432 they feed on stem bases and roots before pupating underground, usually in June (Waring and  
433 Townsend 2009). The long period spent underground, when the larvae are susceptible to water  
434 logging, is a likely explanation for rainfall correlating negatively with abundance and may  
435 contribute to their preference for light, calcareous soils. The period of peak sensitivity to

436 rainfall comes during pupation, whilst the period of least sensitivity occurs during mid-winter  
437 when the larvae are likely to be least active.

438

439 The syntheses of results across all species in our study threw up some interesting generalities.

440 First, the lack of uniformity in the histograms of  $p$ -values provides evidence in support  
441 of all three models  $E_1$ ,  $E_2$  and  $E_3$ , for both the weather variables considered. Effects of  
442 temperature are more strongly supported by the data than effects of rainfall, and the evidence  
443 supporting the augmentation of the null model  $E_0$  to  $E_1$  model with the four additional  
444 underlying parameters was considerably greater than either of the elaborations considered (the  
445 additional two underlying parameters in the cyclic model that extend  $E_1$  to either  $E_2$  or  $E_3$ ).

446 Second, the benefit of including more than the most recent 12 months of weather data  
447 was often considerable, with AIC differences greater than 2.0 in favour of having 480 monthly  
448 weather covariates outweighing AIC differences greater than 2.0 in favour of having 12  
449 monthly weather covariates exceeding 5 to 1 for mean temperature and exceeding 15 to 1 for  
450 precipitation.

451 Third, the estimated annualised decay parameter values,  $\lambda^{12}$ , are bimodal, and tend to  
452 be estimated approximately equally often in the intervals from 0 to 0.1, from 0.1 to 0.9 and  
453 from 0.9 to 1. For example, with model  $E_1$  the percentage of species for which  $\lambda^{12} < 0.1$  is 43%  
454 for mean temperature and 38% for rainfall, whereas the equivalent figures for  $\lambda^{12} > 0.9$  are 24%  
455 and 32% respectively. Having  $\lambda$  estimated as being close to 0 is an indication that the influence  
456 of the weather is confined to the 12 months leading up to the index value. Biologically, this  
457 would relate to a species with a low survival and high turnover of individuals and a strong  
458 effect of weather on productivity and or survival. Conversely, having  $\lambda$  close to 1 means that  
459 the effect of any departure in the index value due to variation in the weather is long-lasting,  
460 and corresponds to the situation for which Freeman and Newson (2008) noted that models for

461 differences in log abundance with a single covariate are equivalent to models for log abundance  
462 using as explanatory variable the cumulative sums of the original covariate. Biologically, this  
463 might relate to situations in which weather impacts productivity or juvenile survival, and in  
464 which individuals have high survival and long-life spans. Therefore the impact on abundance  
465 of weather from 5 years ago is almost as great as the impact on abundance of weather from last  
466 year, because both years have contributed reasonably similar numbers to the current  
467 population. It was precisely to provide a bridge between the use of a single covariate and its  
468 cumulative sum that we began considering the exponential decay term which forms an integral  
469 part of our models, hence by construction the models described cater for both situations and  
470 intermediates in a manner determined by the data.

471 Fourth, the SWMCRC values from the  $E_1$  model indicate that associations between  
472 abundance indices and temperature are on average consistently positive across species in the  
473 summer of the index year from May to August, whereas the associations with precipitation then  
474 are on average consistently negative across species. Whilst this observation ignores the  
475 potential benefit of the more elaborate models and does not apply to those species with early  
476 reference months, the main benefits of including weather data in the models are derived from  
477 the step from  $E_0$  to  $E_1$  and some 94% of species investigated had reference months of May or  
478 later: hence there is certainly a suggestion that variation between years in summer weather  
479 tends to be important for the species we selected for inclusion in this study.

480

481 Although data for the two exemplar species were well-behaved in terms of underlying  
482 parameter estimation, fitting the models to data from all 501 species involved in our study was  
483 not always so straightforward. To implement all model fitting in a single loop required a  
484 system to trap non-convergence errors and to follow these with conditional continuation steps  
485 so that parameter estimates were always obtained, albeit with some error flags. There were

486 also difficulties with constructing confidence intervals for species when the plausible range of  
487 the decay parameter  $\lambda$  was not constrained both above and below by the likelihood, in which  
488 case confidence intervals could be calculated conditional on the value of the  $\lambda$ , but these need  
489 interpreting with considerable caution.

490

491 The modelling approach described above can potentially be extended in many different  
492 directions.

493         One possibility is to investigate the use of error structures with more complex forms of  
494 long-range dependency than the Gaussian AR(1) relationships assumed here.

495         A second possibility is to return to the use of penalised spline regressions for defining  
496 the covariate regression coefficients, but doing so separately for the periodic term and the decay  
497 term. Estimation of the two smoothing terms could either be performed simultaneously or  
498 using sequential iteration between each using the back-fitting algorithm (Hastie and Tibshirani,  
499 1990), allowing limited flexibility in the decay term to avoid overlap between the two terms.

500         A third possibility is to embed our models for abundance into a state space framework,  
501 thereby separating the effect of weather on population dynamics from the effect of weather on  
502 the observation process. This distinction is most acutely required for abundance indices which  
503 are derived from a summation of records over a long period of the year and are hence most  
504 likely to be influenced by both population size and the longevity of adults.

505         A fourth possibility would be to take a multi-species approach to the analysis, in  
506 combination with a state-space population model in the manner of Mutshinda, O'Hara &  
507 Woiwod (2011). Whilst multi-species modelling would have to be restricted to small numbers  
508 of species at a time, this would allow exploration of the extent to which changes in abundance  
509 are the result of species-weather interactions or due to inter-species interactions (Ockendon *et*

510 *al.* 2014), the latter having been postulated as a cause of lagged population responses to  
511 variation in weather variables (e.g. Pearce-Higgins *et al.* 2010).

512

513 In conclusion, we believe that this paper represents a considerable advance on previous  
514 approaches to modelling the effect of weather on species abundance indices by making a more  
515 holistic use of historical weather records and relying less on potentially arbitrary *a priori*  
516 decisions about variable selection in the absence of much ecological information.

517

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529 Council for Nature Conservation and Countryside and SNH) and Royal Society for Protection  
530 of Birds); and the UK Butterfly Monitoring Scheme operated by CEH, Butterfly Conservation  
531 and funded by a consortium of government agencies.

532

### 533 **Data accessibility**

534 The weather data used in this manuscript can be obtained from the Met Office website  
535 <http://www.metoffice.gov.uk/climate/uk/datasets/> . The wren data used as an example in this  
536 manuscript are available through the BTO's standard data request procedure (see  
537 <http://www.bto.org/research-data-services/data-services/data-and-information-policy>), whilst  
538 the flounced rustic data extracted from the Rothamsted Insect Survey (a BBSRC-supported  
539 National Capability) are available through <http://www.rothamsted.ac.uk/insect-survey/>.

540

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## 622 **Tables and Figures**

### 623 **Table 1**

624 Summary of results from the model fitting, indicating for each species and each model: the  
625 maximised log likelihood; the estimated AR(1) correlation coefficient; and twelfth power (ie  
626 annual influence) of the estimated decay rate parameter.

Model (number of fixed effect parameters)	Term	Species	
		Wren	Flounced rustic
$E_0$ (2)	log likelihood	10.09	-21.96
	AR(1) correlation	0.44	0.56
$E_1$ (6)	log likelihood	29.99	-4.32
	AR(1) correlation	0.47	0.53
	$\lambda^{12}$	0.51	0.73
$E_2$ (8)	log likelihood	32.10	-3.09
	AR(1) correlation	0.44	0.52
	$\lambda^{12}$	0.42	0.73
$E_3$ (10)	log likelihood	30.95	-2.52
	AR(1) correlation	0.46	0.57
	$\lambda^{12}$	0.59	0.69
DLM (14)	log likelihood	33.70	-0.48
	AR(1) correlation	0.38	0.57

628

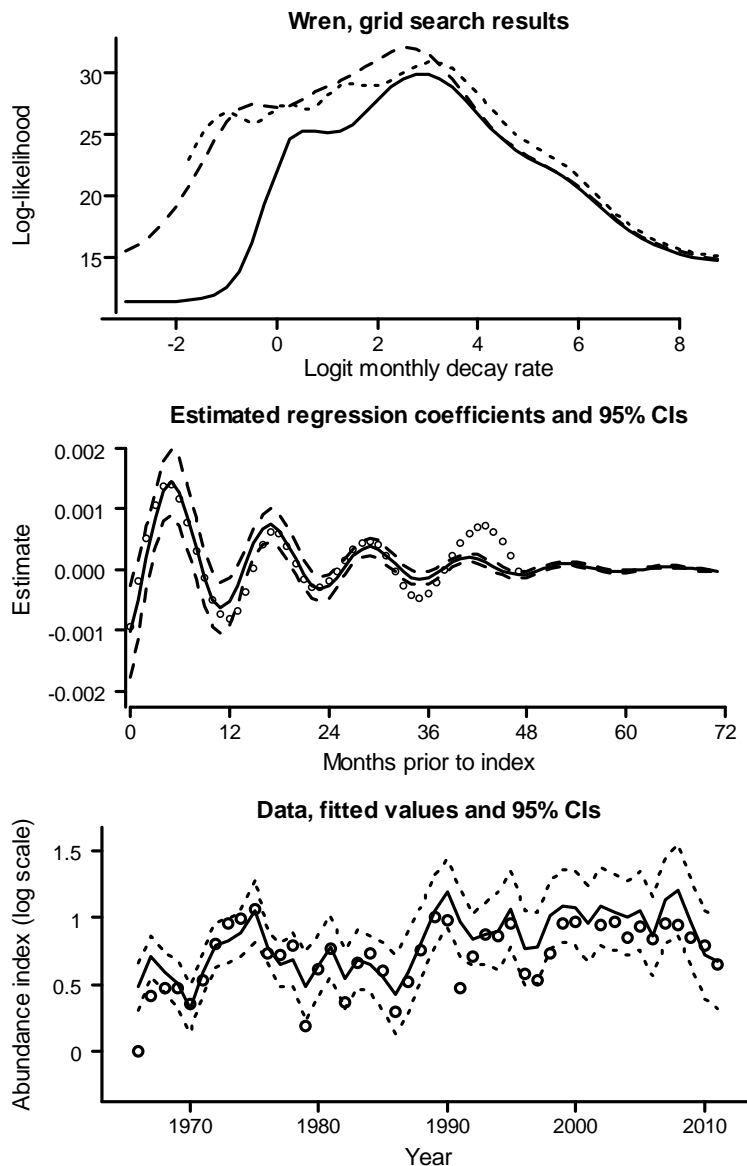
629

630

631

632 **Fig. 1**

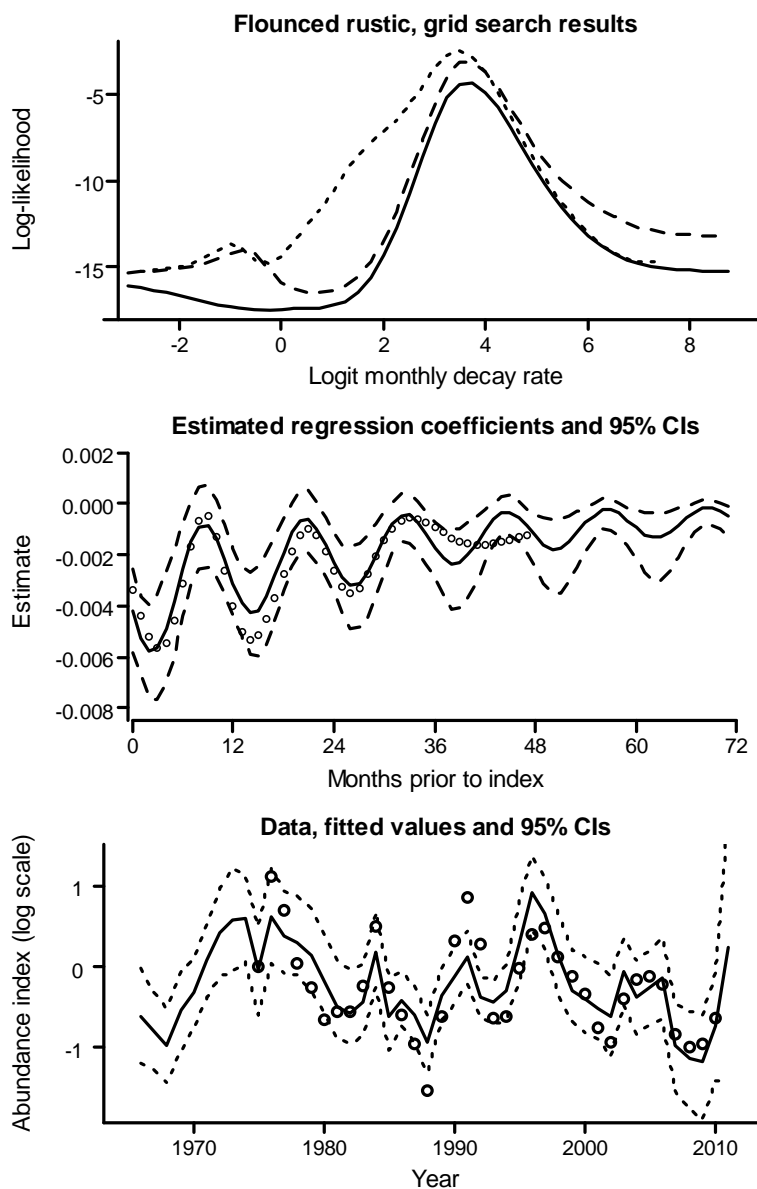
633 Results of fitting the models to wren data: profile likelihood from initial grid search for the  
634 logit of the monthly decay rate parameter  $\kappa$  (top), for models  $E_1$  (solid line),  $E_2$  (dashed) and  
635  $E_3$  (dotted); covariate regression coefficients  $b_m$  (centre) in model  $E_1$  for 72 monthly  
636 temperature covariates up to the month to which the index relates (June,  $m=1$ ,  $r=6$ ) (with 95%  
637 confidence intervals), along with values derived from DLM (circles) using 48 monthly  
638 temperature covariates; observed time series, showing fitted values from model  $E_1$  with 95%  
639 confidence intervals for the fitted values (bottom).



640

641 **Fig. 2**

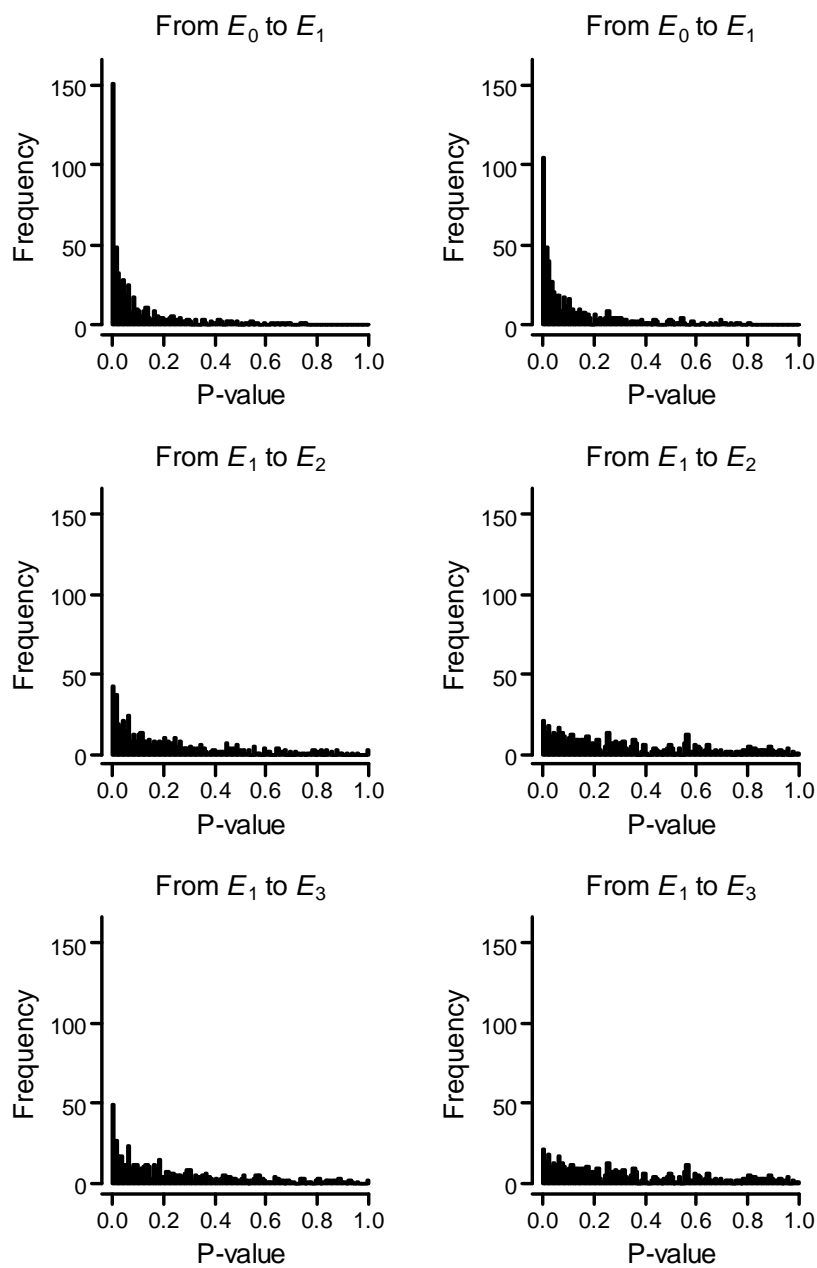
642 Results of fitting the models to flounced rustic data: profile likelihood from initial grid search  
643 for the logit of the monthly decay rate parameter  $\kappa$  (top), for models  $E_1$  (solid line),  $E_2$  (dashed)  
644 and  $E_3$  (dotted); covariate regression coefficients  $b_m$  (centre) in model  $E_1$  shown for 60 monthly  
645 precipitation covariates up to the month to which the index relates (September,  $m=1$ ,  $r=9$ ) (with  
646 95% confidence intervals), along with values derived from DLM (circles) using 48 monthly  
647 temperature covariates; observed time series, showing fitted values from model  $E_1$  with 95%  
648 confidence intervals for the fitted values (bottom).



649

650 **Fig. 3**

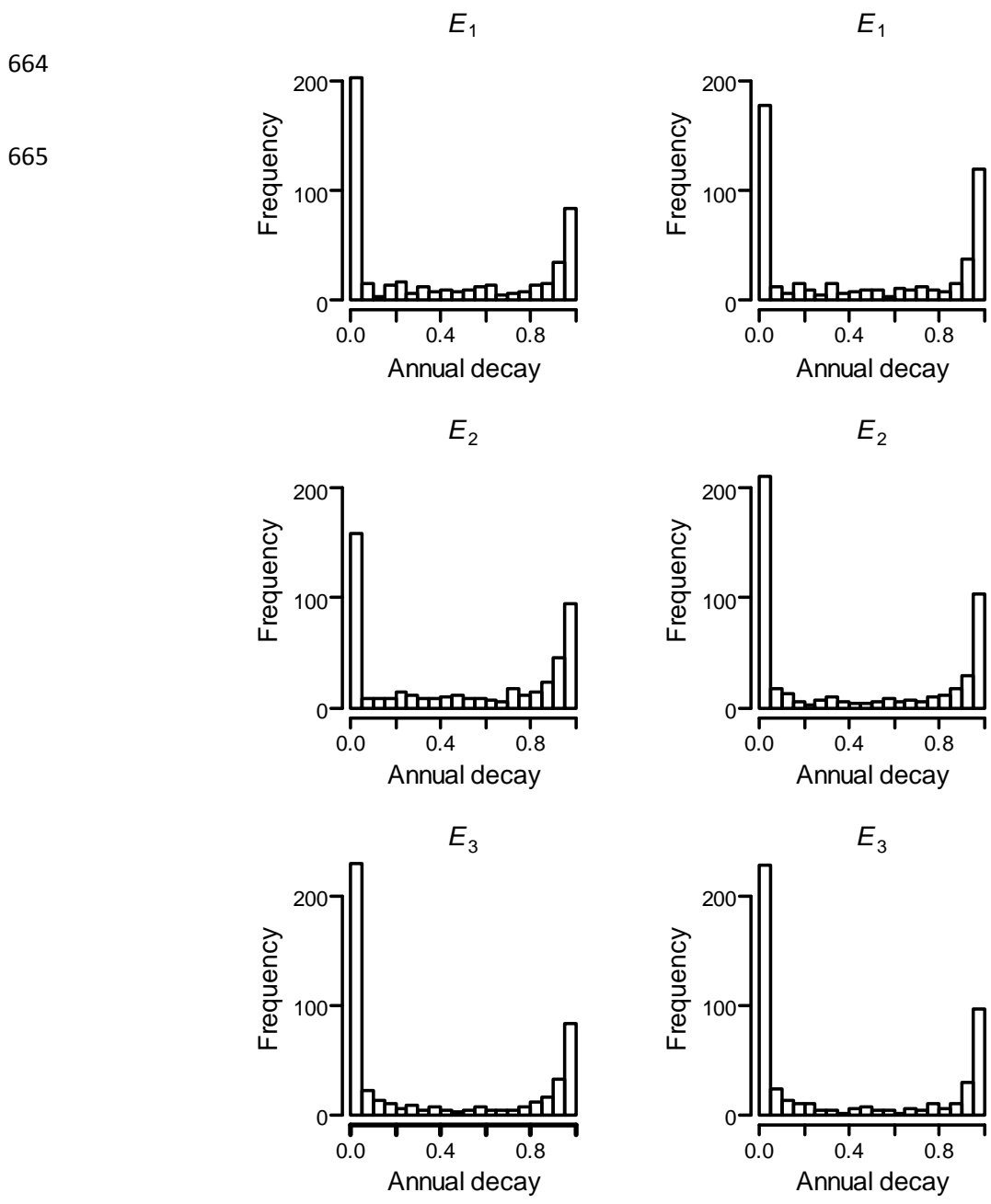
651 Histograms of  $p$ -values across all species using mean temperature (left) and precipitation  
652 (right) as covariates, for augmentation from: the null to first order models ( $E_0$  to  $E_1$ , top, using  
653 all 501 species); the first order to the second order model by addition of a periodic term with  
654 period 6 months ( $E_1$  to  $E_2$ , middle, using those 484 species with at least 20 abundance index  
655 values); and the first order to the second order model by addition of a periodic term with period  
656 24 months ( $E_1$  to  $E_3$ , bottom, same 484 species).



657

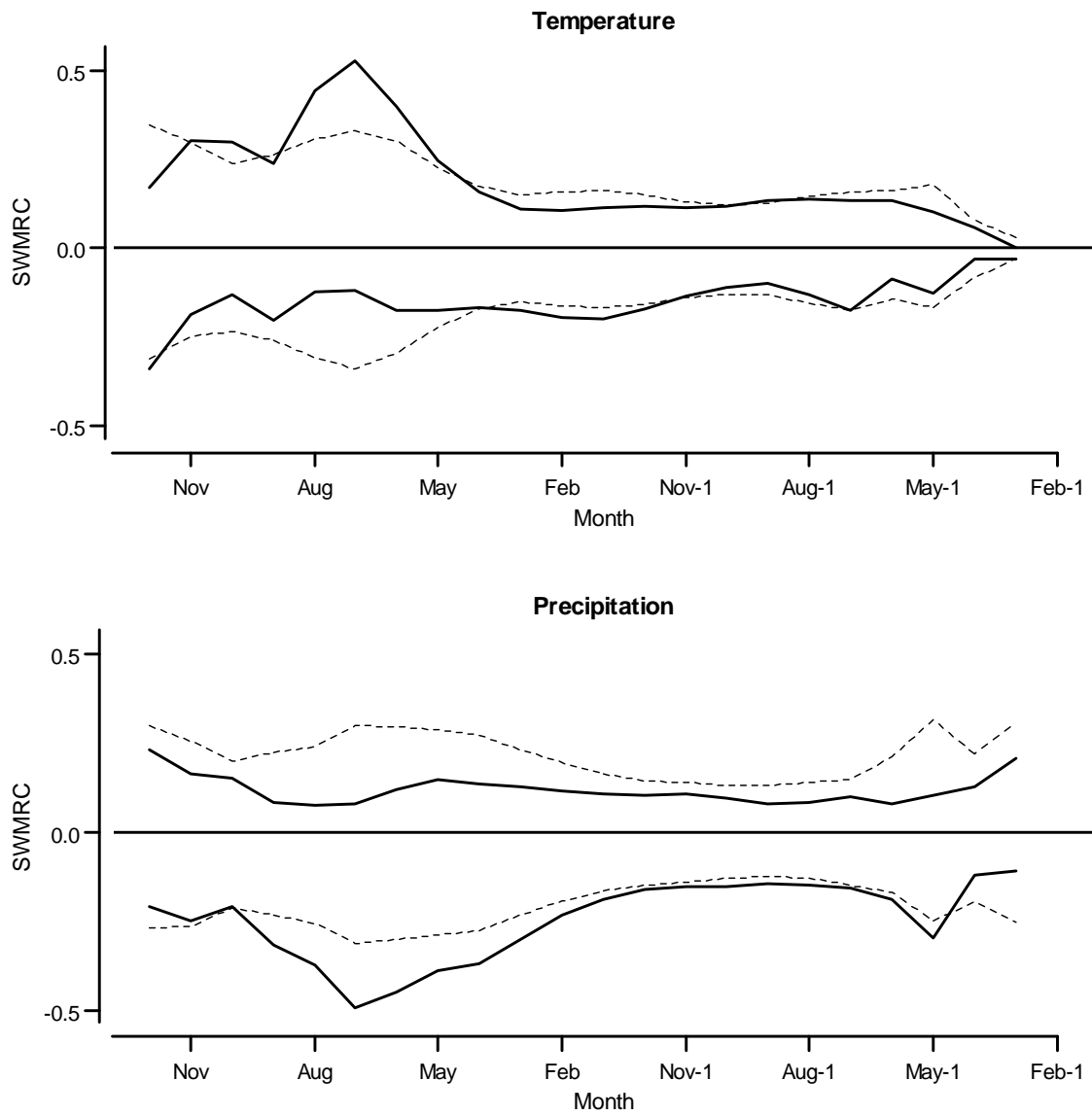
658 **Fig. 4**

659 Histograms of estimated annualised decay coefficients ( $\lambda^{12}$ ) using mean temperature (left) and  
660 precipitation (right) as covariates for: the first order model  $E_1$  (top, using all 501 species); and  
661 the second order models with a periodic term with period 6 months ( $E_2$ , middle, using those  
662 484 species with at least 20 abundance index values); and with period 24 months ( $E_3$ , bottom,  
663 same 484 species).





666 **Fig. 5**  
 667 Standardised weighted mean covariate regression coefficients (SWMCRC, see text for details)  
 668 constructed across all 501 species for model  $E_1$  using mean temperature covariate data (top)  
 669 and precipitation (bottom), showing calculated values for positive ( $A^{S^+}_m$ ) and negative ( $A^{S^-}_m$ )  
 670 coefficients (solid lines) and one-sided 95% confidence intervals (dashed lines).



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