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6 **Identifying multi-species synchrony in response to**
7 **environmental covariates.**

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Abstract

1. The importance of multi-species models for understanding complex ecological processes and interactions is beginning to be realised. Recent developments, such as those by Lahoz-Monfort *et al.* (2011), have enabled synchrony in demographic parameters across multiple species to be explored. Species in a similar environment would be expected to be subject to similar exogenous factors, although their response to each of these factors may be quite different. The ability to group species together according to how they respond to a particular measured covariate may be of particular interest to ecologists.
2. We fit a multi-species model to two sets of similar species of garden bird monitored under the British Trust for Ornithology's Garden Bird Feeding Survey. Posterior model probabilities were estimated using the reversible jump algorithm to compare posterior support for competing models with different species sharing different subsets of regression coefficients.
3. There was frequently good agreement between species with small asynchronous random effect components and those with posterior support for models with shared regression coefficients; however, this was not always the case. When groups of species were less correlated, greater uncertainty was found in whether regression coefficients should be shared or not.
4. The methods outlined in this paper can test additional hypotheses about the similarities or synchrony across multiple species that share the same environment. Through the use of posterior model probabilities, estimated using the reversible jump algorithm, we can detect multi-species responses in rela-

49 tion to measured covariates across any combination of species
50 and covariates under consideration. The method can account
51 for synchrony across species in relation to measured covariates,
52 as well as unexplained variation accounted for using random
53 effects. For more flexible, multi-parameter distributions, the
54 support for species-specific parameters can also be measured.

55 **Key-words: ecosystem modelling, multi-species, predation, syn-**
56 **chrony, Tweedie.**

57 **1 Introduction**

58 When modelling the dynamics of ecological populations, most standard ap-
59 proaches have tended to consider species independently of each other by fitting
60 a single model to each of the species (Harris, 2015; Lecomte *et al.*, 2013). Para-
61 meters in these models are then estimated and interpreted independently of
62 each other. However, this approach oversimplifies the complex interactions that
63 inevitably underpin the ecological dynamics present within such ecosystems.
64 The ability to understand these ecological dynamics is often difficult in practice
65 because traditional models typically estimate just a single set of demographic
66 rates (for example survival or productivity, but not both). Linking demographic
67 rates across numerous species, without merely measuring associations between
68 species, adds an additional non-trivial level of complexity (Ovaskainen *et al.*,
69 2010; Buonaccorsi *et al.*, 2001).

70 In order to better understand such dynamics at an ecosystem level, it is
71 important to account for these multi-species interactions. Further extensions to
72 standard single-species models must be made if one is to account for more com-
73 plex dependencies and correlation structures. Joint species distribution models
74 (JSDMs), which pool data from multiple sources (Fithian *et al.*, 2015) or from
75 multiple species (Thorson *et al.*, 2015; Clark *et al.*, 2013; Pollock *et al.*, 2014),
76 allow more parsimonious models to be fitted whilst also propagating all forms of

77 uncertainty throughout the model. The development of such models outside of
78 the JSDM literature has been slow; however, recent advances by Lahoz-Monfort
79 *et al.* (2011) have enabled such models to be formulated. The authors, extend-
80 ing the work of Grosbois *et al.* (2009), proposed a statistical model in which
81 random effects were used to estimate the level of synchrony across multiple
82 species. Within the model, a synchronous component is used to represent the
83 common response of all the species considered, whilst an asynchronous com-
84 ponent accounts for any additional variation specific to each species. However,
85 these components are conditional on environmental covariates in the model,
86 which then only estimate synchrony in unexplained variation.

87 Lahoz-Monfort *et al.* (2011) fitted the model with species-specific coefficients
88 for all covariates. Only modelling synchrony in variance unexplained by the
89 covariates in the model risks under-estimating the magnitude of the synchrony
90 inherent in the modelled species. If the variation explained by any covariates
91 in the model is largely synchronous across species, then corresponding species-
92 invariant random effect variances will consequently be reduced in relation to
93 the species-specific ones, and the amount of synchrony estimated across the
94 species will be lower than in reality. Additionally, in this case, precision in
95 parameter estimates will be lower if they could realistically be shared across
96 multiple species.

97 To estimate the degree of synchrony with respect to the covariates, Lahoz-
98 Monfort *et al.* (2011) fitted two models, one with covariates and one without
99 (the null model), and then compared the random effect variances in each case.
100 Changes in the observed magnitude of the random effect variances were then
101 used to indicate whether the additional unexplained variation was largely syn-
102 chronous or asynchronous. If the species-invariant random effect variance in-
103 creases, then this suggests that the response to covariates is overall largely
104 synchronous. Conversely, if the species-specific variances increase then it can be
105 concluded that the response to covariates is largely asynchronous. However, in
106 neither case can the synchronous aspect of the response to each individual co-

107 variate be easily analysed for each species-covariate combination. Fitting every
108 model with unique species-covariate combinations in order to compare the ratio
109 of random effect variances would be completely infeasible. Apart from the ob-
110 vious computational demand of this approach, which increases proportionally
111 with each covariate added to the model, this approach also assumes that unex-
112 plained variation no longer attributed to a given covariate will be completely
113 absorbed into either of the two random effects. In reality, it is highly likely that
114 part or all of this variation could be attributed to either a fixed intercept and/or
115 other covariates in the model.

116 We propose an alternative approach, estimating posterior model probabilities
117 associated with different models, where each regression coefficient can be shared
118 across subsets of the species considered. The method explores uncertainty across
119 both parameter and model space; posterior support for models with regression
120 coefficients shared across different subsets of the species under consideration can
121 be estimated. Each covariate is allowed to be shared across different subsets
122 of the species considered, such that species with ‘similar’ parameter estimates
123 associated with each covariate can be grouped together.

124 The covariate synchrony method is applied to long-term longitudinal data
125 relating to numbers of six species of birds visiting garden feeding stations across
126 the UK. These six species are split into two ecologically similar groups, namely
127 blue tit (BT) *Cyanistes caeruleus*, great tit (GT) *Parus major* and coal tit (CT)
128 *Periparus ater* in the first, and house sparrow (HS) *Passer domesticus*, green-
129 finch (GF) *Chloris chloris* and chaffinch (CF) *Fringilla coelebs* in the second.
130 Some of these species have shown severe declines over the past few decades,
131 whilst others have remained stable or are increasing (Newson *et al.*, 2010).
132 Various explanations have been put forward to explain the declines observed
133 in some of these species, but there have been disagreements over what the main
134 drivers are. This has been particularly apparent in relation to the possible role
135 of predation. Whilst previous studies have attempted to understand the changes
136 in numbers of some small passerines (e.g. Thomson *et al.*, 1998; Chamberlain

137 *et al.*, 2009; Newson *et al.*, 2010; Bell *et al.*, 2010; Swallow *et al.*, 2015), there
138 has been little attempt to understand these populations at a multi-species level,
139 though see Sullivan *et al.* (2015). As the species concerned share a similar envir-
140 onment and are susceptible to the same exogenous factors, it would be expected
141 that some or all of these species may interact with each other or respond in a
142 similar way to the environment around them.

143 In particular we concentrate on spatial synchrony in species' response to
144 covariates using log-linear models, however the method is easily applicable to
145 many other cases and to model frameworks where parameters or coefficients can
146 be shared across species, locations or time periods.

147 **2 Materials and methods**

148 2.1 DATA DESCRIPTION

149 The data used come from the British Trust for Ornithology's (BTO) Garden
150 Bird Feeding Survey (GBFS) and relate to an annual mean of up to 26 weekly
151 maximum counts conducted between October and March each year at approxi-
152 mately 200 sites. Inevitably, given the long time period involved, there is a degree
153 of site turnover; however, replacement sites are selected to match as closely
154 as possible - in terms of location and garden type - the site being replaced.
155 The data analysed in this paper span the years 1970/71 to 2005/06 inclusive
156 (henceforth the year 1970 signifies the winter of 1970/71), and correspond to
157 693 individually monitored sites spanning the UK. The spatial distribution of
158 GBFS sites reflects that of the human population, such that there are more
159 sites in areas with greater densities of people. Participants in the survey note
160 the maximum number of each species they observe at any given time feeding
161 at their garden feeding stations or, in the case of predators, hunting the birds
162 visiting the feeders, in up to 26 weeks each winter season.

163 In particular, we chose two distinct sets of three species of potential sparrow-
164 hawk prey monitored under the GBFS that would be expected to have similar

165 ecological requirements (Newton, 1986). The first is a group of closely-related
166 species of the same family, namely blue tit, great tit and coal tit. The second are
167 three species largely associated with a winter diet of medium to large-sized seeds,
168 namely house sparrow, greenfinch and chaffinch. An average over the weekly
169 maxima was calculated for each site and year, giving an essentially continuous
170 distribution.

171 Annual averages across all sites monitored under the GBFS surveys show
172 similar peaks and troughs for each of the three tit species, as well as similarities
173 for greenfinch and chaffinch (Figure 1). Marginal correlations across both sites
174 and years between the observations of each pair of species in the two groups
175 were calculated (Table 1). For the tit species, significant positive correlation
176 was found between all pairings when averages across years were used (0.78 [BT
177 vs GT], 0.46 [BT vs CT] and 0.60 [GT vs CT], Table 1a). This suggests that
178 sites that can, on average, support or attract greater numbers of one of these
179 species also attract greater numbers of the other species too. Correlation across
180 years was also significant and positive for the blue tit-great tit and great tit-
181 coal tit pairings, but not so for blue tit-coal tit. For the other three species,
182 results were more variable. There was strong positive correlation between the
183 finch species across both space and time (0.4 and 0.84 respectively), but less so
184 for house sparrow (Table 1a), a species whose populations have been in long-
185 term decline within the study period, and for which there has been a change
186 in the temporal pattern of peak garden use (Robinson *et al.*, 2005). In fact,
187 temporal correlation between house sparrow and each of the finch species was
188 strongly negative in both (-0.81 [HS vs GF] and -0.84 [HS vs CF]). Populations
189 of both finches are likely to be augmented over the winter with migrants from
190 the continent. As house sparrows are largely sedentary, we would not expect
191 the years where the finch populations are particularly large to correspond to
192 high numbers of sparrows.

193 In gardens across the UK, these species are all subject to similar exogenous
194 factors and it may be that the different species are responding similarly or

195 differently to these same factors. We would expect, due to the similarities in
196 ecology of these three species in each group, that there would be some degree of
197 synchrony across them in relation to their response to environmental covariates.
198 However, the results of Swallow *et al.* (unpublished data) indicate that the
199 species within each of the two groups studied here also respond differently in
200 response to some of the covariates. As such, they offer ideal groups to analyse
201 both synchronous and asynchronous aspects of their population dynamics.

202 2.2 THE MODEL

203 The model is an extension of that presented in Swallow *et al.* (2015), to in-
204 corporate the simultaneous modelling of more than one response species and
205 the sharing of relevant parameters where possible. We extended the modelling
206 framework of Lahoz-Monfort *et al.* (2011) and Grosbois *et al.* (2009), which ac-
207 counts for variation not explained by the fixed effects through two independent
208 random effects. The method adds to previous work done on multi-species syn-
209 chrony by Lahoz-Monfort *et al.* (2013), who studied multi-species productivity
210 and Schaub *et al.* (2015), who studied multi-site synchrony in demographic rates
211 and populations.

212 Formally, let $y_{s,i,t}$ be the observed mean of weekly maxima of species s at
213 site i in year t , \mathbf{x}_i spatially-explicit covariates with associated parameter vector
214 $\beta\{s\}$, and $\mathbf{v}_{i,t}$ spatially- and time-explicit covariates with associated parameter
215 vector $\gamma\{s\}$. We denote $\theta\{s_1, s_2\}$ to be the parameter θ shared over species s_1
216 and s_2 . The covariates \mathbf{x}_i and $\mathbf{v}_{i,t}$ could also be species-specific but in this ap-
217 plication they are not. In addition, we tested for interactions within and between
218 prey species by including a year-lagged measure of each species as a covariate
219 $\tilde{y}_{s,i,t-1}$. The associated coefficient $\nu_{j,k}$ corresponds to the effect of species j on
220 species k . In the case where $j = k$, this parameter is equivalent to the concept
221 of density dependence (Dennis & Taper, 1994). As the empirical distributions
222 for each of the three species have a non-zero probability of exact zeros, whilst
223 also being bounded below by zero, effectively continuous with discrete mass at

224 zero and positively skewed, special consideration was given to the distributional
 225 form of the model. To account for each of these aspects of the data, we used the
 226 Tweedie distributions (here denoted Tw) (Jørgensen, 1987). Given a positive
 227 dispersion parameter ϕ and index parameter $p \notin (0, 1)$, the Tweedie distribu-
 228 tions are defined by the power mean-variance relationship $Var(y) = \phi\mu^p$. For
 229 values of $p \in (1, 2)$, the distributions are non-negative-continuous with a discrete
 230 probability mass at the origin. The model is then defined as follows:

$$y_{s,i,t} \sim Tw(\mu_{s,i,t}, \phi\{s\}, p\{s\})$$

231 where

$$\mu_{s,i,t} = \mu_{s,i,t-1} \exp\{\alpha_s + \mathbf{x}_i^\top \boldsymbol{\beta}\{s\} + \mathbf{v}_{i,t}^\top \boldsymbol{\gamma}\{s\} + \sum_{l=1}^{n_s} \tilde{y}_{l,i,t-1}^\top \nu_{l,s} + \epsilon(i) + \delta_s(i)\}, \quad (1)$$

$$\epsilon(i) \sim N(0, \sigma_\epsilon^2)$$

232 and

$$\delta_s(i) \sim N(0, \sigma_s^2).$$

233 The first random effect, $\epsilon(i)$, is a site-specific random effect that is con-
 234 stant across species, accounting for synchronous variation that is common to
 235 all species. The second, $\delta_s(i)$, is a site-specific random effect that is estimated
 236 separately for each species and accounts for additional variation that is asyn-
 237 chronous. The $\delta_s(i)$ were assumed to be independent of each other and of the
 238 $\epsilon(i)$.

239 Additional intra- and inter-specific interactions between response species can
 240 also be added to the model where appropriate to create an even more flexible
 241 model that accounts for all levels of interactions between the species considered.

242 Following some simple algebraic manipulation and implementing the hier-

243 archical centring reparameterisation method (Browne, 2004; Browne *et al.*, 2009),

244 Equation (1) can be rewritten as:

$$\log\left(\frac{\mu_{s,i,t}}{\mu_{s,i,t-1}}\right) = \mathbf{v}_{i,t}^\top \boldsymbol{\gamma}\{s\} + \sum_{l=1}^{n_s} \nu_{ls} \tilde{y}_{lit-1}^\top + \epsilon(i) + \delta_s(i), \quad (2)$$

245 where

$$\epsilon_i \sim N(0, \sigma_\epsilon^2)$$

246 and

$$\delta_s(i) \sim N(\alpha_s + \mathbf{x}_i^\top \boldsymbol{\beta}\{s\}, \sigma_s^2).$$

247 That is we modelled the difference in log abundance of species s as a function
248 of environmental covariates and random effects. The model also requires the
249 estimation of $\mu_{s,i,0}$, which is a site- and species-specific offset corresponding to
250 the expected value in the year prior to the survey commencing at each site. As in
251 Swallow *et al.* (2015), we used a data augmentation approach to estimate these
252 parameters. That is they are treated as additional unknowns to be estimated
253 from the rest of the data. This methodology allows both zero observations
254 and the first observation at each site to contribute to estimating the remaining
255 regression parameters. This method can also be used when covariate values
256 are missing or for missing years of observations during the survey (although
257 that was not necessary here). The data-augmented μ_{i0} are also used as the
258 density-dependence covariate for the initial year of observations.

259 The analyses are conducted in a Bayesian framework using a Markov chain
260 Monte Carlo (MCMC) approach to obtain inference on the model parameters
261 of interest. A single-update Metropolis-Hastings algorithm is used to update
262 the parameters, with an adaptive tuning approach used for the proposal distri-
263 butions to improve efficiency of the algorithm. More details can be found in
264 Swallow *et al.* (2015).

265 Estimates of the proportion of variance for each species that is synchronous
266 with the other species considered in the model can be calculated. That is the
267 intra-class correlation coefficient (ICC) defined as:

$$\text{ICC}_s = \frac{\sigma_\epsilon^2}{\sigma_\epsilon^2 + \sigma_s^2}.$$

268 Values close to one suggest largely synchronous unexplained variation, whilst
269 values close to zero suggest mostly asynchronous unexplained variation. This
270 measure of synchrony, however, does not take into consideration any variation
271 explained by the covariates. This variation may be an important driver of
272 the synchrony or asynchrony inherent in the species population dynamics and
273 therefore being able to identify which species responds similarly or differently
274 to any of the measured covariates considered should also be of interest.

275 2.3 DETECTING SYNCHRONY TO MEASURED COVARIATES

276 In order to group together species with similar responses to the environmental
277 covariates presented in Swallow *et al.* (2015) (or similar mean-variance rela-
278 tionships in the case of the Tweedie parameters), we used the reversible jump
279 algorithm (e.g. King *et al.*, 2010) to estimate posterior model probabilities asso-
280 ciated with different species groupings for each of the covariate coefficients and
281 the two Tweedie parameters ϕ and p . The particular reversible jump algorithm
282 used is based on that described by King & Brooks (2002), who fit a model for
283 detecting age dependency in mark-recapture parameters. We used a similar
284 algorithm here to group together species with similar responses to measured
285 covariates. The full algorithm is detailed in the supporting information. The
286 algorithm essentially selects one of the parameters that can be shared across spe-
287 cies at random and then proposes to move to a model where either an existing
288 shared group is split into two distinct groups with different parameter values,
289 or two existing groups of species with distinct parameter values are merged into
290 one group with a single shared parameter value.

291 To test for interactions within and between prey species, a covariate-dependence
292 approach was taken to model selection. We estimated the posterior model prob-
293 abilities associated with the model where $\nu_{j,k} = 0$ vs $\nu_{j,k} \neq 0$. Further details
294 can also be found in Swallow *et al.* (2015).

295 2.4 PRIOR DISTRIBUTIONS

296 Conducting the analysis in a Bayesian framework requires prior distributions to
297 be specified on all model parameters. We used uninformative priors for para-
298 meter distributions (Table 2). Prior distributions for each species were assumed
299 equal and specified independently of each other. Density dependence was for-
300 mulated in such a way that it can only intuitively have a negative coefficient,
301 hence a half normal prior is specified for these parameters. All species-covariate
302 combinations were assumed equal *a priori*, however this could easily be relaxed
303 to give zero mass to ecologically infeasible combinations.

304 To aid with specifying the parameters of the proposal distributions for the
305 parameter update step, we initially ran the full model without the revers-
306 ible jump step for 50,000 iterations of which the first 30,000 iterations were
307 discarded as burn-in. The posterior means and standard deviations for the
308 density-dependence and inter-specific interactions coefficients were then used as
309 the proposal distribution means and standard deviations for the corresponding
310 parameters in the full analysis. Independent normal distributions with a zero
311 mean and standard deviation 10^{-3} were used as the proposal distributions for
312 the reversible jump step. Good mixing between models appeared to be achieved
313 when using these proposals. The full model defined above including model un-
314 certainty was then run independently for 100,000 iterations with the first 50,000
315 iterations discarded as burn-in for the two sets of species discussed above. Con-
316 vergence was checked using visual observation of trace plots, which gave no
317 evidence to suggest a lack of convergence.

318 **3 Results**

319 Marginal posterior means and 95% credible intervals for the model parameters
320 and intra-class correlation coefficients, together with their marginal posterior
321 model probabilities are given in Tables 3 - 7 (tits) and 8 - 12 (ground feeding
322 species).

323 Only synchrony across a maximum of two species was found for any covariate
324 in either of the analyses. For the three tit species, most synchrony was across
325 blue tit and great tit, with distinct coefficients for coal tit. The model with
326 shared coefficients for blue tit and great tit was the model with highest posterior
327 probability for all covariates aside from the suburban or rural and ground frost
328 covariates. In the case of the former, the model with blue tit and coal tit shared
329 had the highest posterior mass whilst the latter was shared across great tit and
330 coal tit.

331 The posterior means of the ICC coefficients were close to 1 for blue tit and
332 great tit (0.903, 95% credible interval (0.852,0.947) and 0.912, 95% credible
333 interval (0.857,0.957) respectively), suggesting that the majority of unexplained
334 variation for these species was largely synchronous with the other two species
335 in the joint model. The estimate for coal tit, however, was lower at 0.494 (with
336 95% credible interval (0.411,0.591)) suggesting that additional asynchronous
337 variation was inherent in the data for this species. This does agree largely with
338 the species that were most frequently shared for the regression coefficients.

339 In the second analysis, much more of the unexplained variation on aver-
340 age was asynchronous and the magnitude of the random effect variances were
341 also greater, probably reflecting the greater tendency of these species to form
342 flocks at feeding sites. This was particularly the case for house sparrow, with
343 posterior mean of 0.205 (0.154,0.256) for the ICC associated with this species.
344 Greenfinch and chaffinch showed comparatively more synchrony (ICCs of 0.308
345 (0.211,0.399) and 0.495 (0.344,0.648) respectively), but these were both still be-
346 low the lowest value estimated for the three species of tits. Similarly, greater

347 uncertainty was found across models with regards to which coefficients should
348 be shared, with the preferred pairwise combination only having around 50%
349 posterior support for each of the three time-invariant covariates. In these three
350 covariates, all three pairwise combinations had greater than 10% posterior sup-
351 port. For each of these coefficients, however, the greenfinch and chaffinch shared
352 parameter had the highest posterior support. For the time-varying covariates
353 greater certainty was attributed to a single model but the shared pair of spe-
354 cies in each case was different. For the sparrowhawk covariate, greenfinch and
355 chaffinch shared a parameter value. For collared dove this pair was house spar-
356 row and greenfinch, whilst for ground frost it was house sparrow and chaffinch.

357 The results also suggest that the Tweedie variance parameters, namely ϕ
358 and p should have distinct values for all three species in the first analysis, with
359 marginal posterior probabilities of 1 in each case. In the second analysis, the
360 data supported the model with unique values for ϕ (posterior marginal of 1) and
361 p shared across house sparrow and chaffinch (posterior marginal 0.835). The tit
362 species analysis was re-run without model selection on the Tweedie parameters,
363 that is a single parameter value was assumed across all three species, the results
364 of which can be found in the supporting information.

365 Density dependence, that is intra-specific interactions, was found to be
366 highly significant for each of the three tit species (BT: -0.0260, (-0.0298,-0.0221);
367 GT: -0.0298, (-0.0339,-0.0260); CT: -0.0333, (-0.0404,-0.0464)). In the grain-
368 feeding species analysis, no evidence in support of density dependence was found
369 for house sparrow, but there was strong evidence to suggest density-dependent
370 mechanisms present in greenfinch and chaffinch dynamics (-0.0142, (-0.0195,
371 -0.0093) and -0.0282, (-0.0330,-0.0228) respectively). These results agree well
372 with the analyses conducted in Swallow *et al.* (2015), where once again no evi-
373 dence supporting the presence of density dependence effects was found in house
374 sparrow. No significant inter-specific interactions were found for any combina-
375 tion of the three tit species. In the second analysis, the inter-specific interactions
376 were found between some of the species pairs. Both positive and negative in-

377 teractions were found between different species in the second analysis. The
378 posterior means suggest there is a significant positive effect of greenfinch on
379 house sparrow (0.0327, (0.0258, 0.0401)), whilst similarly there is a negative
380 effect of chaffinch on house sparrow (-0.0462, (-0.0555,-0.0367)).

381 4 Discussion

382 The model presented in this paper is a highly flexible model that can account
383 for and estimate numerous types of interactions that are inherent in many eco-
384 logical data sets. The method extends the work of Lahoz-Monfort *et al.* (2011)
385 and Grosbois *et al.* (2009) to allow synchrony across species to be estimated
386 in both their response to environmental covariates fitted as fixed effects in the
387 model, as well as in unexplained variation accounted for through random effects.
388 The use of posterior model probabilities estimated using the reversible jump al-
389 gorithm ensures that all aspects of synchrony are modelled, and enables more
390 specific conclusions to be drawn as to the nature of the synchrony and to which
391 measured covariates this synchrony relates. This method allows species to be
392 grouped together quantitatively according to how they respond to any covari-
393 ate under consideration, whilst estimating distinct coefficients for those species
394 that respond in a significantly different way. Although this is possible through
395 comparison of parameter estimates from single-species models, our framework
396 is a method that quantitatively discriminates between competing models with
397 different combinations of species grouped together according to their response to
398 covariates. It also takes advantage of the increased precision that sharing para-
399 meters affords, with synchrony in response to covariates predominantly relating
400 to species with the highest overlap in credible intervals in the single species
401 models. Synchrony to covariates in these analyses relates both to species that
402 show no significant relationship with a given covariate as well as those covariates
403 that have a significant but similar manner.

404 There has been a recent trend in joint modelling approaches to multi-species

405 assemblages. Harris (2015) fitted a joint species distribution model and provided
406 more accurate estimates than were obtained through comparison of results from
407 independent, single-species models. Single-species models ignore much of the
408 dependencies and correlations that exist between each of the different species
409 and therefore risk attributing some of the variation spuriously to a covariate
410 that may not be having an overall effect.

411 The ratio of the unexplained variation can also indicate potential covariates
412 that may be missing from the model. If the unexplained variance is largely
413 synchronous, as is the case in blue and great tits, this suggests that any missing
414 covariates (if there are any), are most likely largely global covariates that have
415 a wide-ranging effect. In the case of coal tit, where the unexplained variation
416 was largely asynchronous, the indication would be that any missing covariates
417 affect this species alone. As a species, the coal tit has more specific habitat
418 requirements than the other tit species considered. McKenzie *et al.* (2007)
419 showed that numbers of coal tits visiting gardens was negatively correlated with
420 a measure of the success of conifer cone production. A covariate measuring the
421 distance to the nearest coniferous forest or the success of the cone crop locally
422 may account for a greater amount of variation than the one fitted here.

423 The flexibility of the model does not come without computational cost. How-
424 ever, the flexibility can be reduced depending on the nature of the application of
425 interest. In this application, greater flexibility was added to the model through
426 species-specific dependencies of the Tweedie variance parameters. In the case
427 where a single parameter distribution is used, such as in Lahoz-Monfort *et al.*
428 (2011), this additional complexity would not be required. In these analyses,
429 posterior support for species-specific parameters was found and, as such, it
430 seems that the greater computational cost of allowing this flexibility was war-
431 ranted. Compared to models that did not allow these Tweedie parameters to be
432 species-specific, the corresponding estimates of the species-specific random effect
433 variances were reduced. This suggests that accounting for these differences at
434 the distribution level allows a greater proportion of the variation between spe-

435 cies to be directly accounted for and should therefore lead to improved model
436 performance.

437 In addition, this framework does not require two separate models to be fit-
438 ted to detect synchrony in relation to measured covariates, something that is re-
439 quired in the model of Lahoz-Monfort *et al.* (2011). Simultaneously, the method
440 also calculates synchrony within any species-covariate combination. The abil-
441 ity to detect how species respond similarly or differently to various exogenous
442 factors can provide important information on possible causes of wide-ranging,
443 ecosystem-level changes in populations. It can also account for varying levels of
444 interactions and similarities between species. The need to consider changes in
445 biodiversity at an ecosystem level has been suggested previously (e.g. McCarthy,
446 2011) and this modelling framework allows such modelling to be conducted. The
447 dynamics underpinning the changes in ecological species are inevitably linked
448 and failing to take these links into consideration will oversimplify or even in-
449 correctly identify drivers of population change. Lahoz-Monfort *et al.* (2011)
450 compare the ICCs for models with and without covariates however, such an ap-
451 proach does not take in consideration the fact that, when removing covariates,
452 some of that additional variation could be absorbed by the intercept or alter the
453 dynamics of the remaining variation that was previously attributed to one of
454 the random effects. The method outlined here prevents this problem by directly
455 accounting for the synchrony to measured covariates in a unified approach.

456 Although fitting independent models or a joint multi-species model with
457 unique coefficients, followed by post-analysis comparison of credible intervals,
458 could be used as a more simplistic method for detecting synchrony in covariates,
459 the approach outlined here offers a more robust method for comparing simil-
460 arities between coefficient estimates. The agreement between methods is good,
461 but there were occasions when parameters with distinct credible intervals in the
462 independent models were then shared across multiple species in the joint model
463 (for example p in the ground feeding species analysis).

464 In both analyses, there tended to be little support for models with no syn-

465 chrony in response to each covariate - that is unique coefficients for each of the
466 three species - suggesting that synchrony in response to covariates is a phe-
467 nomenon that should be taken into consideration in models of this type. Merely
468 using the proportion of unexplained variation as a means for estimating total
469 synchrony will therefore tend to underestimate the total level of synchrony in-
470 herent in the data, whilst also reducing precision in comparison to models with
471 shared coefficients.

472 The posterior means of the regression coefficients were consistent with those
473 from independent species analyses Swallow *et al.* (unpublished data). Where
474 coefficients were shared these were usually equal to roughly the average of
475 the two corresponding estimates from the independent analyses. The coeffi-
476 cients that were shared corresponded to either cases where the effect was non-
477 significant - that is where 95% credible intervals included zero - and significant
478 coefficients whose 95% credible intervals did not include zero. In comparing
479 the results from the multi-species analyses with those from independent models
480 the parameters that were shared almost always corresponded with those whose
481 95% credible intervals had the largest degree of overlap (Table 13). The biggest
482 exception to this was the suburban/rural covariate in the ground feeding spe-
483 cies, with the model with the highest posterior model probability relating to
484 the two species having the least overlap in credible intervals in the independent
485 analyses. Secondly, the index parameter p was shared between house sparrow
486 and chaffinch, which had quite distinct values in the independent models. All
487 parameters that were shared had a large degree of overlap, although there were
488 some with reasonable overlap that were not shared.

489 Accounting for the different shape distributions for each species - that is
490 allowing p and ϕ to be species invariant - also reduced the magnitude of asyn-
491 chronous variance compared to models with these parameters constrained to be
492 equal, particularly for coal tit whose posterior means for these two parameters
493 were most different from the others. The posterior mean of ICC_{ct} decreased
494 from 0.494 to 0.414 when the Tweedie parameters remained shared across all

495 species, a bigger change than the other two species suggesting more asynchron-
496 ous variance in the shared parameter model. As these parameters determine
497 the variance of the Tweedie distribution, allowing them to differ for each species
498 will directly account for differences in variance for each species and, as such, a
499 smaller amount of asynchronous variation would then be expected in the means
500 for each species.

501 In some cases it appears that the model is unable to differentiate between
502 inter- and intra-specific interactions. Once the interaction with conspecifics
503 has been accounted for, that is density dependence, there appears to be little
504 additional variation left that can be explained by the number of other spe-
505 cies observed at that site. The two species groups considered in the two models
506 were chosen largely because they have similar ecological requirements and hence
507 we would expect these interaction covariates to be highly correlated. It seems
508 positive, though, that the model is predominately selecting the number of con-
509 specific over the number of the other species in the model as the best predictor
510 of variation. No species showed significant density dependence in addition to an
511 effect of another species on it. That is the changes observed in species counts
512 were either affected by the presence of conspecifics *or* of at most one other spe-
513 cies. This may highlight a difficulty of separating out some of the high level
514 interactions between species that are inherent in these multi-species models.
515 However, modelling the simpler ones clearly adds to the understanding of the
516 ecology, rather than ignoring the effects of other birds visiting the feeders at the
517 same time.

518 The results presented in this analysis suggest that there is indeed a large
519 degree of synchrony in many of the species studied. The drivers of numbers of
520 blue tit and great tit visiting garden feeding stations appear to be particularly
521 strongly correlated, observed through both their tendency for shared covariate
522 parameters and their ICC values. The shared northing and easting parameters
523 suggest similar spatial trends for the two species, which is supported by inform-
524 ation presented within Bird Atlas 2007-11 (Balmer *et al.*, 2013, pp. 496-499).

525 Coal tits have shown negative trends in the southeast of the UK (Balmer *et al.*,
526 2013, pp. 502-503) which is reflected in their unique parameter values. The
527 effect of sparrowhawks and collared doves on the three species seems to be neg-
528 ligible in blue and great tits, but with a small but significant positive association
529 with coal tits. The latter could represent confounding factors that led to spar-
530 rowhawks and collared doves recolonising sites that were also more attractive to
531 coal tits, such as a preference for larger gardens, rather than a causal relation-
532 ship. All three species have a tendency to make use of garden feeders more in
533 conditions of cold weather Chamberlain *et al.* (2005), when natural food sources
534 can be harder to access. The positive effect of ground frost on numbers of ob-
535 served birds suggests a behavioural response of birds entering gardens to access
536 food sources that will be independent of the weather. The strongest effect of
537 this covariate was found in blue tits, with a smaller and equivalent effect on the
538 other two species.

539 In the case of the ground-feeding species, our results have shown that there
540 are frequently similar effects of environmental factors on the numbers visiting
541 garden feeding stations. However, in this case the differences between ICCs
542 were much smaller than in the other species group. Greenfinch and chaffinch
543 unsurprisingly were the two species showing most synchrony in their response
544 to environmental covariates. The exceptions to this were in their relationship
545 with collared doves and ground frost. In the former case, numbers of chaffinches
546 were more positively associated with collared doves than the other two species,
547 whilst greenfinches were less affected by ground frost. Chaffinch and collared
548 dove are more strongly ground feeding than greenfinch and frost would be ex-
549 pected to effect ground feeders more than those species using perched feeders.
550 These individual differences in responses to covariates would have been missed
551 if covariate synchrony had not been added to the modelling process.

552 Multi-species models that account for the complex interactions within and
553 between species have the potential to offer a much greater understanding of
554 the underlying dynamics to which species are responding, either individually

555 or at an ecosystem level. Although the subtleties of the complex processes
556 will always be simplified to some degree when using mathematical models, the
557 method outlined here allows some of those complexities to be accounted for
558 directly. Joint-species responses to specific covariates may suggest areas for
559 further research or indicate areas for management that can benefit a whole
560 ecosystem rather than just its constituent parts. Long-term studies, such as
561 the GBFS, provide invaluable insight into a communities of species that are
562 subject to the same environmental factors; the methods used to analyse such
563 data should really take this into consideration. Given the increasing pressures on
564 land, and a growing degree of urbanisation, there is a clear need to understand
565 the ecological processes driving the changes that we are seeing within wild bird
566 populations. New statistical approaches, such as this, provide an opportunity
567 to look at these processes across species in a more effective manner.

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665 **Figures**

Fig. 1 Average trends in the number of each of the three tit species (left) and grain feeding birds (right) observed across sites monitored by the GBFS from 1970 to 2005.

666 **Tables**

Table 1 Pairwise Pearson’s correlations between site annual means for blue tit (BT), great tit (GT) and coal tit (CT) (left-hand columns) and house sparrow (HS), greenfinch (GF) and chaffinch (CF) (right-hand columns).

Species pair	Correlation (p-value)	Species pair	Correlation (p-value)
BT vs GT	0.78 (<0.001)	HS vs GF	0.09 (0.023)
BT vs CT	0.46 (<0.001)	HS vs CF	-0.08 (0.028)
GT vs CT	0.60 (<0.001)	GF vs CF	0.40 (<0.001)

(a) Marginal correlation between sites, that is means are taken across years within sites and compared between species pairs.

Species pair	Correlation (p-value)	Species pair	Correlation (p-value)
BT vs GT	0.57 (<0.001)	HS vs GF	-0.81 (<0.001)
BT vs CT	0.00 (0.986)	HS vs CF	-0.84 (<0.001)
GT vs CT	0.57 (<0.001)	GF vs CF	0.84 (<0.001)

(b) Marginal correlation between years, that is means are taken across sites for each year and compared between species pairs.

Table 2 Prior distributions for the model parameters.

Parameter	Prior distribution
α_s	$N(0, 10^{-2})$
$\beta_j\{s\}$	$N(0, 10^{-2})$
$\gamma_j\{s\}$	$N(0, 10^{-2})$
$\nu_{i,j} \quad (i = j)$	$HN^{-}(0, 10^{-2})$
$\nu_{i,j} \quad (i \neq j)$	$N(0, 10^{-2})$
$\mu_{s,i,0}$	$U[0, 200]$
$\phi\{s\}$	$U[0, 5]$
$p\{s\}$	$U[1, 2]$
σ_ϵ^2	$\Gamma^{-1}(10^{-3}, 10^{-3})$
σ_s^2	$\Gamma^{-1}(10^{-3}, 10^{-3})$

Table 3 Blue tit, great tit and coal tit multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Covariate	Posterior mean	95%CI
α_{bt}	Intercept	-0.0352	(-0.0414,-0.0284)
α_{gt}	Intercept	-0.0269	(-0.0326,-0.0202)
α_{ct}	Intercept	-0.0477	(-0.0575,-0.0378)
$\beta_1\{bt\}$	Northing	-0.0102	(-0.0177,-0.0039)
$\beta_1\{gt\}$	Northing	-0.0102	(-0.0176,-0.0039)
$\beta_1\{ct\}$	Northing	0.0076	(-0.0026,0.0180)
$\beta_2\{bt\}$	Easting	-0.0080	(-0.0143,-0.0009)
$\beta_2\{gt\}$	Easting	-0.0080	(-0.0142,-0.0009)
$\beta_2\{ct\}$	Easting	-0.0275	(-0.0375,-0.0172)
$\beta_3\{bt\}$	Sub/rur	-0.0155	(-0.0209,-0.0101)
$\beta_3\{gt\}$	Sub/rur	-0.0169	(-0.0228,-0.0114)
$\beta_3\{ct\}$	Sub/rur	-0.0133	(-0.0200,-0.0038)
$\nu_{bt,bt}$	Dens dep	-0.0260	(-0.0298,-0.0221)
$\nu_{gt,gt}$	Dens dep	-0.0298	(-0.0339,-0.0260)
$\nu_{ct,ct}$	Dens dep	-0.0333	(-0.0404,-0.0464)
$\gamma_1\{bt\}$	Sparrowhawk	-0.0032	(-0.0073,0.0010)
$\gamma_1\{gt\}$	Sparrowhawk	-0.0030	(-0.0070,0.0012)
$\gamma_1\{ct\}$	Sparrowhawk	0.0170	(0.0088,0.0255)
$\gamma_2\{bt\}$	Collared dove	-0.0005	(-0.0042,0.0033)
$\gamma_2\{gt\}$	Collared dove	-0.0004	(-0.0042,0.0034)
$\gamma_2\{ct\}$	Collared dove	0.0160	(0.0082,0.0238)
$\gamma_3\{bt\}$	Ground frost	0.0185	(0.0133,0.0238)
$\gamma_3\{gt\}$	Ground frost	0.0126	(0.0074,0.0183)
$\gamma_3\{ct\}$	Ground frost	0.0134	(0.0073,0.0197)
$\phi\{bt\}$	-	0.1654	(0.1567,0.1749)
$\phi\{gt\}$	-	0.1985	(0.1912,0.2060)
$\phi\{ct\}$	-	0.3439	(0.3298,0.3584)
$p\{bt\}$	-	1.4469	(1.4106,1.4814)
$p\{gt\}$	-	1.1797	(1.1656,1.1938)
$p\{ct\}$	-	1.2714	(1.2595,1.2831)

Table 4 Blue tit, great tit and coal tit multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Posterior mean	95%CI
σ_ϵ^2	0.0043	(0.0036,0.0051)
σ_{bt}^2	0.0005	(0.0003,0.0007)
σ_{gt}^2	0.0004	(0.0002,0.0007)
σ_{ct}^2	0.0049	(0.0032,0.0059)
ICC _{bt}	0.903	(0.852,0.947)
ICC _{gt}	0.912	(0.857,0.957)
ICC _{ct}	0.494	(0.411,0.591)

Table 5 β_s marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 3, corresponding to northing easting, and suburban/rural respectively. $\{bt, gt\}$ denotes that the parameter shared across blue tit and great tit.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\{bt, gt\}, \{ct\}$	0.931	$\{bt, gt\}, \{ct\}$	0.979	$\{bt, ct\}, \{gt\}$	0.892
$\{bt, ct\}, \{gt\}$	0.041	$\{bt\}, \{gt\}, \{ct\}$	0.021	$\{gt, ct\}, \{bt\}$	0.107
$\{bt\}, \{gt\}, \{ct\}$	0.028			$\{bt\}, \{gt\}, \{ct\}$	0.001

Table 6 γ_s marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 3, corresponding to sparrowhawk collared dove and ground frost respectively. $\{bt, gt\}$ denotes the parameter shared across blue tit and great tit.

Sparrowhawk		Collared dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\{bt, gt\}, \{ct\}$	0.968	$\{bt, gt\}, \{ct\}$	0.997	$\{gt, ct\}, \{bt\}$	0.994
$\{bt\}, \{gt\}, \{ct\}$	0.032	$\{bt\}, \{gt\}, \{ct\}$	0.003	$\{bt, ct\}, \{gt\}$	0.006

Table 7 Marginal posterior probabilities relating to the sharing of the two Tweedie variance parameters across tit species from the model in Table 3. $\{bt, gt\}$ denotes the parameter shared across blue tit and great tit.

ϕ		p	
Model	MPP	Model	MPP
$\{bt\}, \{gt\}, \{ct\}$	1.000	$\{bt\}, \{gt\}, \{ct\}$	1.000

Table 8 House sparrow, greenfinch and chaffinch multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Covariate	Posterior mean	95%CI
α_{hs}	Intercept	-0.0600	(-0.0720,-0.0485)
α_{gf}	Intercept	-0.0353	(-0.0453,-0.0250)
α_{cf}	Intercept	-0.0058	(-0.0138,0.0021)
$\beta_1\{hs\}$	Northing	-0.0060	(-0.0192,0.0048)
$\beta_1\{gf\}$	Northing	-0.0012	(-0.0102,0.0076)
$\beta_1\{cf\}$	Northing	-0.0008	(-0.0084,0.0072)
$\beta_2\{hs\}$	Easting	-0.0285	(-0.0400,-0.0178)
$\beta_2\{gf\}$	Easting	-0.0246	(-0.0360,-0.0146)
$\beta_2\{cf\}$	Easting	-0.0226	(-0.0315,-0.0138)
$\beta_3\{hs\}$	Sub/rur	-0.0156	(-0.0252,-0.0043)
$\beta_3\{gf\}$	Sub/rur	-0.0181	(-0.0266,-0.0087)
$\beta_3\{cf\}$	Sub/rur	-0.0202	(-0.0277,-0.0129)
$\nu_{hs,hs}$	Dens dep	NA	NA
$\nu_{gf,gf}$	Dens dep	-0.0142	(-0.0195,-0.0093)
$\nu_{cf,cf}$	Dens dep	-0.0282	(-0.0330,-0.0228)
$\nu_{gf,hs}$	Interaction	0.0327	(0.0258,0.0401)
$\nu_{cf,hs}$	Interaction	-0.0462	(-0.0555,-0.0367)
$\gamma_1\{hs\}$	Sparrowhawk	-0.0459	(-0.0532,-0.0387)
$\gamma_1\{gf\}$	Sparrowhawk	-0.0016	(-0.0064,0.0035)
$\gamma_1\{cf\}$	Sparrowhawk	-0.0016	(-0.0063,0.0036)
$\gamma_2\{hs\}$	Collared dove	0.0037	(0.0003,0.0071)
$\gamma_2\{gf\}$	Collared dove	0.0036	(0.0001,0.0071)
$\gamma_2\{cf\}$	Collared dove	0.0118	(0.0070,0.0175)
$\gamma_3\{hs\}$	Ground frost	0.0375	(0.0321,0.0431)
$\gamma_3\{gf\}$	Ground frost	0.0145	(0.0046,0.0238)
$\gamma_3\{cf\}$	Ground frost	0.0375	(0.0321,0.0431)
$\phi\{hs\}$	-	0.6867	(0.6619,0.7121)
$\phi\{gf\}$	-	0.5360	(0.5182,0.5545)
$\phi\{cf\}$	-	0.3890	(0.3754,0.4029)
$p\{hs\}$	-	1.3534	(1.3407,1.3639)
$p\{gf\}$	-	1.4218	(1.4069,1.4370)
$p\{cf\}$	-	1.3563	(1.3450,1.3731)

Table 9 House sparrow, greenfinch and chaffinch multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Posterior mean	95%CI
σ_ϵ^2	0.0037	(0.0027,0.0050)
σ_{hs}^2	0.0145	(0.0120,0.0173)
σ_{gf}^2	0.0084	(0.0068,0.0103)
σ_{cf}^2	0.0039	(0.0025,0.0055)
ICC _{hs}	0.205	(0.154,0.256)
ICC _{gf}	0.308	(0.221,0.398)
ICC _{cf}	0.495	(0.344,0.648)

Table 10 β_s marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 8, corresponding to northing, easting, and suburban/rural respectively. $\{hs, gf\}$ denotes that the parameter shared across house sparrow and greenfinch.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\{gf, cf\}, \{hs\}$	0.591	$\{gf, cf\}, \{hs\}$	0.649	$\{gf, cf\}, \{hs\}$	0.494
$\{hs, cf\}, \{gf\}$	0.223	$\{hs, gf\}, \{cf\}$	0.238	$\{hs, cf\}, \{gf\}$	0.252
$\{hs, gf\}, \{cf\}$	0.175	$\{hs, cf\}, \{gf\}$	0.105	$\{hs, gf\}, \{cf\}$	0.250
$\{hs\}, \{gf\}, \{cf\}$	0.010	$\{hs\}, \{gf\}, \{cf\}$	0.008	$\{hs\}, \{gf\}, \{cf\}$	0.003

Table 11 γ_s marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 8, corresponding to sparrowhawk collared dove and ground frost respectively. $\{hs, gf\}$ denotes the parameter shared across house sparrow and greenfinch.

Sparrowhawk		Collared dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\{gf, cf\}, \{hs\}$	0.991	$\{hs, gf\}, \{cf\}$	0.981	$\{hs, cf\}, \{gf\}$	0.994
$\{hs\}, \{gf\}, \{cf\}$	0.009	$\{hs\}, \{gf\}, \{cf\}$	0.019	$\{hs\}, \{gf\}, \{cf\}$	0.006

Table 12 Marginal posterior probabilities relating to the sharing of the two Tweedie variance parameters across tit species from the model in Table 8. $\{hs, gt\}$ denotes the parameter shared across blue tit and great tit.

ϕ		p	
Model	MPP	Model	MPP
$\{hs\}, \{gf\}, \{cf\}$	1.000	$\{hs, cf\}, \{gf\}$	0.835
		$\{hs\}, \{gf\}, \{cf\}$	0.165

Table 13 Proportion of overlap of 95% credible intervals from the independent analyses from Swallow *et al.* (unpublished data) for each pairwise combination of species. The negative values indicate distinct intervals for each of that pairwise species comparison. Bold values relate to the species pair with the highest posterior model probability for that covariate from the joint model.

Species	North	East	Sub/rur	S.hawk	C. dove	Grd. frost	p	ϕ
BT/GT	0.87	0.59	0.82	-0.02	0.62	0.57	-2.75	-0.69
BT/CT	0.03	0.11	0.34	-0.70	0.11	0.46	-1.67	-5.40
GT/CT	0.10	0.05	0.24	-0.31	0.20	0.53	-2.23	-4.34
HS/GF	0.28	0.68	0.82	-1.15	0.22	-0.73	-1.44	-2.18
HS/CF	-0.18	0.51	0.33	-2.58	0.29	-1.37	-2.32	-5.96
GF/CF	0.51	0.82	0.16	-0.11	0.02	0.58	-4.26	-4.43