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1 **The effects of woodland habitat and biogeography on blue tit (*Cyanistes caeruleus*)**  
2 **territory occupancy and productivity along a 220km transect**

3

4

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19

20 **Key words:** occupancy, productivity, spatial autocorrelation, latitude, elevation, habitat, prey  
21 availability, clutch size

22 **Abstract**

23

24 The nesting phenology and productivity of hole-nesting woodland passerines, such as tit  
25 species (*Paridae*), has been the subject of many studies and played a central role in advancing  
26 our understanding of the causes and consequences of trophic mismatch. However, as most  
27 studies have been conducted in mature, oak-rich (*Quercus* sp.) woodlands, it is unknown  
28 whether insights from such studies generalise to other habitats used by woodland generalist  
29 species. Here we applied spatial mixed models to data collected over three years (2014-2016)  
30 from 238 nestboxes across 40 sites – that vary in woodland habitat and elevation – along a  
31 220km transect in Scotland. We evaluate the importance of habitat, biogeography and food  
32 availability as predictors of mesoscale among-site variation in blue tit (*Cyanistes caeruleus*)  
33 nestbox occupancy and two components of productivity (clutch size and fledging success). We  
34 found that habitat was not a significant predictor of occupancy or clutch size but that occupancy  
35 exhibited pronounced biogeographic trends, declining with increasing latitude and elevation.  
36 However, fledging success, defined as the proportion of a clutch that fledged, was positively  
37 correlated with site level availability of birch, oak and sycamore, and tree diversity. The lack  
38 of correspondence between the effects of habitat on fledging success versus occupancy and  
39 clutch size may indicate that blue tits do not accurately predict the future quality of their  
40 breeding sites when selecting territories and laying clutches. We found little evidence of spatial  
41 autocorrelation in occupancy or clutch size, whereas spatial autocorrelation in fledging success  
42 extends over multiple sites, albeit non-significantly. Taken together, our findings suggest that  
43 the relationship between breeding decisions and breeding outcomes varies among habitats, and  
44 we urge caution when extrapolating inferences from one habitat to others.

45

## 46 **Introduction**

47

48 Temperate hole-nesting woodland passerines, such as tits (*Paridae*) and flycatchers  
49 (*Muscicapidae*), have become well used model systems for understanding trophic mismatch,  
50 specifically examining the effects of spring temperature on trophic interactions and fitness  
51 (Visser et al. 1998, Thomas et al. 2001, Both et al. 2004, Charmantier et al. 2008). Many studies  
52 addressing trophic mismatch in these birds have been conducted in single-site mature  
53 woodlands dominated by a single tree species, usually oak (*Quercus* sp.) (Charmantier et al.  
54 2008, Wilkin et al. 2009). However, many of these bird species are woodland generalists,  
55 occupying a wide variety of woodland types across their range and not all individuals within a  
56 population will experience similar environments. Therefore in order to extrapolate findings  
57 obtained in oak woodlands on a landscape- or meso-scale we first need to understand how  
58 habitat affects occupancy and productivity (Visser et al. 2003, Burger et al. 2012, Cole et al.  
59 2015), as habitat can be a key determinant of fitness (Pärt 2001, Wilkin et al. 2007, Atiénzar et  
60 al. 2010). For instance, if a species is found to be most abundant and productive in oak  
61 woodland, by gaining an understanding of climate-mediated mismatch in this habitat we can  
62 better predict the metapopulation level impacts of mismatch. Alternatively, if habitats other  
63 than oak are found to benefit occupancy and productivity then to understand the impacts of  
64 mismatch on the metapopulation we may also need to understand how mismatch operates in  
65 these different habitats.

66

67 Previous work examining the effect of breeding habitat on tit productivity has typically  
68 considered variation among territories at a single site (Perrins 1979, Wilkin et al. 2009,  
69 Amininasab et al. 2016) or between two or three sites (Blondel et al. 1991, Tremblay et al.  
70 2003, Marciniak et al. 2007). For the two most frequently studied tit species, great tit (*Parus*

71 *major*) and blue tit (*Cyanistes caeruleus*), differences among major woodland types are widely  
72 documented, with clutch sizes and fledgling numbers approximately one third larger in  
73 deciduous compared with coniferous (Gibb and Betts 1963, Perrins 1965, Van Balen 1973) or  
74 sclerophyllous (Blondel et al. 1993, Lambrechts et al. 1997) woodlands. Breeding densities  
75 show a similar pattern, being several times higher in deciduous woodland (Cramp and Perrins  
76 1993). However, great tits seem more able to produce two successful clutches in coniferous  
77 woodland than deciduous (Van Balen 1973), whilst in blue tits second clutches are rare (Gibb  
78 and Betts 1963, Perrins 1979).

79

80 Within deciduous woodlands tree species composition and maturity can vary substantially,  
81 though the effect of this fine-scale habitat variation on tit abundance and breeding performance  
82 has received little attention. Oak (*Quercus* sp.) is widely regarded to be the optimal breeding  
83 habitat for great and blue tits (Perrins 1979), with some studies defining territory quality on the  
84 basis of the number of oak trees they contain (Wilkin et al. 2007, Bell et al. 2014). In support  
85 of this assumption, great and blue tits forage more frequently in oaks than other tree species  
86 when they are present during the breeding season, but also visit a wide variety of other trees  
87 (Gibb 1954) and blue tit breeding densities and clutch sizes are higher in mature oak habitats  
88 than beech (*Fagus sylvatica*) (Amininasab et al. 2016). However, the relationship between the  
89 abundance of other tree species and tit breeding parameters remains largely unexplored,  
90 possibly a consequence of limited habitat variation within the typical single site study. A few  
91 studies have also examined the effect of other aspects of woodland composition and find that  
92 woodland maturity positively affects blue tit fledging success (Arriero et al. 2006), whilst  
93 clutch size and occupancy are unaffected by woodland structure and management (Hinsley et  
94 al. 2002, Arriero et al. 2006, Burgess 2014).

95

96 On a mesoscale, as latitude and elevation increases, abiotic conditions such as temperature,  
97 rainfall and photoperiod may covary, which in turn may affect habitat composition and food  
98 availability. Orell and Ojanen (1983) found no latitudinal trends in great tit clutch sizes across  
99 Europe whereas Sanz (1998) found that they lay marginally lower clutch sizes at the extremes  
100 of their European latitudinal distribution, a result corroborated in blue tits (Fargallo 2004), but  
101 that on the scale of country-wide latitudinal ranges these effects were very weak. Evans et al  
102 (2009) also found little evidence for latitudinal gradients in clutch size at a country-wide (UK)  
103 latitudinal range across a variety of species, including tits. Increasing elevation has been shown  
104 to predict a small but significant reduction in the clutch size of great and blue tits (Sanz 1998,  
105 Fargallo 2004). While the mechanistic underpinnings of any relationship between these  
106 biogeographic variables and breeding parameters is unclear, if after controlling for local habitat  
107 such trends exist, this may imply either that the abiotic environment has a direct or indirect  
108 effect, or that habitat on a broader scale is important.

109

110 Food availability is one component of the biotic environment that may have profound impacts  
111 on geographic variation in species occurrence and productivity. Tits are mainly insectivorous  
112 during the breeding season (Betts 1955, Cholewa and Wesołowski 2011), and whilst they have  
113 been shown to rely heavily on an ephemeral peak in caterpillar abundance (Feeny 1970, van  
114 Dongen et al. 1997, Southwood et al. 2004) for provisioning of nestlings (Visser et al. 1998,  
115 Charmantier et al. 2008), at other times during the spring adult birds prey upon a broad range  
116 of additional taxa that includes flying invertebrates such as *Hemiptera*, *Diptera* and  
117 *Hymenoptera* (Betts 1955, Cowie and Hinsley 1988). Woodland invertebrate diversity and  
118 abundance varies considerably between tree species (Southwood et al. 1982, Kennedy and  
119 Southwood 1984). Given that different invertebrate taxa vary in their phenology (Niemela and  
120 Haukioja 1982, Southwood et al. 2004), the abundance and temporal availability of prey may

121 vary in space (Fielding et al. 1999, Smith et al. 2011), which could affect productivity (Wilkin  
122 et al. 2009) and nest site selection decisions. Indeed, a positive effect of resource availability  
123 on productivity has been revealed via supplementary feeding experiments (Nager et al. 1997,  
124 Robb et al. 2008), although this effect could be dependent upon the existing natural resource  
125 level (Bourgault et al. 2009).

126

127 The focus of this study is on identifying the effects of habitat and biogeography on blue tit  
128 occupancy and productivity. We aim to establish the relative importance of fine-scale  
129 woodland habitat versus food availability, and larger scale biogeography, as predictors of tit  
130 occupancy and on two components of productivity, clutch size and the proportion of the clutch  
131 that fledges. This knowledge will also help form a baseline from which to explore the how  
132 trophic mismatch operates across habitats. We focus on blue tits, which are single-brooded  
133 woodland generalists that often exist in high density across Europe (Perrins 1979, Blair and  
134 Hagemeyer 1997). This species is relatively sedentary, with natal dispersal probably of more  
135 importance to occupancy decisions than breeding dispersal at the scale we evaluate (Paradis et  
136 al. 1998). Rather than focusing on the effects of among territory habitat variation within a single  
137 site, we consider among site habitat variation on a mesoscale. Specifically, we analyse data  
138 arising from a transect extending 220km in Scotland, which incorporates 40 woodlands, spans  
139 two degrees of latitude and almost 450m of elevation. It encompasses a broad sample of  
140 habitats occupied by blue tits, rather than focussing solely on large mature woodlands, with the  
141 aim of providing a more representative sample of blue tit habitat than previous work.

142

143

## 144 **Methods**

145

146 **Transect study design**

147

148 We conducted fieldwork along a 40-site transect from Edinburgh (55.98°N, -3.40°E) to  
149 Dornoch (57.89°N, -4.08°E), in Scotland, spanning 220km (Fig 1A, supplementary material  
150 Table A1). We aimed to spread sites evenly along the transect (mean distance between  
151 neighbouring sites = 6.0 km, min = 0.2 km, max = 13.9 km) and varied in both elevation (Fig  
152 1B, supplementary material Table A1) and the type of deciduous woodland habitat. At each  
153 site we erected six Schwegler 1B 26mm entrance diameter bird nestboxes at approximately  
154 40m intervals in any configuration. All deciduous-dominated woodlands large enough to  
155 accommodate six nestboxes were considered. The sole exception to this is the highest site,  
156 where there was only sufficient woodland area for four nestboxes, as this is the only available  
157 option at this elevation and point of the transect. All sites are outside urban settlements. We  
158 used small hole nestboxes to favour use by blue tits and exclude common non-focal species  
159 such as great tits and erected them at c.1.5m from the floor with the hole facing away from the  
160 prevailing wind. The location of each nestbox was determined using a handheld GPS (Garmin  
161 eTrex High Sensitivity) and we obtained elevation (meters above sea level (m.a.s.l)) via the  
162 Google Maps elevation API. The elevation of the lowest field site was only slightly above sea  
163 level and the highest field site was around the suitable deciduous woodland treeline in Scotland  
164 (Pears 1967) (Fig 1B, supplementary material Table A1).

165

166 The study was carried out during the springs of 2014-16, with different sites studied intensively  
167 in different years (supplementary material Table A1) and intensive study of 24 sites across all  
168 three years of the study, 14 sites across two years and two sites for a single year. Intensively  
169 studied field sites were visited every other day throughout the field season (mid-March to late-  
170 June) and we monitored alternate sites on each day where possible. Sites with installed



171 nestboxes that were not intensively studied in 2015 and 2016 (those un-ticked in these years in  
172 supplementary material Table A1) were omitted from intensive study due to access  
173 complications but were visited at least four times during the field season to collect data on blue  
174 tit occupancy, clutch size and fledging success. All dates used in this study, unless explicitly  
175 indicated otherwise, are ordinal dates counted from January 1st, meaning that April 1<sup>st</sup> is day  
176 91 in most years and 92 in a leap year.

177

## 178 **Habitat**

179

180 We recorded habitat around each nestbox at 39 field sites in June-July 2015 and one site in  
181 June 2016. We sampled the woodland habitat within a 15m radius of each nestbox. This  
182 distance was selected because we found it provided a fair representation of surrounding habitat  
183 and avoided cases of the same trees contributing to the habitat of different nestboxes. To  
184 capture variation in tree maturity we assigned every tree with part of its trunk within the 15m  
185 radius of the nestbox and a trunk over 40cm in diameter at breast height (approximately 150cm  
186 from the ground) to one of three size categories: small (40-99cm girth at breast height (gbh)),  
187 medium (100-249cm gbh) and large (>250cm gbh). All measurements of tree size were taken  
188 at breast height, so if a tree split below this measure the size of each separate trunk was  
189 recorded.

190

191 At some sites there were few trunks that qualified under our definition of a tree, but there were  
192 stands of shrub cover (e.g., Hazel *Corylus avellana* and Willow *Salix sp.*) that provided feeding  
193 habitat. To accommodate this we constructed three 'stand' classes. (1) Stand6-20: where 6-20  
194 separate branches emanated from within 20cm of the base of the shrub stand; (2) stand21+:  
195 where >20 branches split; (3) When the shrub stand was too impenetrable to count the stems

196 for a stand score, we measured the length and width of the thicket to create a rectangle full of  
197 thicket, and estimated the maximum height of the thicket. While converting these stand scores  
198 to the foliage provided by a number of trees will only be very approximate, based on visual  
199 inspection we used the following equivalences: stand6-20 = 0.5 small trees, stand21+ = 1 small  
200 tree and thicket volume  $\times 1/30 = n$  small trees.

201

202 We identified each tree or shrub to genus level and then assigned to focal taxon categories  
203 (Table 1). Tree identification was to genus level due to substantial evidence of intra-genus  
204 hybridisation (e.g. *Betula pubescens x pendula*, *Quercus robur x patraea*, *Salix caprea x*  
205 *cinerea*) along the transect and similar intra-genus ecological properties and associated  
206 invertebrate communities (Kennedy and Southwood 1984, Southwood et al. 2004). We  
207 weighted large, medium and small trees of each genus by the minimum diameter (e.g.,  
208  $\pi[250/(2\pi)]^2$  for large trees) to obtain an approximate ‘foliage score’ for each tree genus at each  
209 nestbox (see Fig 2 for site means). Our intention here was to represent the ability of larger trees  
210 to afford a greater habitat resource and foraging space for blue tits than smaller trees.

211

212 We characterised variation in woodland habitat based on five measures of the amount of foliage  
213 (total, birch, oak, sycamore, willow) and one measure of tree diversity. Foliage scores were  
214 calculated at the site level as the mean of the nestbox scores. Our motivation for focussing on  
215 these four tree species is that birch, oak and sycamore were the three most common focal tree  
216 taxa by foliage score along the transect (Table 1), and, along with willow, constitute the  
217 dominant species at the majority of sites (Fig 2, supplementary material Table A1). Total  
218 foliage provides a metric for the total foraging resource available to blue tits and is in effect  
219 the product of woodland density and maturity, accounting for increases in trees in general of  
220 species not included in models individually. Tree diversity was quantified as Simpson’s

221 diversity index at the site level across all genera (i.e. ‘other deciduous’ and ‘conifers’ categories  
222 were split into their constituent genera (Table 1)) via the R package ‘vegan’ (Oksanen et al.  
223 2012). We included this variable as greater tree diversity may be correlated with greater prey  
224 diversity and abundance (Southwood et al. 1982, Fuentes-Montemayor et al. 2012) and/or  
225 increase the temporal spread of prey availability (Kennedy and Southwood 1984). Across sites  
226 the pairwise correlations among habitat variables was  $< 0.52$ , implying that co-linearity should  
227 not present a problem in our analyses.

228

## 229 **Invertebrates**

230

231 To monitor (mostly flying) invertebrates we installed 2 x 245 x 100mm double-sided yellow  
232 sticky traps at c.1.75m above the ground on two randomly selected trees at each intensively  
233 studied site, with the same trees, and when possible branches, used each year. Each sticky trap  
234 had a protective cage constructed from 25 x 12mm wire mesh that slotted over it to prevent  
235 bird and bat mortalities. Every four days each sticky trap was collected and replaced. Sticky  
236 trap use was for the period 22/23 March – 14/15 June 2014, 24/25 March – 16/17 June 2015  
237 and 28/29 March – 16/17 June 2016. One observer (JDS) counted all invertebrates over 3mm  
238 in length (n=98772) collected by the traps (both sides) and assigned each to at least order level,  
239 with *Hemiptera*, *Diptera* and *Hymenoptera* the most frequent and known to contribute  
240 substantially to blue tit diet (Betts 1955, Cowie and Hinsley 1988).. To quantify repeatability  
241 58 sticky traps were randomly sampled and counted for a second time (26 from 2014, 16 each  
242 from 2015 and 2016). Repeatability of total invertebrates on a given sticky trap was then  
243 estimated using a generalised linear mixed model (GLMM) (Bates et al. 2015) with Poisson  
244 error structure containing year as a fixed effect and site, date, sticky trap ID, sticky trap ID date  
245 and residual error as random effects. Regardless of whether repeatability on the latent scale

246 was estimated at the site and date level (i.e. sticky trap ID in the numerator) or transect level  
247 (i.e. site, date and sticky trap ID in the numerator), the estimate was > 99%. We subdivided the  
248 invertebrate dataset into two roughly equal time periods to partially take into account the major  
249 phenological changes in invertebrate abundance over the course of spring. The early time  
250 period contained all sticky traps collected from 26th March – 4th May, whilst the late time  
251 period constituted those collected from 5th May – 17th June in each year. Site level predictions  
252 (ln-scale) for total invertebrate availability in early spring and late spring were estimated using  
253 Poisson GLMM's in the MCMCglmm package (Hadfield 2010) that included site as a fixed  
254 effect and sticky trap ID, year and sampling date as random effects.

255

## 256 **Birds**

257

258 At all intensively studied sites, nestboxes were checked every other day prior to egg-laying.  
259 We considered a nestbox as occupied if there was at least one egg laid in a lined nest. Clutch  
260 size was counted post-incubation initiation and prior to hatching. All nestlings were  
261 individually ringed under license from the British Trust for Ornithology and nests were  
262 revisited after chicks were 20 days old to ascertain the fledging success/failure of individual  
263 nestlings. We had evidence of one second brood in 2014 and this was discounted from all  
264 analyses.

265

## 266 **Statistical Analyses**

267

268 All analyses were conducted in R version 3.1.1 (R Core Team 2014). We used spatial GLMMs  
269 to study the effects of habitat, biogeography and invertebrate availability on blue tit occupancy  
270 (proportion of available nestboxes at a site that were occupied by blue tits), clutch size and

271 fledging success (proportion of a clutch that fledged). Our motivation for focussing on clutch  
272 size and fledging success (rather than total fledglings) is that it allows us to examine the effects  
273 of drivers on these two largely independent components of productivity (with total fledglings  
274 the product of the two). However, we also considered a model with total fledglings, presented  
275 in the supplementary material. Spatial GLMM's were constructed via the spaMM package  
276 (Rousset and Ferdy 2014), which treats spatial correlation among sites as random effects and  
277 we assumed that spatial autocorrelation among sites declines exponentially with distance by  
278 fixing  $\nu$  at 0.5. Occupancy and fledging success were modelled with binomial family errors,  
279 and clutch size and total fledglings were log-transformed and modelled with Gaussian family  
280 errors. We excluded from analyses nestboxes occupied by coal tits (*Parus ater*, one in each  
281 of 2015 and 2016) and stolen or unavailable nestboxes (two in 2015, one in 2016). Models  
282 included habitat variables, latitude, elevation and year as fixed effects. It was possible to  
283 include latitude and spatial autocorrelation in the same model as the former describes a linear  
284 trend, whereas the latter allows for the correlation to decay with distance over an estimated  
285 range in two dimensions. We also included site level predictions of early season total  
286 invertebrates in the occupancy and clutch size models and late season total invertebrates in the  
287 fledging success and total fledglings models. Nestbox ID was included as a random term in all  
288 models.

289

290 Nestbox provision can result in blue tit breeding densities that are double natural levels (Dhondt  
291 et al. 1992) and blue tits preferentially select territories with few neighbours (Serrano-Davies  
292 et al. 2017). For the occupancy model we tested whether nestboxes led to an increase in blue  
293 tit density, by including a two-level factor distinguishing first versus subsequent seasons.  
294 Breeding density has been shown to reduce clutch size and fledging success in tit populations  
295 across different habitats (Both 1998, Wilkin et al. 2006, Dhondt 2010, Sæther et al. 2016) and

296 to accommodate such an effect we included blue tit density as the proportion of operational  
297 nestboxes occupied at a site in the clutch size, fledging success and total fledglings models.

298

299 In all of the above models, site means were used for all predictor variables and all numeric  
300 predictor variables were mean-centred for ease of interpretation (Schielzeth 2010). Latitude  
301 values were expressed as northing values in units of metres. Maximum likelihood was used for  
302 GLMM optimisation. Our modelling approach was to construct a full model including all  
303 terms, which we did not then seek to simplify. We included no interactions as we had no strong  
304 *a priori* reasons for including them. To test the significance of specific individual terms where  
305  $t > 1.5$  we used term deletion and likelihood ratio tests to obtain P values. As our model includes  
306 multiple terms there is a high probability that some terms will be significant even if the null  
307 hypothesis were true. Whilst we do not correct for this, we suggest that this should be borne in  
308 mind when interpreting our results. To ascertain whether habitat in general had a significant  
309 effect we deleted all habitat terms as a group predictor and compared models with a likelihood  
310 ratio test to the full model, with the degrees of freedom equal to the difference in number of  
311 estimated parameters.

312

313 To evaluate the importance of spatial autocorrelation in each model, we fixed  $\rho = 10000$  to  
314 simulate negligible autocorrelation and then compared with a likelihood ratio test to the full  
315 model. To test the sensitivity of our results to our use of habitat stand scores, these data were  
316 excluded and models were re-run and parameter estimates compared. Finally, to contextualise  
317 the amount of spatial variance explained by (i) all habitat variables, (ii) the two biogeographic  
318 variables and (iii) invertebrate resource availability, each of these predictor blocks were  
319 independently removed from the full model and the spatial variance compared with both the

320 full model and a null model that contained only year as a fixed effect and the random and spatial  
321 autocorrelation terms.

322

## 323 **Results**

324

325 Total foliage, oak, sycamore and tree diversity all appear to decrease at higher elevations, with  
326 birch and willow displaying the opposite trend (supplementary material Fig. A1). Whereas,  
327 birch increases with latitude but the other habitat variables exhibited no clear trend  
328 (supplementary material Fig. A1).

329

330 The total number of flying invertebrates sampled on sticky traps varied substantially among  
331 sites and dates (supplementary Fig. A2). Across sites we see that there is little evidence for any  
332 latitudinal trend in the amount of invertebrates, whereas there is a decrease in invertebrate  
333 abundance with elevation in the early time period (supplementary material Fig.A3B), with the  
334 opposite pattern in the late time period (supplementary material Fig. A3D).

335

336 Occupancy was not significantly predicted by habitat in general, or by any individual habitat  
337 variable (Table 2A). Instead there was support for biogeographic variables, with occupancy  
338 decreasing with latitude, such that holding other predictors constant (for the year 2014 and with  
339 all other variables at their means – we took the same approach with all other predictions that  
340 we report below), 70% of nestboxes were predicted to be occupied in the far south of the  
341 transect declining to 33% in the far north (Fig 3A). Elevation was also a significant predictor  
342 of occupancy, and the probability of occupancy decreased from 79% at sea level to just 13%  
343 at the highest elevation (Fig 3B). In a *post-hoc* test, described in the supplementary material,  
344 we found no evidence that the effects of latitude or elevation were simply acting as a proxy for

345 the multi-year spring average temperatures at each site (supplementary material Table A3). The  
346 environmental availability of invertebrates early in the spring, whether the nestbox was in its  
347 first available year or a subsequent year, and year, were all non-significant predictors.

348

349 The mean clutch size was just over eight and varied within years (2014:  $8.63 \pm 2.07$  (mean  $\pm$   
350 sd, 2015:  $7.62 \pm 1.82$ , 2016:  $8.08 \pm 1.49$ , total range: 2-14). Habitat was not a significant  
351 predictor of clutch size in general (Table 2B). Willow was the only significant habitat term,  
352 such that clutch size was predicted to increase from 8.3 with no willow present to 10.4 with the  
353 highest amount of willow found on the transect. We found no significant biogeographic trend  
354 in clutch size across latitudes or elevations and no effect of invertebrate availability early in  
355 the year, or of blue tit density. Differences in clutch sizes among years were pronounced, with  
356 clutch sizes highest in 2014 and predicted to be 12% and 6% lower in 2015 and 2016,  
357 respectively.

358

359 Fledging success, unlike occupancy and clutch size, was predicted by several habitat variables  
360 (Table 2C, Fig 4). Amongst the individual habitat variables, birch, oak, sycamore and  
361 increasing tree diversity all predicted a significant increase in the proportion of eggs that  
362 survived to fledging. Where oak foliage was at the highest levels found on the transect it  
363 predicted fledging rates of 100%, whilst zero oak predicted 80%. The equivalent figures for  
364 sycamore and birch were very similar at 97%, 80%, 96% and 79% respectively. Fledging  
365 success also increased with tree diversity, with predicted success of 97% at the highest levels  
366 of tree diversity on the transect, versus 71% at the lowest. Of the six habitat variables  
367 considered, the coefficients for five of these switched sign between the fledgling success and  
368 clutch size model. Providing further evidence that site level habitat indices are important  
369 predictors of fledging success, when we removed all habitat variables from the full model the



370 spatial variance increased considerably and much more than when biogeographic variables or  
371 food availability were removed (Table 2). These effects of habitat on fledging success are not  
372 dominated by year effects, being in the same direction each year (supplementary material Table  
373 A2A-C). In addition to habitat, the availability of late spring flying invertebrates also predicted  
374 increased fledging success (from 62% to 97%). Fledging success also increased significantly  
375 with increasing elevation, with predictions ranging from 68% to 97% from the lowest to highest  
376 elevations, though the latitudinal trend was very shallow and non-significant. Year had a  
377 substantial effect on fledging success, with predicted fledging success of 86%, 49% and 73%  
378 in 2014, 2015 and 2016, respectively. We found no evidence that blue tit density had any effect  
379 on fledging success within the parameters of this study. Quantitatively, the results for the total  
380 number of fledglings were congruent to those described here for fledging success, with all  
381 coefficients in the same direction and of comparable significance (supplementary material  
382 Table A2D).

383

384 Spatial autocorrelation was very weak for both occupancy and clutch size, where the  
385 correlation declined to 0.1 by just 959m and 606m respectively, considerably less than the  
386 mean distance between adjacent sites along the transect. In comparison spatial autocorrelation  
387 was much stronger for fledging success (range at which correlation declined to 0.1 = 200km),  
388 which implies that fledging success at even distant sites is correlated. However, a likelihood  
389 ratio test comparing these models to a model with very weak spatial autocorrelation was non-  
390 significant for all three models ( $p > 0.8$  in all models), from which we infer that spatial  
391 autocorrelation is either weak or we lack the power to estimate it well. Of the predictor variable  
392 ‘blocks’, spatial variance was best explained by biogeography for occupancy and habitat for  
393 clutch size and fledging success (Table 2 footnotes).

394

395 **Discussion**

396

397 We find that habitat plays a critical role in predicting the fledging success of blue tits, with  
398 increasing availability of birch, oak and sycamore and higher tree diversity all having a positive  
399 effect. That these patterns are consistent across years provides substantial evidence in support  
400 of a robust and general effect in Scotland (Table 2, supplementary material Table A2). In  
401 contrast, habitat did not predict occupancy or clutch size. We propose that this discrepancy  
402 between the habitat predictors of early-season breeding decisions and late-season breeding  
403 outcomes could suggest that blue tits may not be accurately assessing, or accounting for, the  
404 future quality of their breeding habitat when occupying territories and laying clutches.  
405 Occupancy is better predicted by biogeography, and declines as elevation and latitude increase,  
406 whereas inter-annual variation, probably in the form of untested environmental factors (e.g.  
407 rainfall, temperature), is the strongest predictor of clutch size.

408

409 Blue tit fledging success was highly sensitive to habitat variables, with the site-level  
410 availability of birch, oak and sycamore all positive predictors. Our findings broadly agree with  
411 earlier work that reports that whilst blue tits are woodland generalists, productivity is highest  
412 when certain species are present, particularly oak (Wilkin et al. 2009, Amininasab et al. 2016).  
413 However, whilst previous work has concentrated on differences between major woodland  
414 types, such as deciduous versus coniferous (Gibb and Betts 1963, Van Balen 1973) or  
415 sclerophyllous (Blondel et al. 1993, Lambrechts et al. 2004), we have demonstrated more  
416 nuanced effects of different constituent species within deciduous woodland, and over a much  
417 larger geographic scale.

418

419 Oak has previously been used in studies as a proxy for blue tit habitat quality (Wilkin et al.  
420 2007, Bell et al. 2014), justified on the basis of oak woodland supporting higher abundances  
421 of winter moth caterpillars, a critical dietary component for rearing nestlings. Our study  
422 corroborates the use of oak availability as a proxy for habitat quality and provides some of the  
423 most comprehensive results to date that an increase in the availability of oak predicts an  
424 increase in fledging success. However, sycamore and birch also predict increased fledging  
425 success, and this demonstrates that other species in addition to oak provide high quality blue  
426 tit habitat. As total foliage, capturing the effect of an increase in the average tree after  
427 accounting for the individually analysed tree species, elicits no significant effects on the birds,  
428 it can be surmised that the positive effects of oak, birch and sycamore are due to these species  
429 providing exceptionally productive habitat rather than this effect simply being a product of an  
430 increase in trees in general. Biogeographic variables and breeding density did not significantly  
431 predict fledging success, the latter differing from some previous studies (Dhondt et al. 1992,  
432 Wilkin et al. 2006). However, our maximum number of nestboxes per site was low ( $n=6$ ) and  
433 we modelled the effect of breeding density as a consistent effect across sites, which does not  
434 take into account among site differences in average tit density and may explain why we do not  
435 detect an effect of density.

436

437 In contrast to fledging success, the other component of productivity that we studied, clutch  
438 size, was not significantly predicted by habitat, or any individual habitat variables, with the  
439 exception of a slight positive effect of willow availability. The apparent lack of variation in  
440 clutch sizes across habitats is consistent with earlier work comparing plots within a site  
441 (Dhondt et al. 1990) and may imply that high rates of gene flow among habitats prevents local  
442 adaptation (Postma and Van Noordwijk 2005). One possibility is that clutch size is adapted to  
443 the dominant, or most productive habitat in the wider landscape, as earlier work on blue tit

444 clutch sizes has found (Blondel et al. 1993, Dias and Blondel 1996), making clutch size less  
445 sensitive than fledging success to habitat variation (Arriero et al. 2006). We also found that  
446 many variables had an opposite directional effect on the predicted slope for clutch size as they  
447 did for productivity; this might be explained by individual females making suboptimal large  
448 reproductive investments in early spring in habitats that later prove to be poor. A challenge  
449 faced by a female blue tit is that the environment that determines fledgling survival (often  
450 termed the environment of selection) is around three weeks after the environment in which the  
451 clutch is laid (the environment of development). The ability of a female to predict future  
452 conditions and plastically adjust clutch size adaptively will depend on the correlation between  
453 the environment of development and selection (Gavrilets and Scheiner 1993) and this  
454 correlation may vary among habitats. For example, habitats with a high quality resource early  
455 in the breeding season differ from those that provide a high quality resource late in the breeding  
456 season. One explanation for this phenomenon is tree phenology, where early leafing trees and  
457 habitats may support higher prey abundances early in the season whilst food peaks tail off later  
458 on, with late leafing trees, or trees with full-season growth (Niemela and Haukioja 1982),  
459 having the opposite tendency. Such temporal asynchronicity in invertebrate abundances across  
460 tree species (Southwood et al. 2004, Veen et al. 2010) could help explain why increasing tree  
461 diversity elevates eventual productivity, providing a suitable environment for the entirety of  
462 the breeding season through the diversity of leafing times maintaining a more sustained and  
463 reliable temporal availability of prey.

464

465 Whilst blue tits did not seem to predict high quality local habitats within a year, clutch size and  
466 fledging success varied substantially among years with coincident trends based on three years  
467 of data. If clutch size and fledging success are genuinely positively correlated, this is consistent  
468 with high quality versus low quality years being a major source of variation in reproductive

469 success within this system (Perrins 1979, Tremblay et al. 2003). A positive correlation would  
470 also imply that birds are more able to predict the relative quality of a breeding season than they  
471 are able to predict the future effects of different habitats. Indeed, previous studies have shown  
472 among year correlations between clutch size and caterpillar abundance, with the latter  
473 providing a proxy for the quality of the year for blue tit reproduction (Perrins 1965, 1991,  
474 Marciniak et al. 2007). That we found no evidence of a latitudinal gradient in clutch size at this  
475 scale agreed with previous studies (Fargallo 2004, Evans et al. 2009).

476

477 Occupancy, like clutch size, was not significantly predicted by habitat. This may imply that  
478 blue tits occupy nestboxes across different habitats at random. However, more likely is that  
479 population densities on larger spatial scales determine occupancy. Blue tit populations in the  
480 UK are currently at a high ebb (Balmer et al. 2013) and this may lead to even low quality 'sink'  
481 habitats becoming occupied (Bellamy et al. 2000). Biogeographic variables did however  
482 predict occupancy, with occupancy highest at low elevations and decreasing further north,  
483 agreeing with other work (Fargallo 2004). Our findings reveal that these biogeographic trends  
484 occur over a finer latitudinal and elevational scale than previously reported. A decrease in  
485 occupancy with latitude and elevation must reflect the impact of environmental variables  
486 beyond those captured by site-level habitat metrics, and could include habitat across broader  
487 spatial scales, tolerance to temperatures at particular times of year (e.g. winter, but not spring  
488 – see supplementary material) or the frequency of supplementary feeding (Robb et al 2008), as  
489 in the focal area human population density decreases with both latitude and elevation and blue  
490 tit density increases between low and moderately high human population densities (Tratalos et  
491 al. 2007).

492

493 To summarise, we find that the availability of oak, birch, sycamore and tree diversity predict  
494 increased blue tit fledging success, whereas the effects of habitat on occupancy and clutch size  
495 are much weaker, which may imply that blue tits are not able to predict among habitat variation  
496 in the future availability of resources. One of the implications of blue tit breeding parameters  
497 differing among habitats is that it may not be appropriate to extrapolate insights from the  
498 commonly-studied mature (often oak) habitats to others and habitat should be taken into  
499 account when predicting demographic changes based on trophic mismatch theory.

500

501

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511

512

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669

**Table 1:** Focal tree taxon categories, detailing the most prevalent tree species along the transect within each category, ordered by mean category foliage score per nestbox (Birch to Aspen) followed by the multi-genera categories (Other Deciduous and Conifers). Categories are at the genus level, or above this level if the taxon is uncommon on the transect (mean genus foliage score per nestbox <1). Total n = 5921.

Category	Species	n	Size (%)			Stand
			Small	Medium	Large	
Birch	Downy Birch ( <i>Betula pubescens</i> )	1929	81	18	1	
	Silver Birch ( <i>Betula pendula</i> )					
Oak	Pedunculate Oak ( <i>Quercus robur</i> )	499	30	66	4	
	Sessile Oak ( <i>Quercus patraea</i> )					
Sycamore	Sycamore Maple ( <i>Acer pseudoplatanus</i> )	858	67	32	1	
Ash	European Ash ( <i>Fraxinus excelsior</i> )	486	73	26	1	
Beech	European Beech ( <i>Fagus sylvatica</i> )	194	65	27	8	
Alder	Common Alder ( <i>Alnus glutinosa</i> )	491	85	14	1	
Willow	Goat Willow ( <i>Salix caprea</i> )	481	70	6	24	
	Grey Willow ( <i>Salix cinerea</i> )					
	Eared Willow ( <i>Salix aurita</i> )					
	White Willow ( <i>Salix alba</i> )					
	Crack Willow ( <i>Salix fragilis</i> )					
Elm	Wych Elm ( <i>Ulmus glabra</i> )	158	73	26	1	
Aspen	Eurasian Aspen ( <i>Populus tremula</i> )	100	71	29		
Other Deciduous	Common Hazel ( <i>Corylus avellana</i> )	330	70	11	19	
	European Rowan ( <i>Sorbus aucuparia</i> )					
	Hawthorn ( <i>Crataegus monogyna</i> )					
	Wild Cherry ( <i>Prunus avium</i> )					
	Sweet Chestnut ( <i>Castanea sativa</i> )					
Small-leaved Lime ( <i>Tilia cordata</i> )						
Conifers	Scots Pine ( <i>Pinus sylvestris</i> )	395	55	43	2	
	Common Yew ( <i>Taxus baccata</i> )					
	European Larch ( <i>Larix decidua</i> )					
	Norway Spruce ( <i>Picea abies</i> )					
	Sitka Spruce ( <i>Picea sitchensis</i> )					

**Table 2** Effects on blue tit occupancy, clutch size and fledging success along the transect. Slopes (coefficient) are shown with their associated standard errors (se) from the respective full GLMM. All significant slopes from fixed effects are presented in bold ( $p \leq 0.05$  \*  $\leq 0.01$  \*\*  $\leq 0.001$  \*\*\*) with individual term p values obtained via term deletion and the habitat group p values (denoted in each column by the bracket wrapping all deleted terms) obtained via group deletion (see methods). No significance asterisk implies that predictor or predictor group is not significant. Intercept year is 2014.

	<b>A. Occupancy</b>	<b>B. Clutch Size</b>	<b>C. Fledging success</b>
<b>Fixed Term</b>	<b>coefficient <math>\pm</math> se</b>	<b>coefficient <math>\pm</math> se</b>	<b>coefficient <math>\pm</math> se</b>
Intercept	0.090 $\pm$ 0.228	2.14 $\pm$ 0.03	1.78 $\pm$ 0.16
Total Foliage	0.0054 $\pm$ 0.0159	0.00069 $\pm$ 0.00108	-0.00027 $\pm$ 0.01059
Birch	-0.0039 $\pm$ 0.0166	-0.00065 $\pm$ 0.00123	<b>0.025 <math>\pm</math> 0.011 *</b>
Oak	0.0029 $\pm$ 0.0145	-0.00041 $\pm$ 0.00105	<b>0.041 <math>\pm</math> 0.010 ***</b>
Sycamore	0.013 $\pm$ 0.024	0.00092 $\pm$ 0.00155	<b>0.044 <math>\pm</math> 0.016 **</b>
Willow	0.0096 $\pm$ 0.0454	<b>0.011 <math>\pm</math> 0.003 **</b>	-0.056 $\pm$ 0.030
Tree Diversity	0.051 $\pm$ 0.218	-0.024 $\pm$ 0.015	<b>0.49 <math>\pm</math> 0.15 **</b>
Latitude	<b>-7.3x10<sup>-6</sup> <math>\pm</math> 3.6x10<sup>-6</sup> *</b>	-3.9x10 <sup>-7</sup> $\pm$ 2.5x10 <sup>-7</sup>	2.7x10 <sup>-6</sup> $\pm$ 2.7x10 <sup>-6</sup>
Elevation	<b>-0.0073 <math>\pm</math> 0.0029 *</b>	-6.6x10 <sup>-6</sup> $\pm$ 2.4x10 <sup>-4</sup>	<b>0.0061 <math>\pm</math> 0.0021 **</b>
Early Invertebrates	-0.25 $\pm$ 0.36	-0.020 $\pm$ 0.024	-
Late Invertebrates	-	-	<b>1.50 <math>\pm</math> 0.37 ***</b>
Subsequent Year	0.12 $\pm$ 0.50	-	-
Blue Tit Density	-	-0.056 $\pm$ 0.068	-0.25 $\pm$ 0.44
Year 2015	0.86 $\pm$ 0.51	<b>-0.13 <math>\pm</math> 0.03 ***</b>	<b>-1.84 <math>\pm</math> 0.16 ***</b>
Year 2016	0.43 $\pm$ 0.59	<b>-0.066 <math>\pm</math> 0.033 ***</b>	<b>-0.80 <math>\pm</math> 0.14 ***</b>
<b>Random Term</b>	<b>variance</b>	<b>variance</b>	<b>variance</b>
Space	0.6	6.5x10 <sup>-9</sup>	1.4x10 <sup>-9</sup>
Nestbox ID	0.2	2.1x10 <sup>-4</sup>	2.0
<b>Spatial Autocorrelation</b>	<b>parameter</b>	<b>parameter</b>	<b>parameter</b>
nu	0.5	0.5	0.5
rho	0.0024	0.0038	5.5x10 <sup>-6</sup>

Spatial variances when predictor blocks were removed: **Occupancy**: - habitat 0.66, - biogeography 0.86, - invertebrates 0.64, null 1.98. **Clutch Size**: - habitat 0.0011, - biogeography  $7 \times 10^{-9}$ , - invertebrates  $6 \times 10^{-9}$ , null 0.0032. **Fledging Success**: - habitat 0.39, - biogeography 0.13, - invertebrates 0.20, null 0.48.



## Figure legends.

Figure 1. A. Map of Scotland showing the locations of all 40 field sites (blue stars), scale, and selected cities as location indicators. B. A latitudinal elevation profile of the transect sites, again with selected cities as location indicators.

Figure 2. Bar plot of mean foliage scores per site for each focal taxon category (Table 1), with 'Otherdecid' referring to other deciduous trees. Site names from left to right correspond to south to north (supplementary material Table A1).

Figure 3. The effect of A. latitude and B. elevation on nestbox occupancy in blue tits, with all other variables at their mean, in 2014 and in the first spring since site installation.

Figure 4. Predictors of fledging success: A. Birch Foliage B. Oak Foliage C. Sycamore Foliage D. Tree Diversity E. Elevation F. Late-spring Invertebrate Abundance (log scale). Lines show the prediction, with all other variables at their mean and in 2014.

Supplementary material Figure A1. Site-level biogeographic patterns in habitat variables.

Supplementary material Figure A2. Raw numbers of invertebrates sampled from sticky traps at each site in each year. Some counts exceed the limits of the constant y axis used for comparison.

Supplementary material Figure A3. Site level predictions (ln-scale) of total invertebrate numbers from a GLMM (see methods). A. Early season total invertebrates by latitude. B. Early season total invertebrates by elevation. C. Late season total invertebrates by latitude. D. Late season total invertebrates by elevation.

**Supplementary material Table A1:** Field site details including location and elevation, when the nestboxes were installed, and the years in which each site was intensively studied. Dominant tree defined as the commonest deciduous tree by foliage score, but see Figure 2 for more detailed habitat information.

Code	Name	Mean Latitude (°N)	Mean Longitude (°E)	Mean Elevation (m.a.s.l)	Nestboxes	Installation Date	2014	2015	2016	Dominant Tree (%)
EDI	Edinburgh	55.98	- 3.40	54	6	04/02/2015		✓	✓	Sycamore (70)
RSY	Rosyth	56.02	- 3.41	37	6	20/01/2015		✓	✓	Sycamore (49)
FOF	Fordell Firs	56.06	- 3.38	87	6	09/12/2013	✓	✓	✓	Sycamore (39)
BAD	Blairadam	56.12	- 3.45	170	6	29/11/2013	✓			Beech (35)
LVN	Loch Leven	56.17	- 3.36	123	6	09/12/2013	✓	✓	✓	Birch (66)
GLF	Glenfarg	56.30	- 3.36	100	6	10/01/2014	✓	✓	✓	Beech (32)
SER	Strathearn	56.35	- 3.40	10	6	20/02/2015		✓	✓	Sycamore (45)
MCH	Moncrieffe Hill	56.36	- 3.38	48	6	29/11/2013	✓		✓	Sycamore (42)
PTH	Perth	56.42	- 3.47	24	6	29/11/2013	✓	✓		Ash (49)
STY	Stanley	56.48	- 3.47	51	6	29/11/2013	✓	✓	✓	Sycamore (30)
BIR	Birnam	56.54	- 3.53	87	6	10/01/2014	✓		✓	Oak (31)
DUN	Dunkeld	56.57	- 3.62	112	6	29/11/2013	✓	✓		Birch (25)
BLG	Ballinluig	56.65	- 3.66	79	6	29/11/2013	✓	✓	✓	Sycamore (46)
KCK	Killiecrankie I	56.73	- 3.77	117	6	09/12/2013	✓	✓	✓	Beech (51)
KCZ	Killiecrankie II	56.73	- 3.78	155	6	20/01/2015		✓	✓	Oak (78)
BLA	Blair Atholl	56.76	- 3.85	175	6	09/12/2013	✓	✓	✓	Beech (38)
CAL	Calvine	56.77	- 3.97	195	6	29/11/2013	✓	✓	✓	Birch (58)
DNM	Dalnamein	56.80	- 4.03	248	6	29/11/2013	✓	✓	✓	Birch (46)
DNC	Dalnacardoch	56.82	- 4.13	363	6	10/01/2014	✓	✓	✓	Willow (42)
DNS	Dalnaspidal	56.83	- 4.22	433	4	19/02/2015		✓	✓	Willow (38)
DLW	Dalwhinnie	56.92	- 4.24	377	6	13/12/2013	✓	✓	✓	Willow (71)
CRU	Crubenmore	56.99	- 4.18	298	6	13/12/2013	✓	✓	✓	Birch (87)
NEW	Newtonmore	57.05	- 4.13	236	6	13/12/2013	✓	✓	✓	Birch (87)
INS	Insh	57.07	- 4.00	248	6	13/12/2013	✓	✓	✓	Birch (68)
FSH	Feshiebridge	57.12	- 3.90	242	6	13/12/2013	✓	✓	✓	Birch (88)
RTH	Rothiemurchus	57.15	- 3.85	228	6	19/01/2015		✓	✓	Oak (87)
AVI	Aviemore	57.19	- 3.84	209	6	13/12/2013	✓	✓	✓	Birch (100)
AVN	Avielochan	57.21	- 3.82	217	6	20/01/2015		✓	✓	Oak (78)
CAR	Carrbridge	57.29	- 3.79	252	6	14/12/2013	✓	✓	✓	Birch (55)
SLS	Slochd Summit	57.30	- 3.92	375	6	19/01/2015		✓	✓	Birch (94)
TOM	Tomatin	57.33	- 3.98	315	6	13/12/2013	✓	✓	✓	Birch (100)
DAV	Daviot	57.41	- 4.15	152	6	14/12/2013	✓	✓	✓	Alder (79)
ART	Artafallie	57.51	- 4.31	60	6	13/10/2015			✓	Oak (73)
MUN	Munloch	57.55	- 4.28	54	6	14/12/2013	✓	✓	✓	Oak (23)
FOU	Foulis Estate	57.64	- 4.35	17	6	14/12/2013	✓	✓	✓	Sycamore (49)
ALN	Alness	57.69	- 4.29	35	6	14/12/2013	✓	✓	✓	Birch (86)
DEL	Delny Muir	57.72	- 4.13	18	6	14/12/2013	✓	✓	✓	Elm (21)
TAI	Tain Pottery	57.80	- 4.04	23	6	14/12/2013	✓		✓	Birch (32)
SPD	Spinningdale	57.87	- 4.26	71	6	19/01/2015		✓	✓	Oak (86)
DOR	Dornoch	57.89	- 4.08	28	6	14/12/2013	✓	✓	✓	Alder (55)

**Supplementary material Table A2 (A-C)** Effects on blue tit fledging success along the transect once the analysis is split into the constituent years, to compare with Table 2C (showing the result for all years). **(D)** Effects on total number of fledglings, as opposed to fledging success as a proportion of clutch size (Table 2C). Slopes (coefficient) are shown with their associated standard errors (se) from GLMM's.

	<b>A. 2014</b>	<b>B. 2015</b>	<b>C. 2016</b>	<b>D. Total Fledglings</b>
<b>Fixed Term</b>	<b>coefficient ± se</b>	<b>coefficient ± se</b>	<b>coefficient ± se</b>	<b>coefficient ± se</b>
Intercept	2.32 ± 0.38	-0.45 ± 0.36	1.20 ± 0.30	1.92 ± 0.05
Total Foliage	-0.0029 ± 0.0229	-0.0097 ± 0.0265	0.025 ± 0.023	-0.00083 ± 0.00283
Birch	0.0029 ± 0.0243	0.033 ± 0.026	0.020 ± 0.027	0.0067 ± 0.0032 *
Oak	0.073 ± 0.056	0.082 ± 0.026	0.029 ± 0.022	0.011 ± 0.003 ***
Sycamore	0.062 ± 0.030	0.053 ± 0.039	0.047 ± 0.035	0.011 ± 0.004 **
Willow	-0.031 ± 0.114	-0.20 ± 0.07	0.10 ± 0.07	-0.00032 ± 0.00794
Tree Diversity	0.33 ± 0.27	0.77 ± 0.35	0.33 ± 0.33	0.10 ± 0.04 **
Latitude	0.57 ± 0.74	0.52 ± 0.35	0.60 ± 0.71	0.038 ± 0.085
Elevation	0.0045 ± 0.0064	0.0084 ± 0.0051	0.011 ± 0.005	0.0015 ± 0.0006 **
Late Invertebrates	1.85 ± 0.96	2.07 ± 0.81	1.92 ± 0.82	0.39 ± 0.10 ***
Blue Tit Density	-3.62 ± 1.65	1.45 ± 1.65	1.53 ± 1.42	0.090 ± 0.159
Year				
2015	-	-	-	-0.71 ± 0.07 ***
2016	-	-	-	-0.30 ± 0.06 ***
<b>Random Term</b>	<b>variance</b>	<b>variance</b>	<b>variance</b>	<b>variance</b>
Space	3.0x10 <sup>-9</sup>	0.3	2.2x10 <sup>-8</sup>	6.1x10 <sup>-9</sup>
Nestbox ID	3.3	7.1	7.3	0.07
<b>Spatial Autocorrelation</b>	<b>parameter</b>	<b>parameter</b>	<b>parameter</b>	<b>parameter</b>
nu	0.5	0.5	0.5	0.5
rho	5.1	82.8	136.6	4.75

**Supplementary material: *Post-hoc* test of the effect of spring temperature on occupancy**

**Methods:** As biogeographic trends in occupancy were strong, we conducted a *post-hoc* test to examine whether latitude and elevation are simply acting as a proxy for the average spring temperatures at a site. Hourly temperature data were collected by two Thermachron iButton’s (model DS1922L-F5, sensitive to 0.0625°C) installed at opposite ends of each active site throughout March and April of each study year. They were secured 1.5m high on the north side of a tree to avoid direct sunlight in a waterproof white pot with a 20mm-diameter hole in the bottom to allow ambient air circulation. To account for the fact that some sites were not monitored in some years, we obtained site mean spring temperatures as best linear unbiased predictors from a linear mixed model. This model included the mean March/April temperature for each logger as the response variable, year as a fixed term and site as a random term. The site mean temperature term was then added to the full occupancy model and this model was then compared to the original occupancy model via a likelihood ratio test to obtain a p value.

**Results:** March/April temperature was a weak and non-significant predictor of occupancy (supplementary material Table A3,  $\chi^2_1 = 0.84$ ,  $p = 0.36$ ) and inclusion of this term did not diminish the effects of latitude or elevation (compare with Table 2A).

**Discussion:** This analysis allows us to discount a simple relationship between temperature and occupancy but it is possible that a more complex relationship may exist. For instance, perhaps minimum winter temperatures are more important than the spring temperatures that we considered. However, minimum winter temperatures and mean spring temperatures are likely to be highly correlated among sites. Alternatively, this may indicate that latitude and elevation are proxy for the effects of one or perhaps several environmental variables besides temperature.

**Supplementary material Table A3** Effect of site-mean March/April temperature on blue tit nestbox occupancy.

<b>Fixed Term</b>		<b>Occupancy coefficient ± se</b>
Intercept		0.088 ± 0.227
Total Foliage		0.0074 ± 0.0159
Birch		-0.0035 ± 0.0165
Oak		0.0041 ± 0.0145
Sycamore		0.019 ± 0.025
Willow		0.019 ± 0.046
Tree Diversity		-0.026 ± 0.232
Latitude		-8.5x10 <sup>-6</sup> ± 3.8x10 <sup>-6</sup>
Elevation		-0.013 ± 0.006
March/April Temperature		-0.83 ± 0.90
Early Invertebrates		-0.28 ± 0.35
Subsequent Year		0.11 ± 0.50
Year	2015	0.88 ± 0.51
	2016	0.44 ± 0.59
<b>Random Term</b>		<b>variance</b>
Space		0.6
Nestbox ID		0.2
<b>Spatial Autocorrelation</b>		<b>parameter</b>
nu		0.5
rho		0.0022



Figure 1

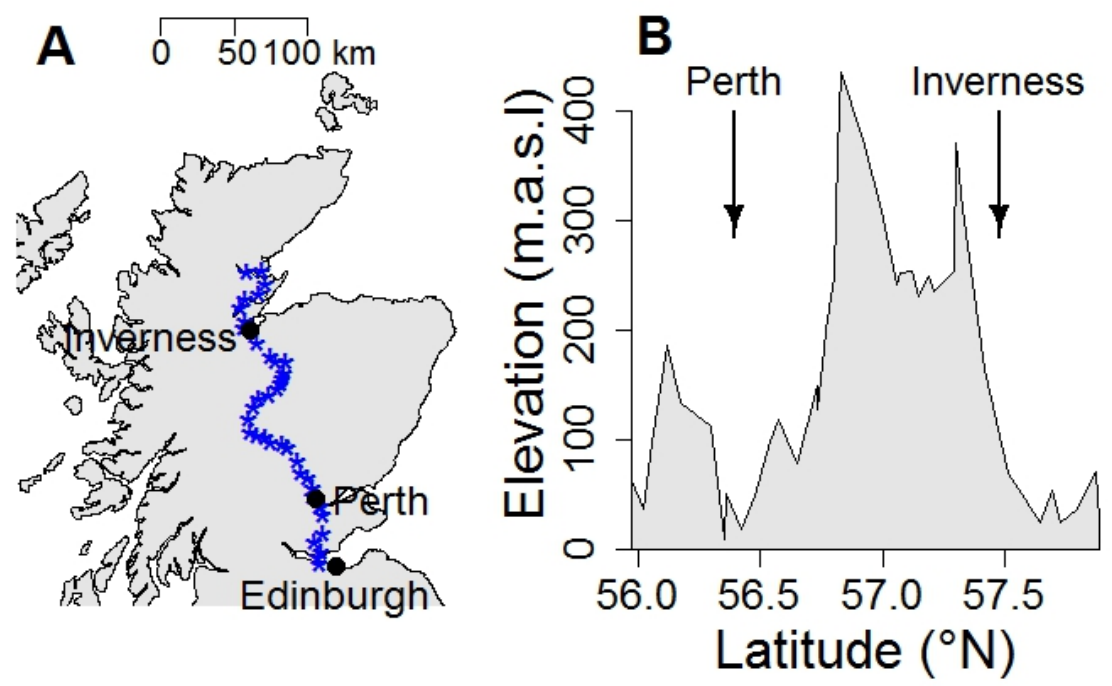


Figure 2.

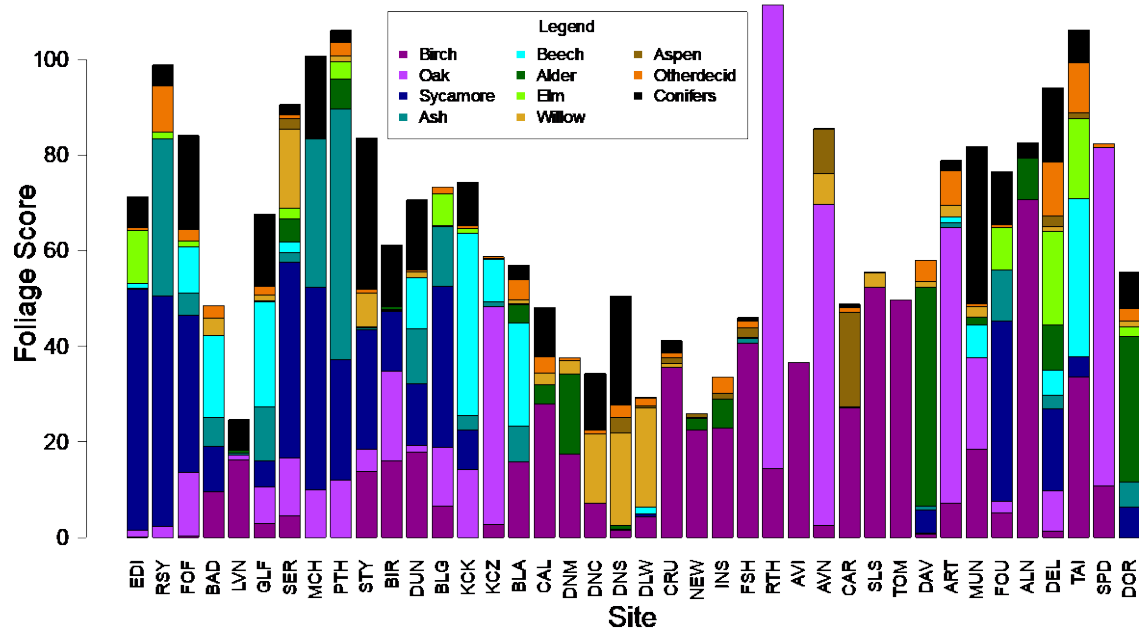


Figure 3.

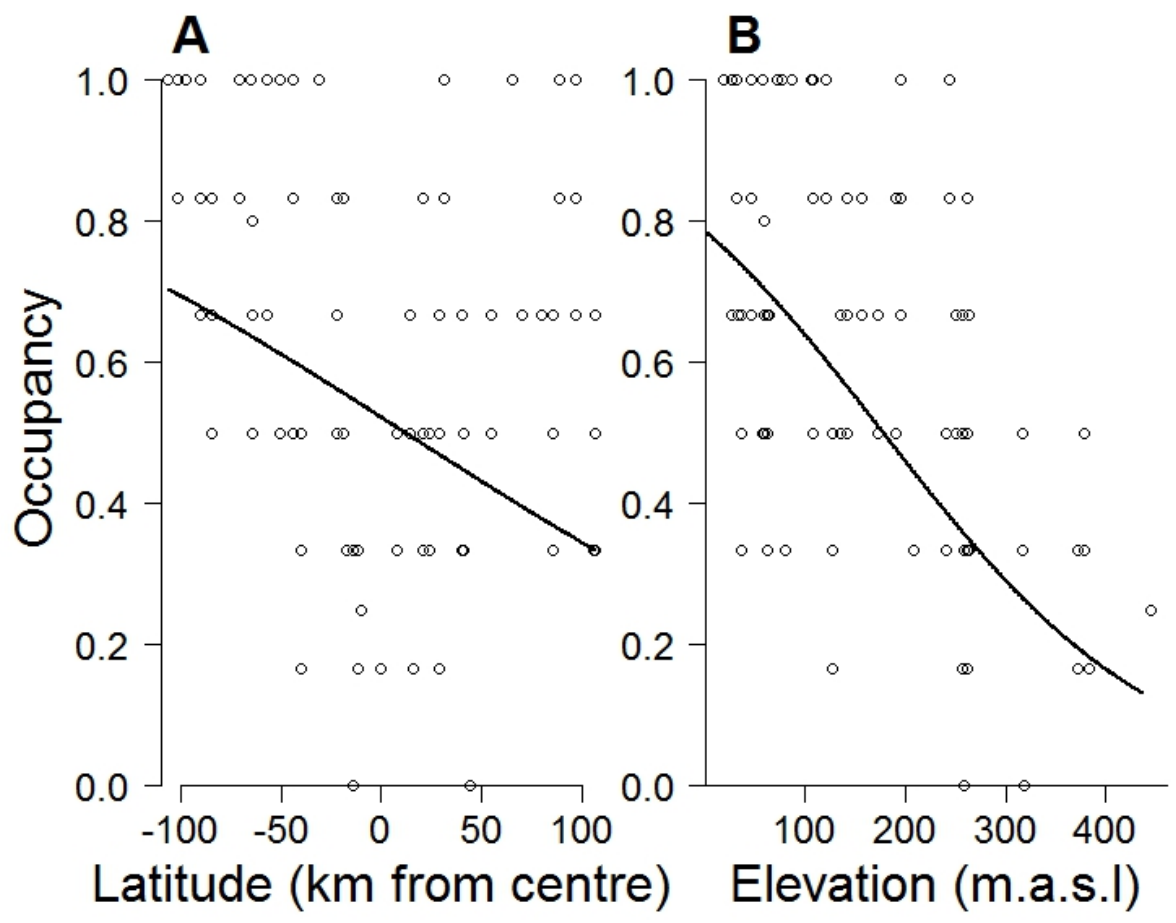




Figure 4.

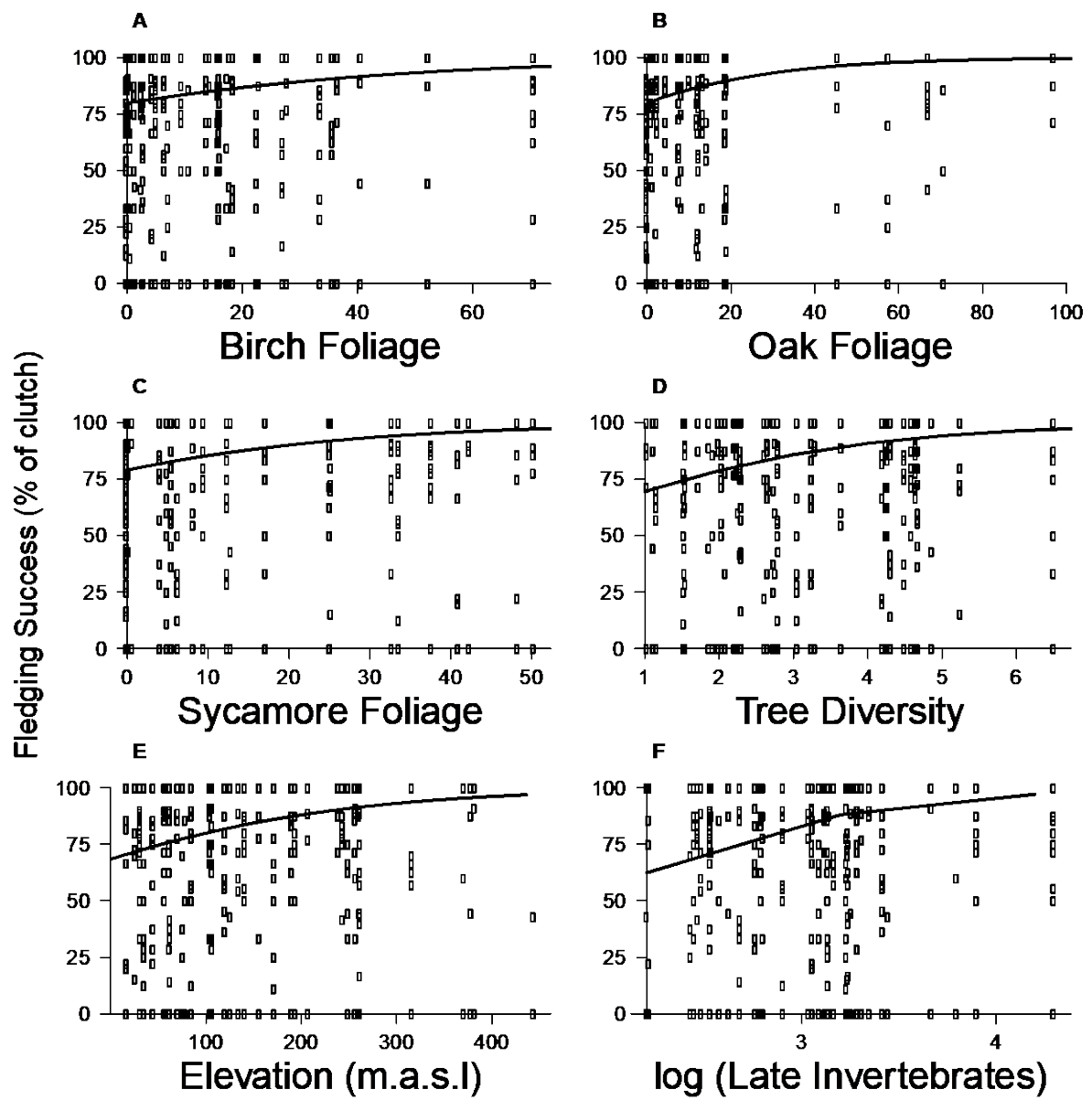


Fig A1.

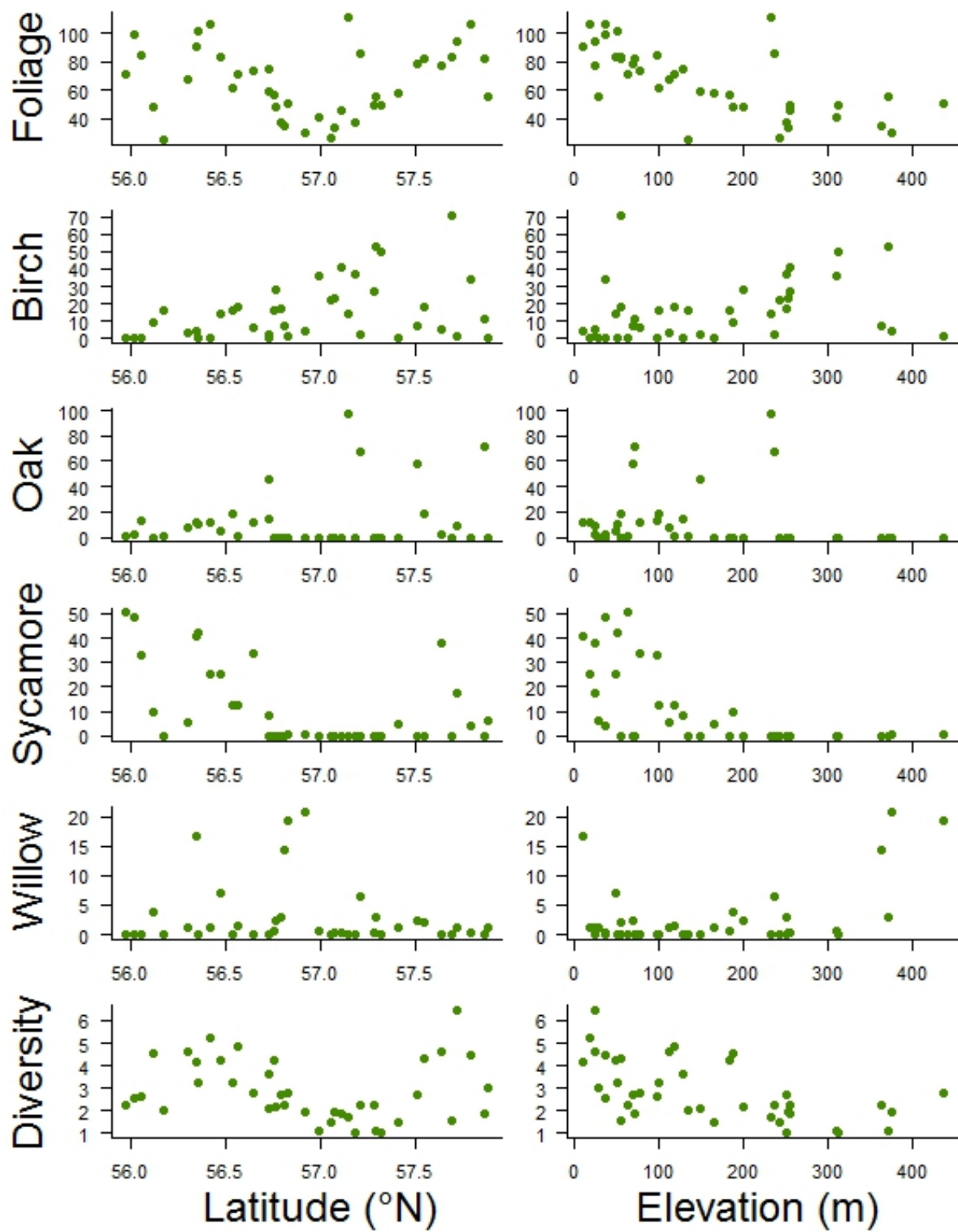


Fig. A2

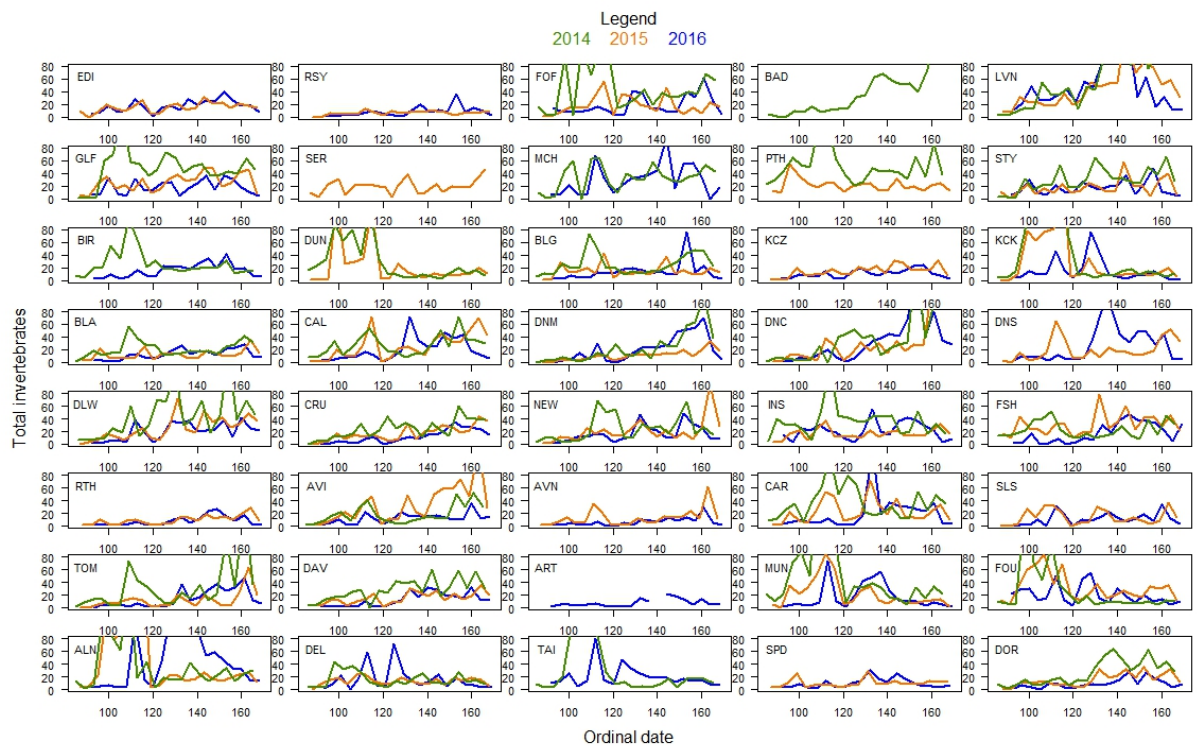


Fig. A3

