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

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Abstract

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

Introduction

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

Previous work examining the effect of breeding habitat on tit productivity has typically considered variation among territories at a single site (Perrins 1979, Wilkin et al. 2009, Amininasab et al. 2016) or between two or three sites (Blondel et al. 1991, Tremblay et al. 2003, Marciniak et al. 2007). For the two most frequently studied tit species, great tit (*Parus* *major*) and blue tit (*Cyanistes caeruleus*), differences among major woodland types are widely documented, with clutch sizes and fledgling numbers approximately one third larger in deciduous compared with coniferous (Gibb and Betts 1963, Perrins 1965, Van Balen 1973) or sclerophyllous (Blondel et al. 1993, Lambrechts et al. 1997) woodlands. Breeding densities show a similar pattern, being several times higher in deciduous woodland (Cramp and Perrins 1993). However, great tits seem more able to produce two successful clutches in coniferous woodland than deciduous (Van Balen 1973), whist in blue tits second clutches are rare (Gibb and Betts 1963, Perrins 1979).

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

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

Food availability is one component of the biotic environment that may have profound impacts on geographic variation in species occurrence and productivity. Tits are mainly insectivorous during the breeding season (Betts 1955, Cholewa and Wesołowski 2011), and whilst they have been shown to rely heavily on an ephemeral peak in caterpillar abundance (Feeny 1970, van Dongen et al. 1997, Southwood et al. 2004) for provisioning of nestlings (Visser et al. 1998, Charmantier et al. 2008), at other times during the spring adult birds prey upon a broad range of additional taxa that includes flying invertebrates such as *Hemiptera*, *Diptera* and *Hymenoptera* (Betts 1955, Cowie and Hinsley 1988). Woodland invertebrate diversity and abundance varies considerably between tree species (Southwood et al. 1982, Kennedy and Southwood 1984). Given that different invertebrate taxa vary in their phenology (Niemela and Haukioja 1982, Southwood et al. 2004), the abundance and temporal availability of prey may vary in space (Fielding et al. 1999, Smith et al. 2011), which could affect productivity (Wilkin et al. 2009) and nest site selection decisions. Indeed, a positive effect of resource availability on productivity has been revealed via supplementary feeding experiments (Nager et al. 1997, Robb et al. 2008), although this effect could be dependent upon the existing natural resource level (Bourgault et al. 2009).

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

Methods

Transect study design

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

The study was carried out during the springs of 2014-16, with different sites studied intensively in different years (supplementary material Table A1) and intensive study of 24 sites across all three years of the study, 14 sites across two years and two sites for a single year. Intensively studied field sites were visited every other day throughout the field season (mid-March to late-June) and we monitored alternate sites on each day where possible. Sites with installed nestboxes that were not intensively studied in 2015 and 2016 (those un-ticked in these years in supplementary material Table A1) were omitted from intensive study due to access complications but were visited at least four times during the field season to collect data on blue tit occupancy, clutch size and fledging success. All dates used in this study, unless explicitly indicated otherwise, are ordinal dates counted from January 1st, meaning that April 1st is day 91 in most years and 92 in a leap year.

Habitat

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

At some sites there were few trunks that qualified under our definition of a tree, but there were stands of shrub cover (e.g., Hazel *Corylus avellana* and Willow *Salix sp.*) that provided feeding habitat. To accommodate this we constructed three 'stand' classes. (1) Stand6-20: where 6-20 separate branches emanated from within 20cm of the base of the shrub stand; (2) stand21+: where >20 branches split; (3) When the shrub stand was too impenetrable to count the stems for a stand score, we measured the length and width of the thicket to create a rectangle full of thicket, and estimated the maximum height of the thicket. While converting these stand scores to the foliage provided by a number of trees will only be very approximate, based on visual inspection we used the following equivalences: stand6-20 = 0.5 small trees, stand21+ = 1 small tree and thicket volume x1/30 = n small trees.

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

We characterised variation in woodland habitat based on five measures of the amount of foliage (total, birch, oak, sycamore, willow) and one measure of tree diversity. Foliage scores were calculated at the site level as the mean of the nestbox scores. Our motivation for focussing on these four tree species is that birch, oak and sycamore were the three most common focal tree taxa by foliage score along the transect (Table 1), and, along with willow, constitute the dominant species at the majority of sites (Fig 2, supplementary material Table A1). Total foliage provides a metric for the total foraging resource available to blue tits and is in effect the product of woodland density and maturity, accounting for increases in trees in general of species not included in models individually. Tree diversity was quantified as Simpson's diversity index at the site level across all genera (i.e. ‘other deciduous’ and ‘conifers’ categories were split into their constituent genera (Table 1)) via the R package ‘vegan’ (Oksanen et al. 2012). We included this variable as greater tree diversity may be correlated with greater prey diversity and abundance (Southwood et al. 1982, Fuentes-Montemayor et al. 2012) and/or increase the temporal spread of prey availability (Kennedy and Southwood 1984). Across sites the pairwise correlations among habitat variables was < 0.52, implying that co-linearity should not present a problem in our analyses.

Invertebrates

To monitor (mostly flying) invertebrates we installed 2 x 245 x 100mm double-sided yellow sticky traps at c.1.75m above the ground on two randomly selected trees at each intensively studied site, with the same trees, and when possible branches, used each year. Each sticky trap had a protective cage constructed from 25 x 12mm wire mesh that slotted over it to prevent bird and bat mortalities. Every four days each sticky trap was collected and replaced. Sticky trap use was for the period 22/23 March – 14/15 June 2014, 24/25 March – 16/17 June 2015 and 28/29 March – 16/17 June 2016. One observer (JDS) counted all invertebrates over 3mm in length (n=98772) collected by the traps (both sides) and assigned each to at least order level, with *Hemiptera*, *Diptera* and *Hymenoptera* the most frequent and known to contribute substantially to blue tit diet (Betts 1955, Cowie and Hinsley 1988).. To quantify repeatability 58 sticky traps were randomly sampled and counted for a second time (26 from 2014, 16 each from 2015 and 2016). Repeatability of total invertebrates on a given sticky trap was then estimated using a generalised linear mixed model (GLMM) (Bates et al. 2015) with Poisson error structure containing year as a fixed effect and site, date, sticky trap ID, sticky trap ID date and residual error as random effects. Regardless of whether repeatability on the latent scale was estimated at the site and date level (i.e. sticky trap ID in the numerator) or transect level (i.e. site, date and sticky trap ID in the numerator), the estimate was > 99%. We subdivided the invertebrate dataset into two roughly equal time periods to partially take into account the major phenological changes in invertebrate abundance over the course of spring. The early time period contained all sticky traps collected from 26th March – 4th May, whilst the late time period constituted those collected from 5th May – 17th June in each year. Site level predictions (ln-scale) for total invertebrate availability in early spring and late spring were estimated using Poisson GLMM's in the MCMCglmm package (Hadfield 2010) that included site as a fixed effect and sticky trap ID, year and sampling date as random effects.

Birds

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

Statistical Analyses

All analyses were conducted in R version 3.1.1 (R Core Team 2014). We used spatial GLMMs to study the effects of habitat, biogeography and invertebrate availability on blue tit occupancy (proportion of available nestboxes at a site that were occupied by blue tits), clutch size and fledging success (proportion of a clutch that fledged). Our motivation for focussing on clutch size and fledging success (rather than total fledglings) is that it allows us to examine the effects of drivers on these two largely independent components of productivity (with total fledglings the product of the two). However, we also considered a model with total fledglings, presented in the supplementary material. Spatial GLMM's were constructed via the spaMM package (Rousset and Ferdy 2014), which treats spatial correlation among sites as random effects and we assumed that spatial autocorrelation among sites declines exponentially with distance by fixing nu at 0.5. Occupancy and fledging success were modelled with binomial family errors, and clutch size and total fledglings were log-transformed and modelled with Gaussian family errors. We excluded from analyses nestboxes occupied by coal tits (*Periparus ater*, one in each of 2015 and 2016) and stolen or unavailable nestboxes (two in 2015, one in 2016). Models included habitat variables, latitude, elevation and year as fixed effects. It was possible to include latitude and spatial autocorrelation in the same model as the former describes a linear trend, whereas the latter allows for the correlation to decay with distance over an estimated range in two dimensions. We also included site level predictions of early season total invertebrates in the occupancy and clutch size models and late season total invertebrates in the fledging success and total fledglings models. Nestbox ID was included as a random term in all models.

Nestbox provision can result in blue tit breeding densities that are double natural levels (Dhondt et al. 1992) and blue tits preferentially select territories with few neighbours (Serrano-Davies et al. 2017). For the occupancy model we tested whether nestboxes led to an increase in blue tit density, by including a two-level factor distinguishing first versus subsequent seasons. Breeding density has been shown to reduce clutch size and fledging success in tit populations across different habitats (Both 1998, Wilkin et al. 2006, Dhondt 2010, Sæther et al. 2016) and to accommodate such an effect we included blue tit density as the proportion of operational nestboxes occupied at a site in the clutch size, fledging success and total fledglings models.

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

To evaluate the importance of spatial autocorrelation in each model, we fixed rho = 10000 to simulate negligible autocorrelation and then compared with a likelihood ratio test to the full model. To test the sensitivity of our results to our use of habitat stand scores, these data were excluded and models were re-run and parameter estimates compared. Finally, to contextualise the amount of spatial variance explained by (i) all habitat variables, (ii) the two biogeographic variables and (iii) invertebrate resource availability, each of these predictor blocks were independently removed from the full model and the spatial variance compared with both the full model and a null model that contained only year as a fixed effect and the random and spatial autocorrelation terms.

Results

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

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

Occupancy was not significantly predicted by habitat in general, or by any individual habitat variable (Table 2A). Instead there was support for biogeographic variables, with occupancy decreasing with latitude, such that holding other predictors constant (for the year 2014 and with all other variables at their means – we took the same approach with all other predictions that we report below), 70% of nestboxes were predicted to be occupied in the far south of the transect declining to 33% in the far north (Fig 3A). Elevation was also a significant predictor of occupancy, and the probability of occupancy decreased from 79% at sea level to just 13% at the highest elevation (Fig 3B). In a *post-hoc* test, described in the supplementary material, we found no evidence that the effects of latitude or elevation were simply acting as a proxy for the multi-year spring average temperatures at each site (supplementary material Table A3). The environmental availability of invertebrates early in the spring, whether the nestbox was in its first available year or a subsequent year, and year, were all non-significant predictors.

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

Fledging success, unlike occupancy and clutch size, was predicted by several habitat variables (Table 2C, Fig 4). Amongst the individual habitat variables, birch, oak, sycamore and increasing tree diversity all predicted a significant increase in the proportion of eggs that survived to fledging. Where oak foliage was at the highest levels found on the transect it predicted fledging rates of 100%, whilst zero oak predicted 80%. The equivalent figures for sycamore and birch were very similar at 97%, 80%, 96% and 79% respectively. Fledging success also increased with tree diversity, with predicted success of 97% at the highest levels of tree diversity on the transect, versus 71% at the lowest. Of the six habitat variables considered, the coefficients for five of these switched sign between the fledgling success and clutch size model. Providing further evidence that site level habitat indices are important predictors of fledging success, when we removed all habitat variables from the full model the spatial variance increased considerably and much more than when biogeographic variables or food availability were removed (Table 2). These effects of habitat on fledging success are not dominated by year effects, being in the same direction each year (supplementary material Table A2A-C). In addition to habitat, the availability of late spring flying invertebrates also predicted increased fledging success (from 62% to 97%). Fledging success also increased significantly with increasing elevation, with predictions ranging from 68% to 97% from the lowest to highest elevations, though the latitudinal trend was very shallow and non-significant. Year had a substantial effect on fledging success, with predicted fledging success of 86%, 49% and 73% in 2014, 2015 and 2016, respectively. We found no evidence that blue tit density had any effect on fledging success within the parameters of this study. Quantitatively, the results for the total number of fledglings were congruent to those described here for fledging success, with all coefficients in the same direction and of comparable significance (supplementary material Table A2D).

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

Discussion

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

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

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

In contrast to fledging success, the other component of productivity that we studied, clutch size, was not significantly predicted by habitat, or any individual habitat variables, with the exception of a slight positive effect of willow availability. The apparent lack of variation in clutch sizes across habitats is consistent with earlier work comparing plots within a site (Dhondt et al. 1990) and may imply that high rates of gene flow among habitats prevents local adaptation (Postma and Van Noordwijk 2005). One possibility is that clutch size is adapted to the dominant, or most productive habitat in the wider landscape, as earlier work on blue tit clutch sizes has found (Blondel et al. 1993, Dias and Blondel 1996), making clutch size less sensitive than fledging success to habitat variation (Arriero et al. 2006). We also found that many variables had an opposite directional effect on the predicted slope for clutch size as they did for productivity; this might be explained by individual females making suboptimal large reproductive investments in early spring in habitats that later prove to be poor. A challenge faced by a female blue tit is that the environment that determines fledgling survival (often termed the environment of selection) is around three weeks after the environment in which the clutch is laid (the environment of development). The ability of a female to predict future conditions and plastically adjust clutch size adaptively will depend on the correlation between the environment of development and selection (Gavrilets and Scheiner 1993) and this correlation may vary among habitats. For example, habitats with a high quality resource early in the breeding season differ from those that provide a high quality resource late in the breeding season. One explanation for this phenomenon is tree phenology, where early leafing trees and habitats may support higher prey abundances early in the season whilst food peaks tail off later on, with late leafing trees, or trees with full-season growth (Niemela and Haukioja 1982), having the opposite tendency. Such temporal asynchronicity in invertebrate abundances across tree species (Southwood et al. 2004, Veen et al. 2010) could help explain why increasing tree diversity elevates eventual productivity, providing a suitable environment for the entirety of the breeding season through the diversity of leafing times maintaining a more sustained and reliable temporal availability of prey.

Whilst blue tits did not seem to predict high quality local habitats within a year, clutch size and fledging success varied substantially among years with coincident trends based on three years of data. If clutch size and fledging success are genuinely positively correlated, this is consistent with high quality versus low quality years being a major source of variation in reproductive success within this system (Perrins 1979, Tremblay et al. 2003). A positive correlation would also imply that birds are more able to predict the relative quality of a breeding season than they are able to predict the future effects of different habitats. Indeed, previous studies have shown among year correlations between clutch size and caterpillar abundance, with the latter providing a proxy for the quality of the year for blue tit reproduction (Perrins 1965, 1991, Marciniak et al. 2007). That we found no evidence of a latitudinal gradient in clutch size at this scale agreed with previous studies (Fargallo 2004, Evans et al. 2009).

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

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

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

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 ≤0.05 * ≤0.01 ** ≤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.

		A. Occupancy	B. Clutch Size	C. Fledging success	
Fixed Term		**coefficient ± se**	**coefficient ± se**	**coefficient ± se**	
Intercept		0.090 ± 0.228	2.14 ± 0.03	1.78 ± 0.16	
Total Foliage		0.0054 ± 0.0159	0.00069 ± 0.00108	-0.00027 ± 0.01059	
Birch		-0.0039 ± 0.0166	-0.00065 ± 0.00123	**0.025 ± 0.011 ***	
Oak		0.0029 ± 0.0145	-0.00041 ± 0.00105	**0.041 ± 0.010 *****	***
Sycamore		0.013 ± 0.024	0.00092 ± 0.00155	**0.044 ± 0.016 ****	
Willow		0.0096 ± 0.0454	**0.011 ± 0.003 ****	-0.056 ± 0.030	
Tree Diversity		0.051 ± 0.218	-0.024 ± 0.015	**0.49 ± 0.15 ****	
Latitude		**$-7.3\times10^{-6} \pm 3.6\times10^{-6}$ ***	$-3.9\times10^{-7} \pm 2.5\times10^{-7}$	$2.7\times10^{-6} \pm 2.7\times10^{-6}$	
Elevation		**-0.0073 ± 0.0029 ***	$-6.6\times10^{-6} \pm 2.4\times10^{-4}$	**0.0061 ± 0.0021 ****	
Early Invertebrates		-0.25 ± 0.36	-0.020 ± 0.024	-	
Late Invertebrates		-	-	**1.50 ± 0.37 *****	
Subsequent Year		0.12 ± 0.50	-	-	
Blue Tit Density		-	-0.056 ± 0.068	-0.25 ± 0.44	
Year	2015	0.86 ± 0.51	**-0.13 ± 0.03 *****	**-1.84 ± 0.16 *****	
	2016	0.43 ± 0.59	**-0.066 ± 0.033 *****	**-0.80 ± 0.14 *****	
Random Term		**variance**	**variance**	**variance**	
Space		0.6	6.5×10^{-9}	1.4×10^{-9}	
Nestbox ID		0.2	2.1×10^{-4}	2.0	
Spatial Autocorrelation		**parameter**	**parameter**	**parameter**	
nu		0.5	0.5	0.5	
rho		0.0024	0.0038	5.5×10^{-6}	

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 $7x10^{-9}$, - invertebrates $6x10^{-9}$, 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	Munlochy	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.

		A. 2014	**B. 2015**	**C. 2016**	**D. Total Fledglings**
Fixed Term		**coefficient ± se**	**coefficient ± se**	**coefficient ± se**	**coefficient ± se**
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 ***
Random Term		**variance**	**variance**	**variance**	**variance**
Space		3.0x10^{-9}	0.3	2.2x10^{-8}	6.1x10^{-9}
Nestbox ID		3.3	7.1	7.3	0.07
Spatial Autocorrelation		**parameter**	**parameter**	**parameter**	**parameter**
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, χ_1^2 = 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.

		Occupancy
Fixed Term		**coefficient ± se**
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		$-8.5\text{x}10^{-6}$ ± $3.8\text{x}10^{-6}$
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
Random Term		**variance**
Space		0.6
Nestbox ID		0.2
Spatial Autocorrelation		**parameter**
nu		0.5
rho		0.0022

Figure 1

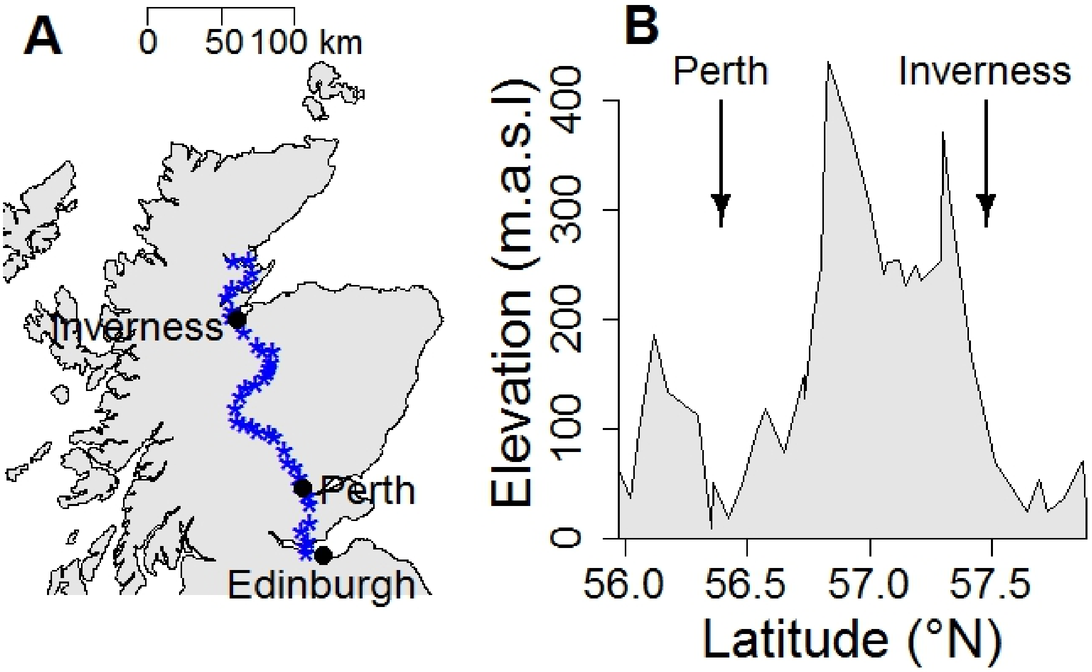

A
0
50
100 km
Inverness
Perth
Edinburgh
B
Perth
Inverness
Elevation (m.a.s.l)
0
100
200
300
400
56.0
56.5
57.0
57.5
Latitude (°N)

Figure 2.

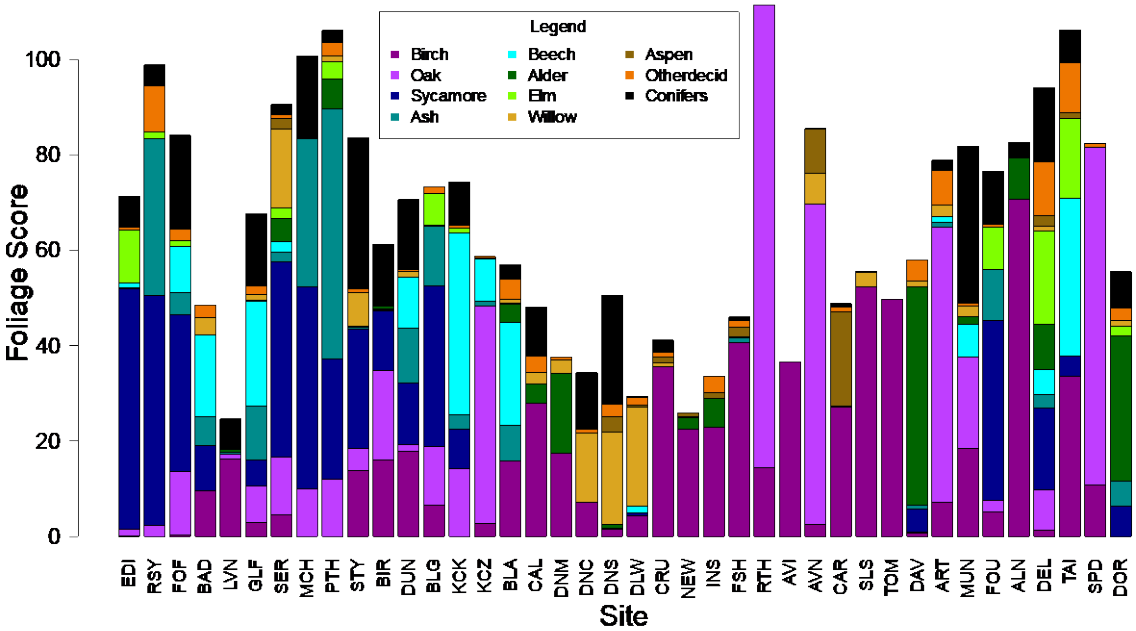

Legend
Birch
Oak
Sycamore
Ash
Beech
Alder
Elm
Willow
Aspen
Otherdecid
Conifers
Foliage Score
0
20
40
60
80
100
Site
EDI
RSY
FOF
BAD
LVN
GLF
SER
MCH
PTH
STY
BIR
DUN
BLG
KCK
KCZ
BLA
CAL
DNM
DNC
DNS
DLW
CRU
NEW
INS
FSH
RTH
AVI
AVN
CAR
SLS
TOM
DAV
ART
MUN
FOU
ALN
DEL
TAI
SPD
DOR

Figure 3.

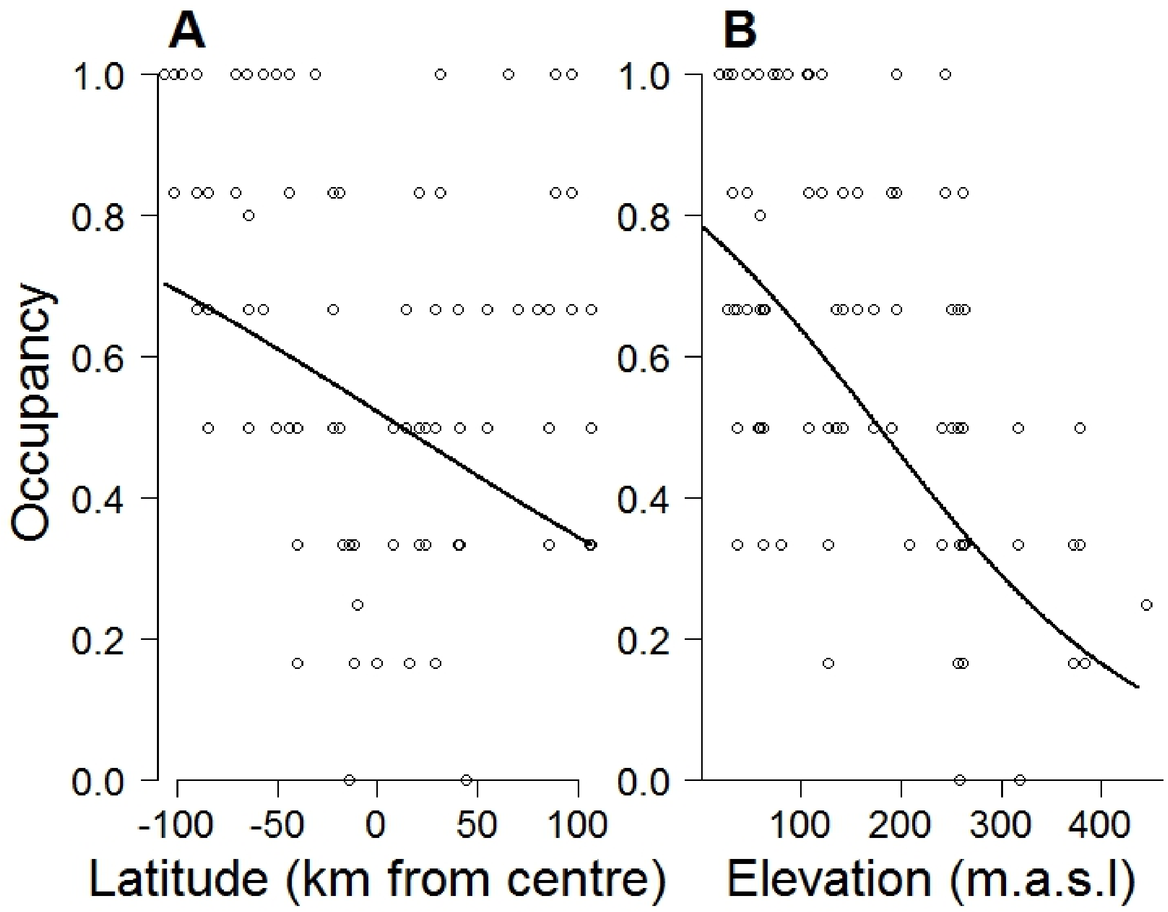
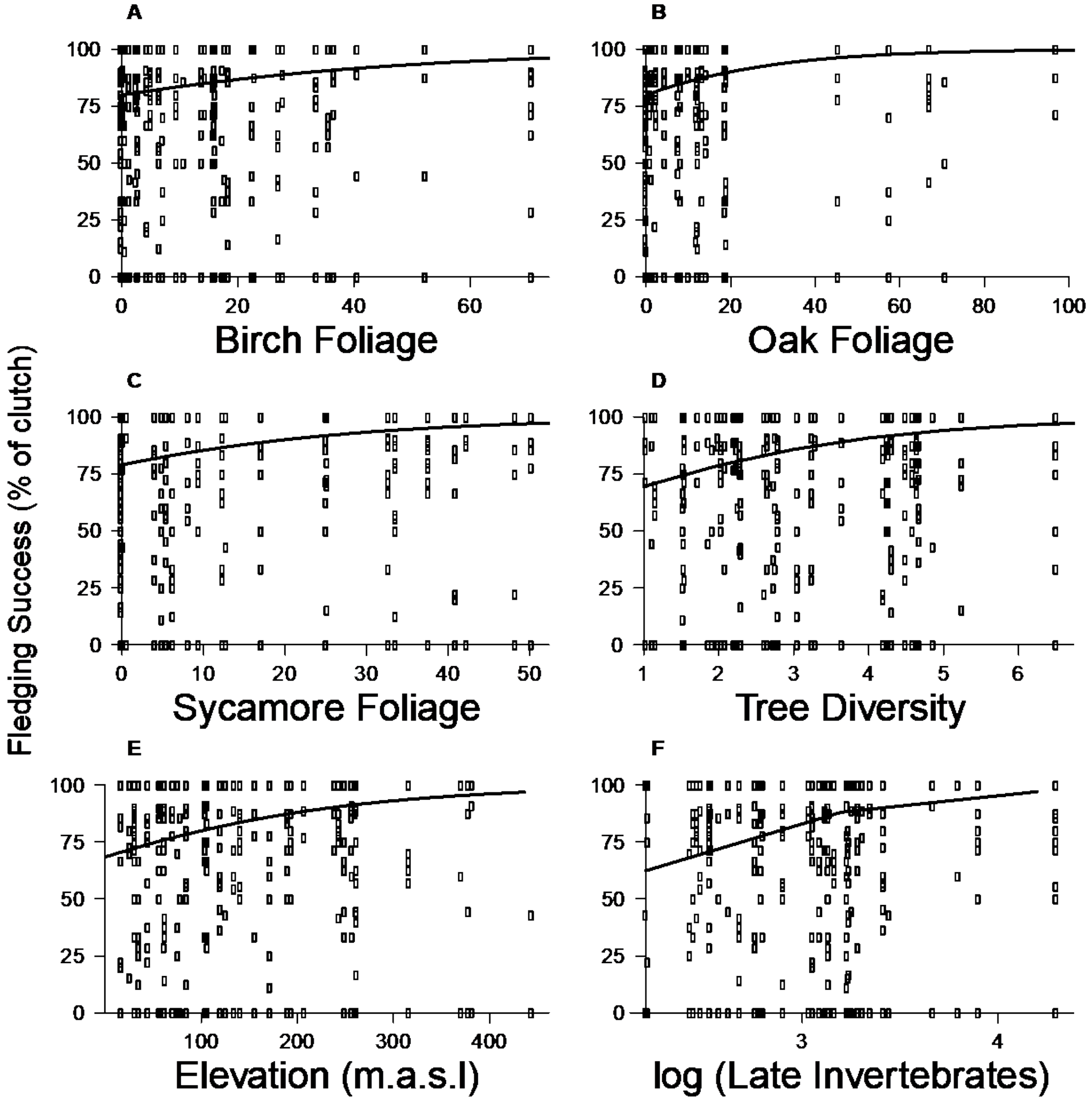

A
B
Occupancy
1.0
0.8
0.6
0.4
0.2
0.0
-100
-50
0
50
100
Latitude (km from centre)
100
200
300
400
Elevation (m.a.s.l)

Figure 4.



A
B
C
D
E
F
Fledging Success (% of clutch)
0
25
50
75
100
0
20
40
60
Birch Foliage
0
20
40
60
80
100
Oak Foliage
0
10
20
30
40
50
Sycamore Foliage
1
2
3
4
5
6
Tree Diversity
100
200
300
400
Elevation (m.a.s.l)
3
4
log (Late Invertebrates)

Fig A1.

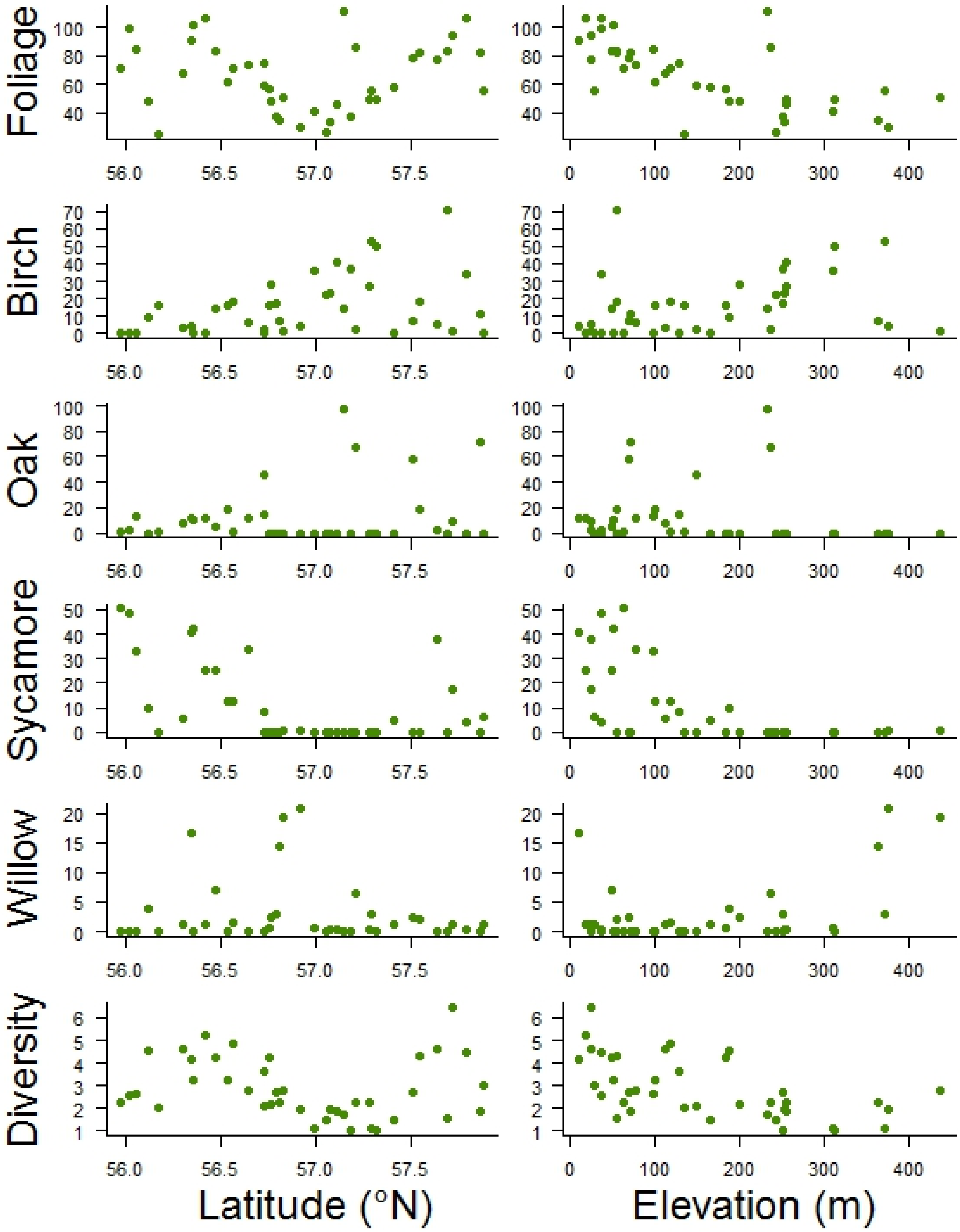

Foliage
Birch
Oak
Sycamore
Willow
Diversity
100
80
60
40
70
60
50
30
20
10
0
15
5
6
4
3
2
1
56.0
56.5
57.0
57.5
0
100
200
300
400
Latitude (°N)
Elevation (m)

Fig. A2

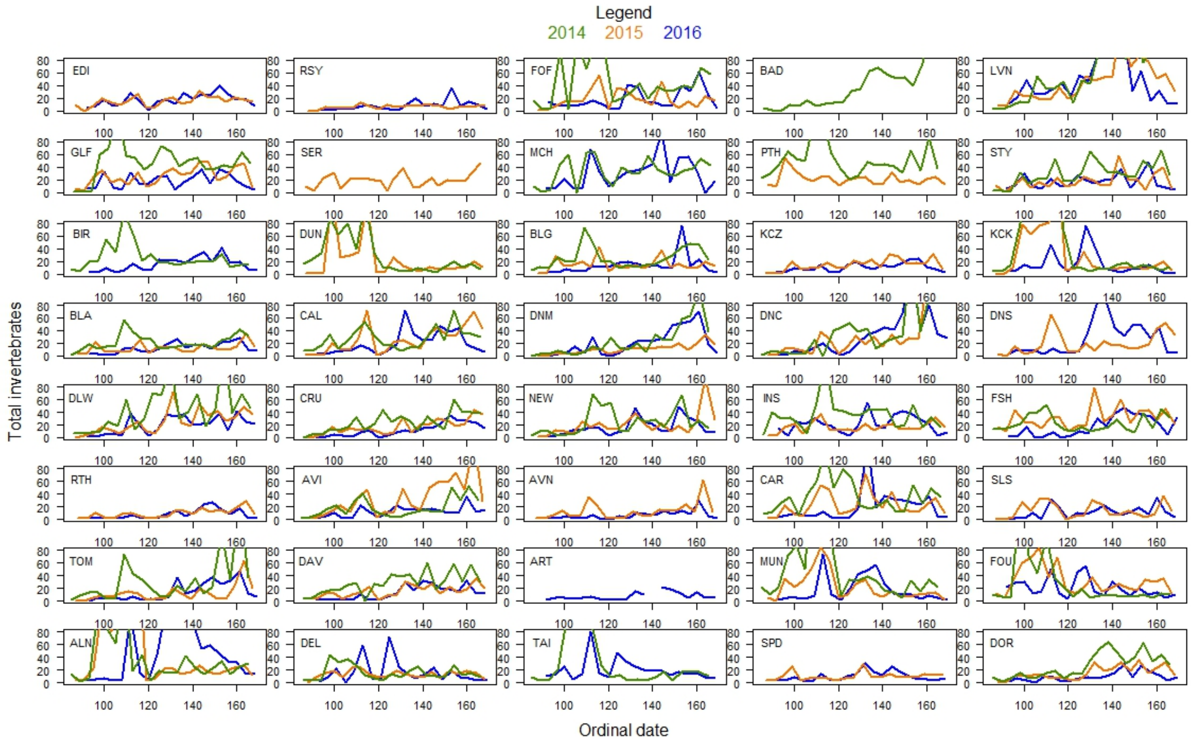
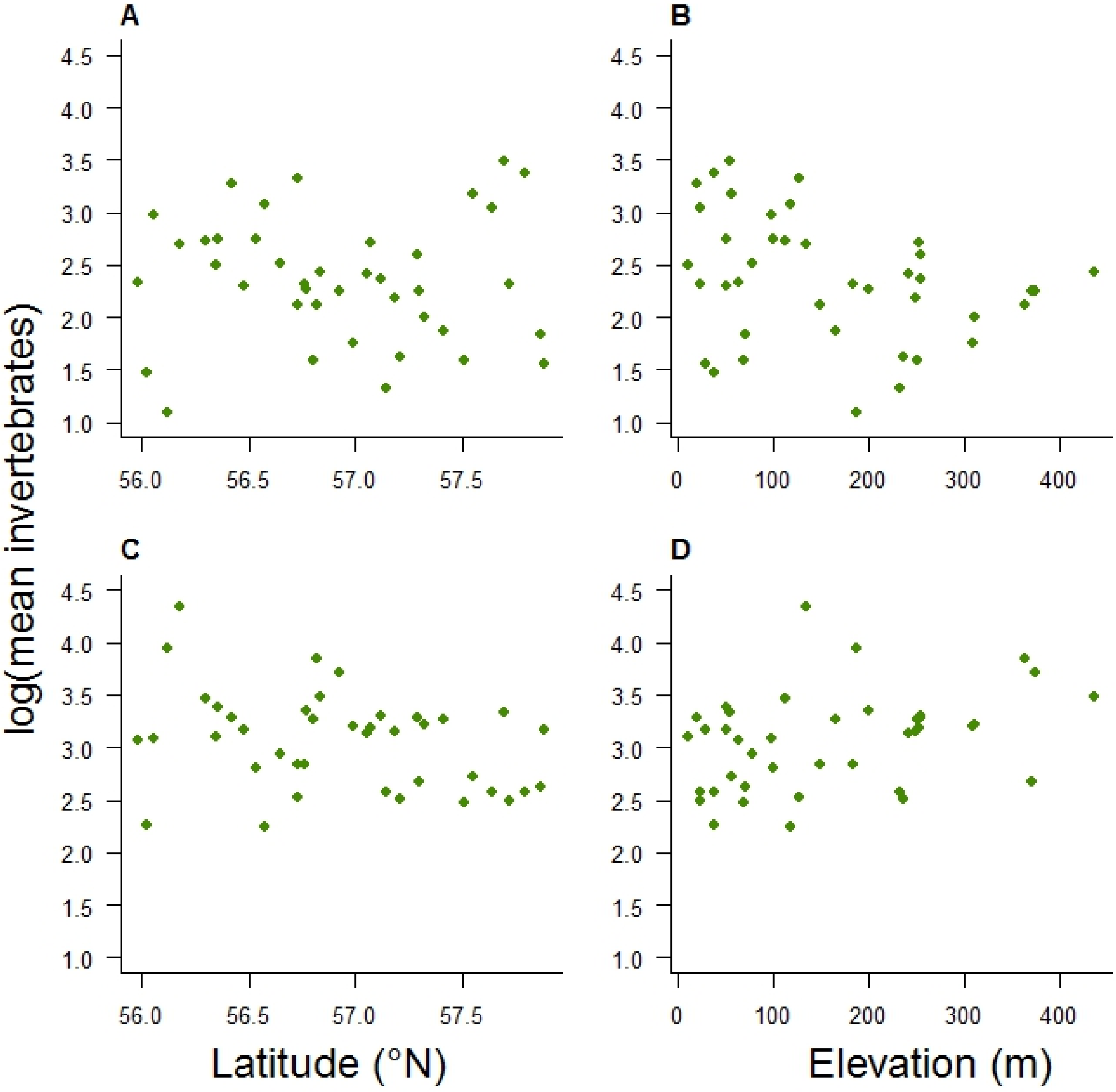

Legend
2014
2015
2016
EDI
RSY
FOF
BAD
LVN
GLF
SER
MCH
PTH
STY
BIR
DUN
BLG
KCZ
KCK
BLA
CAL
DNM
DNC
DNS
DLW
CRU
NEW
INS
FSH
RTH
AVI
AVN
CAR
SLS
TOM
DAV
ART
MUN
FOU
ALN
DEL
TAI
SPD
DOR
0
20
40
60
80
100
120
140
160
Total invertebrates
Ordinal date

Fig. A3


A
B
C
D
log(mean invertebrates)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
56.0
56.5
57.0
57.5
0
100
200
300
400
Latitude (°N)
Elevation (m)