



Microclimate predicts within-season distribution dynamics of montane forest birds

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ABSTRACT

Aim Climate changes are anticipated to have pervasive negative effects on biodiversity and are expected to necessitate widespread range shifts or contractions. Such projections are based upon the assumptions that (1) species respond primarily to broad-scale climatic regimes, or (2) that variation in climate at fine spatial scales is less relevant at coarse spatial scales. However, in montane forest landscapes, high degrees of microclimate variability could influence occupancy dynamics and distributions of forest species. Using high-resolution bird survey and under-canopy air temperature data, we tested the hypothesis that the high vagility of most forest bird species combined with the heterogeneous thermal regime of mountain landscapes would enable them to adjust initial settlement decisions to track their thermal niches.

Location Western Cascade Mountains, Oregon, USA.

Methods We used dynamic occupancy models to test the degree to which microclimate affects the distribution patterns of forest birds in a heterogeneous mountain environment. In all models we statistically accounted for vegetation structure, vegetation composition and potential biases due to imperfect detection of birds. We generated spatial predictions of forest bird distributions in relation to microclimate and vegetation structure.

Results Fine-scale temperature metrics were strong predictors of bird distributions; effects of temperature on within-season occupancy dynamics were as large or larger (1–1.7 times) than vegetation effects. Most species (86.7%) exhibited apparent within-season occupancy dynamics. However, species were almost as likely to be warm associated (i.e., apparent settlement at warmer sites and/or vacancy at cooler sites; 53.3% of species) as cool associated (i.e., apparent settlement at cooler sites and/or vacancy at warmer sites; 46.7% of species), suggesting that microclimate preferences are species specific.

Main conclusions High-resolution temperature data increase the quality of predictions about avian distribution dynamics and should be included in efforts to project future distributions. We hypothesize that microclimate-associated distribution patterns may reflect species' potential for behavioural buffering from climate change in montane forest environments.

Keywords

dynamic occupancy models, forest bird distributions, forest structure and composition, microclimate, mountains, within-season movements.

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INTRODUCTION

Climate change is already exerting a strong influence on species range shifts and population trends (Parmesan & Yohe,

2003; Both *et al.*, 2006; Hitch & Leberg, 2007; Devictor *et al.*, 2008; Gutiérrez Illán *et al.*, 2014). Climate change has also been implicated in inconsistent phenological changes across taxa resulting in the decoupling of trophic interactions (Both

& Visser, 2005). Given that such deviations are expected to amplify over the coming century (IPCC, 2014), a key question is the degree to which biodiversity will be affected as a result (Thomas *et al.*, 2004).

Making reliable predictions about species' responses to climate change has been challenging because responses have not been uniform; empirical studies using historical datasets have revealed high among-species variation in the degree to which populations and species distributions respond over time (Tingley *et al.*, 2012; Gutiérrez Illán *et al.*, 2014). Although some species demonstrate range shifting in response to climate change (Tingley & Beissinger, 2009; Virkкала *et al.*, 2014), many species have not extended their ranges to occupy the geographic extent of apparently 'suitable' climates, either historically (Araújo & Pearson, 2005; Moritz & Agudo, 2013) or during recent rapid climate change (Thuiller *et al.*, 2004b). Although some of this variation in species responses is associated with life-history traits (Sheldon *et al.*, 2011), much variation remains unexplained.

One hypothesis for this mismatch between climate envelope predictions and observed responses to change is that climate data used to define suitable envelopes are collected at resolutions much coarser than those perceived and used by organisms in habitat selection (Pearson & Dawson, 2003; Logan *et al.*, 2013; Storlie *et al.*, 2014). Most temperature data are collected at scales 10^4 -fold larger than the territory sizes of focal organisms (Potter *et al.*, 2013), and there is high potential for hidden microclimate variation within broader regional patterns (Franklin *et al.*, 2013). Climate is assumed to be mainly a driver of distribution patterns at broad spatial scales (Thuiller *et al.*, 2004a; Boucher-Lalonde *et al.*, 2014) although habitat characteristics such as vegetation structure and composition are thought to overwhelm the importance of climate at finer spatial scales (Brown, 1995; Luoto *et al.*, 2007). Therefore, this hidden microclimatic variation and its potential to affect distribution dynamics are often overlooked (Huey *et al.*, 2012; Cumming *et al.*, 2014). Additionally, lack of high-resolution climate data, particularly under-canopy temperatures (Scherrer *et al.*, 2011), has prohibited effective testing of the role of microclimate in fine-scale distribution dynamics.

Environmental heterogeneity offers a range of resources and microclimates that can provide options for 'microrefugia' where an organism can persist in the face of regional warming (Keppel *et al.*, 2012; Patsiou *et al.*, 2013). In addition, microclimate variability at fine spatial scales could provide options for short-distance, adaptive movements and resource tracking within a season (Karr & Freemark, 1983; Dobrowski, 2010). Animals may adjust their use of local habitat in ways that allow them to persist in the face of climate change without necessitating broad-scale range shifts (Kearney *et al.*, 2009). Landscapes with little climatic variability provide fewer possibilities for new behaviour (Bonebrake *et al.*, 2014) such as shifts in habitat or diet.

Direct tracking of individual behaviour to examine within-season movements (e.g., Gow & Stutchbury, 2013) is

logistically challenging, particularly when considering more than a single species. However, dynamic occupancy modelling offers a viable alternative for quantifying within-season distribution changes (MacKenzie *et al.*, 2003). These models allow changes in colonization and extinction processes across a season and have been shown to outperform static occupancy models for many species (McClure & Hill, 2012). Recent work has demonstrated that within-season movements by birds may actually be relatively common (McClure & Hill, 2012; Gow & Stutchbury, 2013), which violates the assumptions of commonly used species' occupancy models (Rota *et al.*, 2009) and necessitates the application of dynamic models. Within-season movements appear to reflect shifts to higher quality sites (Betts *et al.*, 2008; Gilroy *et al.*, 2010) and often represent shifts upwards along elevational gradients (Brambilla & Rubolini, 2009). Given that site quality may change over the breeding season as temperatures warm (Vatka *et al.*, 2011), being sufficiently flexible to take advantage of new favourable microclimates should be adaptive and allow birds to track their thermal niches across space and time. Within-season occupancy dynamics are thought to represent a combination of two important processes: (1) true settlement and vacancy (i.e., birds settling in or shifting away from territories) and (2) temporary immigration/emigration in and out of sampling locations due to the combination of (1) variation in territory density and (2) territories not always falling completely within the sampling radius (Chandler *et al.*, 2011). As both of these processes result from movement at either fine or broad spatial scales due to variation in habitat suitability (i.e., settlement, disproportionate within-territory use, and higher territory densities should all be associated with favoured sites), it is possible to use a dynamic occupancy framework to examine habitat suitability for multiple species across a landscape.

In both 2012 and 2013, we sampled a forest bird community six times during the breeding season at 183 sites in complex mountainous terrain, resulting in 19,171 bird observations. We collected under-canopy temperature data with sensors located at each of the count sites (Frey *et al.*, 2016). We used dynamic occupancy modelling to test the relative roles of fine-scale temperatures and vegetation characteristics on within-season distribution dynamics while accounting for imperfect detection. We hypothesized that high vagility of most forest bird species, combined with the heterogeneous thermal regime of mountain landscapes, would enable within-season distribution dynamics such that birds can track their thermal niches.

METHODS

Study design

We collected bird occurrence data at 183 sample locations within the H. J. Andrews Experimental Forest (HJA). The 6400-ha HJA spans an elevational gradient from 410 to 1630 m.a.s.l. and is located in the western Cascades of Oregon,

USA (44°12' N, 122°15' W, Fig. S2a). It is a forest mosaic comprising a mix of old-growth forest, mature forests, ~60-year-old Douglas-fir (*Pseudotsuga menziesii*) plantations, alpine meadows, Sitka alder (*Alnus viridis*) or vine maple (*Acer circinatum*) shrub fields, and landslides (Fig. S2b).

We used a stratified, systematic, random design to select sample locations. We stratified across elevation, distance to road and habitat type (plantation or mature/old-growth forest). Distance between all sampling points was ≥ 300 m to avoid double sampling. Sample points were categorized as transect, trail or road. Transect points were selected by placing a systematic grid of points across a portion of the watershed using GIS (ESRI, 2011). We separated each transect by 600 m. We placed trail points randomly along existing and abandoned trails (<1 m wide) at 300-m intervals. To select road points, we first placed points randomly along maintained and abandoned gravel roads at 600-m intervals using Hawth's tools (Beyer, 2004). Then, we chose a random direction and distance from the road into the forest (0, 50, or 100 m) for the final point placement. Our final dataset was comprised of 60 transect points, 68 road points and 55 trail points.

Point counts

We conducted point counts on six separate occasions from 14 May to 9 July in 2012 and from 14 May to 10 July in 2013, which corresponded to spring arrival and subsequent breeding period for the majority of bird species at HJA. Point counts were conducted during favourable weather conditions by trained observers. The mean (SD) length of sample occasions was 5 (1.17) and 6 (1.22) days in 2012 and 2013, respectively. Mean (SD) break length between point count rounds was 4 (1.91) days in 2012 and 5 (1.90) days in

2013. Surveys occurred between 05:15 h and 10:30 h and each consisted of a 10-min point count where we recorded all birds seen or heard within a 100-m radius. Each 10-min point count was divided into three 3-min 20-s subcounts where the point count was reinitiated (see Betts *et al.*, 2008 for methods details). We detected a total of 41 species during May–July 2012 and 2013; however, we did not use data from species with <0.2 prevalence because models in these cases often failed to converge. Thus, we modelled occupancy dynamics of 15 species (Table 1).

Environmental covariates

We placed data loggers (Onset HOBO Pendant Temperature/Light Data Logger 64K, model UA-002-64 [$n = 167$] and Onset HOBO Water Temperature Pro v2 Data Logger, model U22-001 [$n = 16$]) that recorded temperature every 20 min at each sample point. We summarized temperature measurements between January 2012 and December 2013 (see Appendix S1 and Frey *et al.*, 2016 for details on logger placement and data processing). We used five temperature metrics that we expected to influence forest birds during the breeding season and/or alter timing of important phenological events upon which birds depend. These metrics included cumulative degree days (CDD) >0 °C January–March and >10 °C April–June, both of which are expected to be important drivers of bud break and insect abundance (Fu *et al.*, 2012), bird phenology (Both *et al.*, 2005) and bird distributions (Araújo *et al.*, 2005). We included mean monthly temperatures (monthly mean, maximum and minimum) from April to June. Mean maximum and mean minimum monthly temperatures capture temperature extremes and have been used to describe avian distributional boundaries (Root, 1988)

Table 1 Species list for the 15 bird species we examined at the H. J. Andrews Experimental Forest. Prevalence (Prev.) is the number of points for which a species was detected at least once throughout the breeding season out of the total points (183) for each year. Home range values were obtained from the online Birds of North America accounts (Poole, 2005). Thermal preference (pref.) is based on model results (see *Results* section).

Species' common name	Species' scientific name	Species code	Prev. 2012	Prev. 2013	Home range (ha)	Thermal pref.
Brown creeper	<i>Certhia americana</i>	BRCR	0.435	0.495	4.2	Warm
Chestnut-backed chickadee	<i>Poecile rufescens</i>	CBCH	0.913	0.826	1.3	Warm
Golden-crowned kinglet	<i>Regulus satrapa</i>	GCKI	0.674	0.647	1.6	Cool
Hammond's flycatcher	<i>Empidonax hammondi</i>	HAFL	0.386	0.446	1	Warm
Hermit thrush	<i>Catharus guttatus</i>	HETH	0.462	0.527	0.7	Cool
Hermit warbler	<i>Setophaga occidentalis</i>	HEWA	0.875	0.951	0.35	Cool
Oregon junco	<i>Junco hyemalis</i>	ORJU	0.620	0.663	0.38	Cool
Pacific wren	<i>Troglodytes pacificus</i>	PAWR	0.821	0.793	1.38	Warm
Pacific-slope flycatcher	<i>Empidonax difficilis</i>	PSFL	0.761	0.853	2.5	Warm
Red-breasted nuthatch	<i>Sitta canadensis</i>	RBNU	0.511	0.783	1.2	Cool
Steller's jay	<i>Cyanocitta stelleri</i>	STJA	0.630	0.625	80	Warm
Swainson's thrush	<i>Catharus ustulatus</i>	SWTH	0.674	0.723	1	Warm
Varied thrush	<i>Ixoreus naevius</i>	VATH	0.609	0.565	7	Cool
Western tanager	<i>Piranga ludoviciana</i>	WETA	0.277	0.342	2.8	Warm
Wilson's warbler	<i>Cardellina pusilla</i>	WIWA	0.299	0.266	0.3	Cool

and predict abundance trends (Gutiérrez Illán *et al.*, 2014). Mean monthly temperature describes the general temperature conditions at a site and is a common metric in species-climate studies (Virkkala *et al.*, 2008; Stralberg *et al.*, 2009). We chose the months of April, May and June since this is the period when we expected the majority of within-breeding season dynamics to take place.

To describe vegetation structure at each of our sites, we used LiDAR-derived metrics and a principal component analysis (PCA, Appendix S2, Table S1, Frey *et al.*, 2016). We used the first two components in our analysis as they explained 75% of the variability in our structure metrics (PC1 = 45%, PC2 = 30%, Table S2). We quantified forest composition by measuring the proportion of deciduous basal area at a site using variable radius prism plots and counting deciduous trees and large shrubs >2 cm DBH (see Table S3 for species list). We chose deciduous vegetation as our composition variable because it is often associated with abundance of leaf-gleaning forest birds and deciduous plant species are typically thought to support higher abundances of insects (Hagar, 2007; Ellis & Betts, 2011).

Occupancy models

We used dynamic occupancy models (MacKenzie *et al.*, 2003) to estimate within-season distribution dynamics as a function of microclimate conditions in the HJA. These models use detection histories from multiple surveys (i.e., our three subcounts) over multiple seasons (i.e., six site visits) to estimate four parameters: (1) detection probability (p), (2) initial site occupancy (ψ), (3) site colonization (γ) and (4) local-site extinction (ϵ). Occupancy models are hierarchical in that they model the observation process (detection) independent from the ecological processes of interest (site occupancy, colonization and extinction; see Appendix S3 for model structure). For our within-season application of dynamic occupancy models, we refer to colonization as site 'settlement' (γ) and extinction as site 'vacancy' (ϵ). We modelled 2012 and 2013 separately for simplicity in model structure (testing for year effects would result in at least an additional nine model parameters).

The resulting parameter estimates for colonization/extinction stem from the combined processes of true settlement/vacancy (i.e., birds settling in or shifting away from sites) and temporary immigration/emigration in and out of the point count circle. For example, species with larger home ranges may be more likely to move out of a count circle while remaining within their original home ranges. In instances with large home ranges, within-territory/home-range movements could cause the appearance that a territory has become vacant when the bird is actually still within its initial home range (i.e., the territory is counted as vacant when it is not). Similarly, in areas of high density, multiple territories could overlap the count circle and the likelihood of detecting at least one individual within the count circle is higher, purely because more individuals are present.

We addressed the role of temporary within-territory movements in estimates of occupancy dynamics in two ways. First, we used information about the average home range size for each species (Table 1, Poole, 2005) to test whether species with larger home ranges show higher levels of within-season dynamics. Higher levels of dynamics for species with larger home ranges would suggest artificially high apparent settlement and vacancy rates due simply to within-home range movements (Betts *et al.*, 2008). Secondly, we used detections within a 100-m radius to increase the likelihood that entire territories were included within the boundaries of the sample plot. The majority of species (12/15) we included in our study have territory sizes that are smaller than our sample plot (Table 1, area of 100-m radius point count circle = 3.14 ha).

Model selection

We selected survey- and site-level covariates we expected to be important in our system *a priori* (see *Environmental covariates* above). In order to reduce our model set, we used a manual forward stepwise approach to select the variables that best explained detection and site occupancy parameters (Chandler & King, 2011). All continuous predictor variables were standardized (z-transformed) to enable comparison of effect sizes. We compared support for models containing different covariates using AIC (Burnham & Anderson, 2002).

The objective of the model selection process was to select the best temperature metric for each parameter while also including important vegetation variables. Our model selection steps for each parameter were as follows: (1) We first ranked univariate models for each of the covariates using AIC. (2) We then constructed additive models including covariates in order of their AIC ranking (highest to lowest). We added variables in order of support until additional covariates resulted in the model being >2 Δ AIC points below the top model. (3) We selected the most parameterized model within 2 AIC points of the top model (this was often the top-ranked model; i.e., Δ AIC = 0). We combined top-ranked temperature and vegetation metrics in additive models. We did include multiple vegetation variables in the same model when there was support for more than one. However, we never combined multiple temperature metrics in any additive models due to intervariable correlation (Table S4). We chose not to use model averaging because it is not recommended for competing models that contain correlated variables (Cade, 2015).

We tested for differences in detection as a function of eight temperature and vegetation variables and six survey-level variables (i.e., survey time, day of year [days since May 1], observer, stream noise, weather conditions [cloud cover and wind] and a temporal autocovariate). We included temperature metrics as covariates for detection to avoid potentially attributing effects of temperature to changes in distributions when, in actuality, they were due to detectability. Also, a site's thermal regime could influence detection

through higher or lower activity levels of birds (which would in turn affect how easily we detect them) at sites that are generally warmer or cooler. We included a temporal autocovariate because subcounts were temporally autocorrelated. This autocovariate indicated whether an individual was detected in the previous subcount. We then used forward stepwise selection as described above to determine the best detection model.

We compared univariate models of our microclimate and vegetation metrics while holding the other dynamic parameter constant (i.e., vacancy was modelled as the mean across all sites while examining settlement and vice versa). We then combined the top variables for both settlement and vacancy to obtain the final model. We created spatial maps of bird distributions as a function of the temperature and vegetation structure variables using the final models (see Appendix S4 for methods). To determine whether the effects of temperature depended on vegetation and vice versa, we tested for interactions between the most-supported temperature and vegetation variables in the final models. All analyses were conducted in R version 3.1.1 (R Development Core Team, 2011) using the 'unmarked' package (Fiske & Chandler, 2011).

Relative importance of microclimate and vegetation

Once we identified the top models for each of the 15 species in each year, we assessed relative importance of the temperature and vegetation metrics using the effect sizes. To account for differences in precision of effect sizes, we divided these by the corresponding standard errors (Ritchie *et al.*, 2009). When more than one vegetation metric was in the top model, we selected, for comparison, the one with the largest effect size. In the rare instance where none of the metrics were useful in explaining variability in occupancy parameters, we considered the effect size to be zero. We did this for initial occupancy, settlement and vacancy.

Model fit

We used parametric bootstrapping to evaluate the goodness-of-fit of the best model for each species in each year (Kéry & Chandler, 2012). For each species, we simulated 250 datasets from its top model in a given year. Each time we refitted the model to these simulated data, we computed a fit statistic (sum of squares error [SSE]). The simulation resulted in a reference distribution of the fit statistic from which we computed a *P*-value indicating the proportion of the reference distribution that was greater than the observed value. We used χ^2 to compare observed and expected fit statistics because it has been shown to perform well at evaluating goodness-of-fit for logistic regression models (Hosmer *et al.*, 1997; MacKenzie & Bailey, 2004; Kéry & Chandler, 2012). Models with fit statistics that are higher than the mean from the simulated distribution are indicative of overdispersion in the data, meaning that there is still unexplained variability.

Spatial autocorrelation, a common property of ecological data, could potentially be problematic due to violation of sample independence assumptions (Legendre, 1993). Therefore, we tested for spatial autocorrelation in our data by calculating Moran's *I* for the residuals from the top model for each species. Moran's *I* values can range from 0 to 1, and values >0.3 are considered relatively large (Lichstein *et al.*, 2002).

RESULTS

Overall, temperature and vegetation metrics were strong predictors of initial bird distributions (Fig. 1, Table S5). Temperature was the most important predictor (largest effect size) for 80% and 47% of species in 2012 and 2013, respectively. Of the species with temperature as an important predictor (95% confidence interval did not overlap 0) in the top model (Fig. 1), roughly equal numbers were associated with warm sites (53%) versus cooler sites (47%) in both years (Table S5). Vegetation (structure and/or composition) was an important predictor of initial occupancy patterns for a substantial proportion of species in both years (2012: 33%, 2013: 47% of species, Fig. 1, Table S5) and was more important than temperature for 20% and 53% of species in 2012 and 2013, respectively. For most species, detection probability was explained well by survey (temporal autocovariate, time of day, day of year and stream noise; Table S6) and site (temperature and vegetation; Table S7) covariates.

In both years, the majority of species showed mean settlement and vacancy rates >0.1 throughout the breeding season indicating that overall occupancy patterns were dynamic (Table S8; settlement – 80.0% of species in both years;

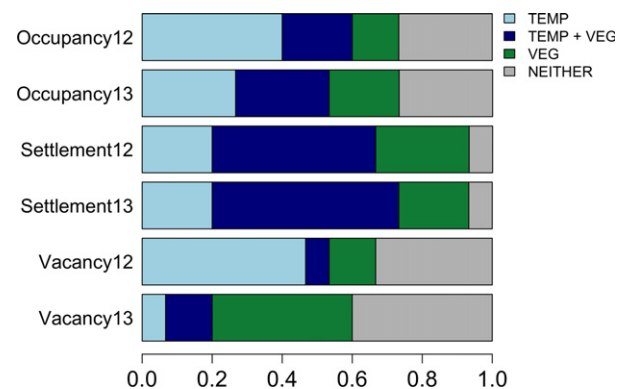


Figure 1 The proportion of species in each year for each of the ecological parameters where the effects of (1) temperature alone (TEMP), (2) both vegetation and temperature (BOTH) or (3) vegetation alone (VEG) were important (95% CIs did not overlap 0) in the top model, or whether (4) neither vegetation nor temperature (TEMP + VEG) was important in the top model. Initial occupancy described the distribution in the first sample session (mid-May). Settlement and vacancy described distribution dynamics between the second and sixth sample sessions (late May until early July).

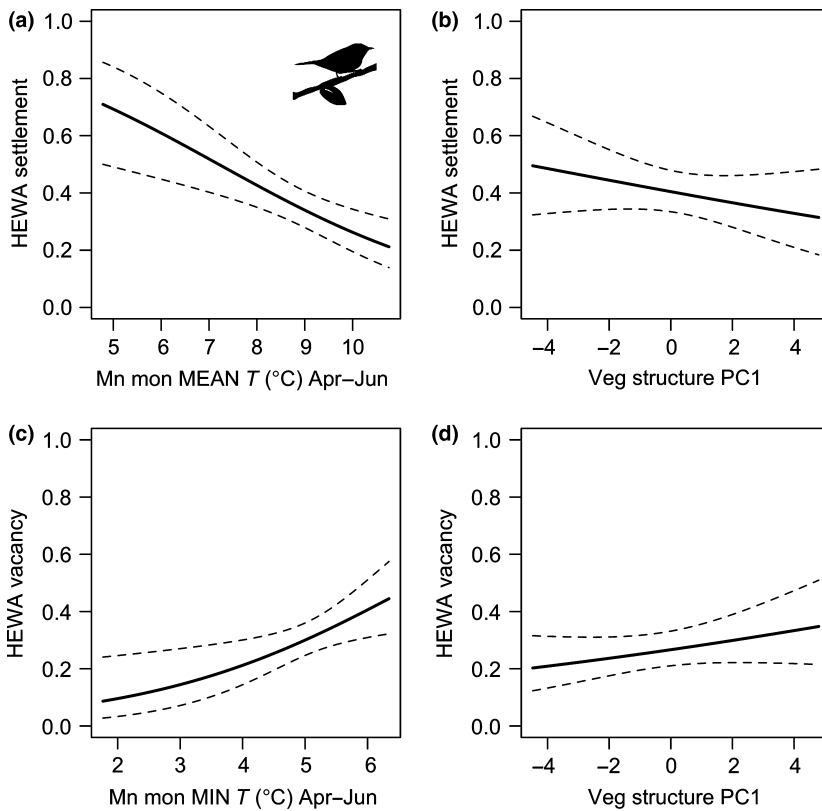


Figure 2 Hermit warbler (*Setophaga occidentalis*, HEWA) is an example of a species where site-level dynamics are largely driven by temperature and vegetation structure to a lesser extent. Hermit warblers were both less likely to settle sites (a) and more likely to vacate sites (c) that were warmer. Vegetation structure was not an important predictor of either vacancy (b) or settlement (d). Mn, mean; mon, monthly; T, temperature; Veg, vegetation; PC, principal component; MIN, minimum.

vacancy – 2012: 86.7%, 2013: 93.3%). On average for all species, mean vacancy probability (mean [SD] – 2012: 0.39 [0.20], 2013: 0.38 [0.21]) tended to be higher than settlement probability (2012: 0.22 [0.14], 2013: 0.22 [0.13]). The mean settlement and vacancy rates are interpreted as the change in occupancy that occurred between each sampling occasion (i.e., between 1 and 2, 2 and 3, etc.), on average, across all sites (not including any covariate effects).

Site-level temperature metrics were strong predictors of the apparent distribution changes we observed, and temperature was equal or more effective (1–1.7 times) than vegetation at predicting local-site occupancy dynamics in both years (Figs. 1–5, Tables 2, 3 and S9). Temperature metrics were the most important predictors (larger effect sizes) for at least one dynamic parameter for 73.3% and 66.7% of species in 2012 and 2013, respectively (see Tables 2 and 3 for coefficients from top models, and see Table S9 for comparison of SE-adjusted effect sizes). Overall, species were almost as likely to be cool associated (i.e., higher apparent settlement at cooler sites and/or vacancy at warmer sites; 53.3% of species, Figs. 2 & 3) as warm associated (i.e., higher apparent settlement at cooler sites and/or vacancy at warmer sites; 46.7% of species; Figs. 4 & 5, Table 1). Preference for cool versus warm sites never switched between years for a species for any of the ecological parameters (Tables 2 and 3, Figs. S3 & S4). However, whether the effects of temperature alone, vegetation alone or both were most important for a given parameter varied within species between years. For species whose apparent settlement patterns were largely temperature

driven, 71.4% (2012) and 62.5% (2013) showed preference for sites with cooler microclimates (Table 2, Fig. S3). For species whose vacancy patterns were driven primarily by temperature, 77.8% (2012) and 55.6% (2013) were those that vacated warmer sites (Table 3, Fig. S4). We found little support for temperature–vegetation interactions (Table S11).

Our goodness-of-fit tests indicated no, or minimal lack of fit due to overdispersion in our models (Table S10). Goodness-of-fit tests for Steller's jay in 2012 and hermit thrush in 2013 suggested slight overdispersion ($P = 0.33$ and 0.11 , respectively). Three species (only in 2012) showed little to no difference between the observed and mean expected fit statistic ($0.25 < P < 0.75$). We did find evidence for underdispersion in our data; the majority of species had fit statistics that were lower than the distribution of bootstrapped values ($P > 0.75$). Underdispersion is generally not considered a problem as it results in inflated standard errors, leading to more conservative estimates of covariate effects (Hosmer *et al.*, 2013). Further, we found no evidence for spatial autocorrelation in the residuals (mean [SD] Moran's I for all species 2012 = -0.002 [0.014], 2013 = 0.001 [0.007]; mean [SD], P -values 2012 = 0.230 [0.046], 2013 = 0.237 [0.031]) indicating that spatial autocorrelation was not prevalent in our study (Table S9).

DISCUSSION

Forest bird distributions in our study responded strongly to fine-scale thermal conditions. Climate is widely accepted to

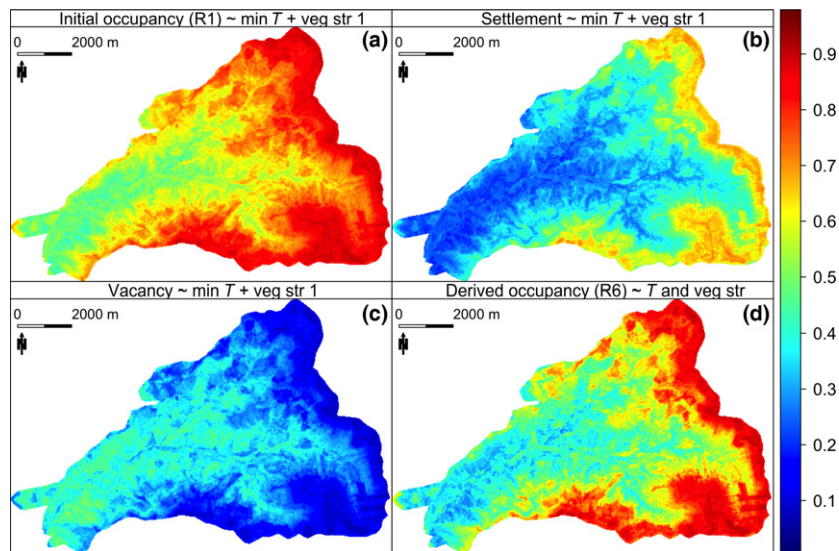


Figure 3 Predicted maps for hermit warbler (a) initial occupancy, (b) settlement, (c) vacancy and (d) final occupancy patterns at the end of the sampling period. Hermit warblers show higher apparent vacancy at warmer sites and higher apparent settlement at cooler sites. By the end of the season, (d) hermit warblers have shifted away from warmer sites towards cooler sites. The Andrews Forest is low elevation to the east and high elevation to the west (see Fig. S2 for elevation and canopy height distributions). T, temperature; veg str 1, vegetation structure variable PC1; mn, mean; min, minimum; R1, round 1 of point counts; R6, round 6 of point counts.

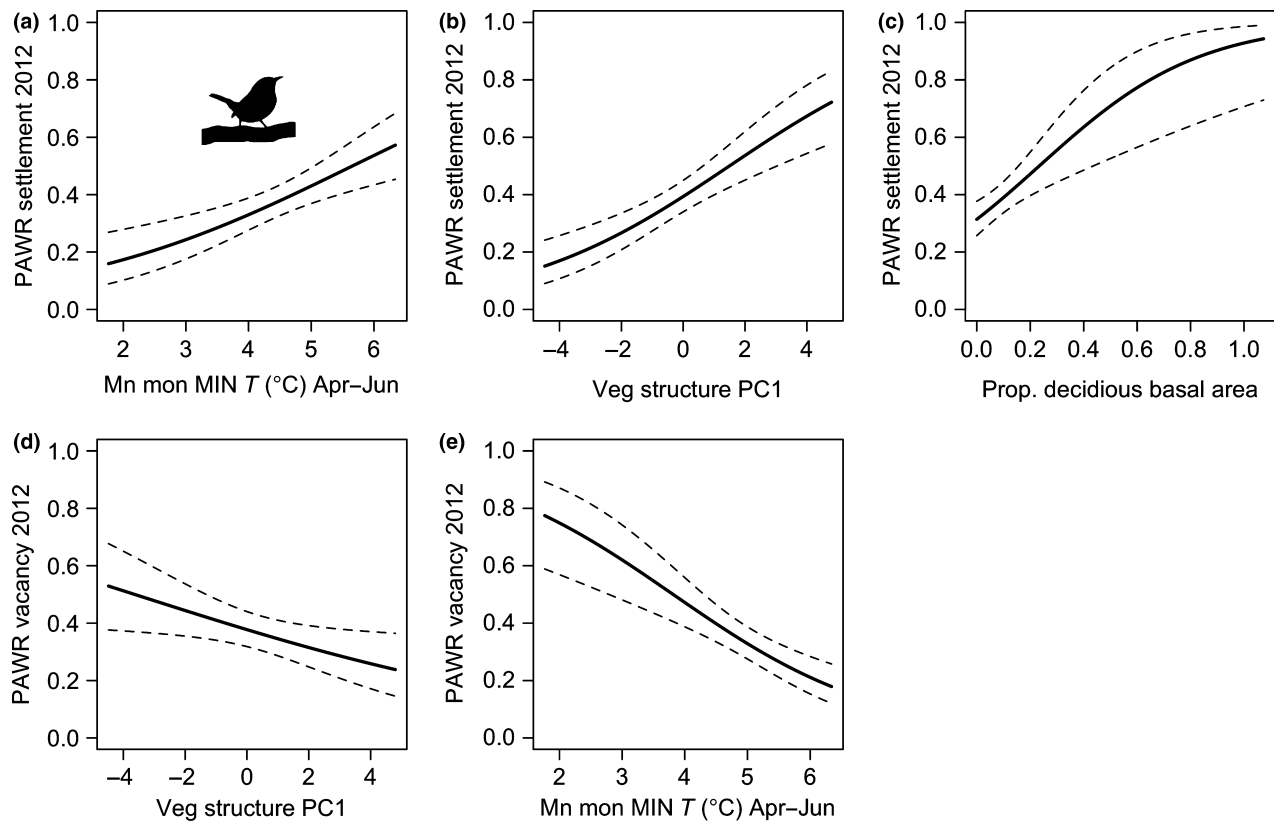


Figure 4 Pacific wren (*Troglodytes pacificus*, PAWR) is an example of a warm-associated species where both temperature and vegetation were important in within-season dynamics. Pacific wrens were more likely to settle warmer sites (a) and vacate cooler sites (e). Pacific wrens were more likely to settle sites with old-growth characteristics (b) and higher deciduous composition (c). Wrens were more likely to vacate even-aged vegetation stands such as plantations (d). Mn, mean; mon, monthly; MIN, minimum; T, temperature; Veg, vegetation; PC, principal component; Prop, proportion.

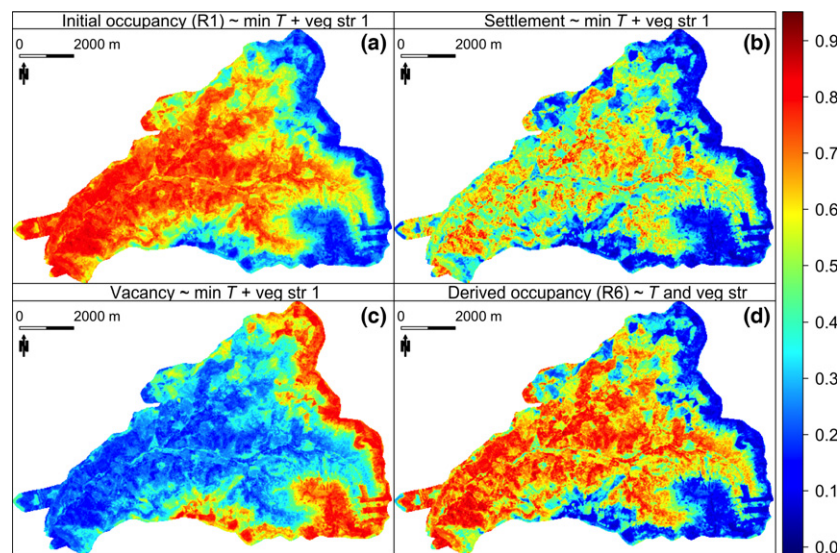


Figure 5 Predicted distribution maps for Pacific wren (a) initial occupancy, (b) settlement, (c) vacancy and (d) final occupancy patterns at the end of the sampling period. By the end of the season, (d) Pacific wrens have shifted away from plantation sites towards older forest sites. The predicted maps for this species highlight the strong vegetation component in addition to temperature. Maps do not include proportion of deciduous basal area since it is a local-site vegetation variable. The Andrews Forest is low elevation to the east and high elevation to the west (see Fig. S2 for elevation and canopy height distributions). T, temperature; veg str 1, vegetation structure variable PC1; min, minimum; R1, round 1 of point counts; R6, round 6 of point counts.

be a major driver of species distributions at broad spatial extents (Thuiller *et al.*, 2004a; Thomas, 2010; Boucher-Lalonde *et al.*, 2014), but to our knowledge, this is the first evidence of fine-scale temperature effects on bird occupancy dynamics. Local habitat selection in birds has often been shown to depend on vegetation characteristics (Hildén, 1965) such as structure (MacArthur *et al.*, 1962; Seavy *et al.*, 2009) and composition (Ellis & Betts, 2011). However, local-scale temperature appears to be of equal or possibly greater importance than vegetation in site selection by forest birds in our system. Clearly our findings do not downplay the important role of vegetation in species distributions; rather, they highlight the need to account for microclimate variability when considering distributional changes. Occupancy dynamics for many species we examined depended on both microclimate and vegetation metrics. Although we do not know of any other bird occupancy studies that have compared the role of local-scale temperature and vegetation in a forest system, there is some previous evidence that the combined effects of vegetation and temperature influence avian occurrence patterns in other systems. For example, in an exurban environment, Lumpkin & Pearson (2013) found that both temperature and habitat characteristics (building density and forest cover) affected bird occurrence patterns. Further, previous work conducted at broad spatial scales has shown a strong influence of both vegetation and temperature on bird distributions (Cumming *et al.*, 2014).

Microclimate is known to be important for ectotherms due to thermoregulation requirements (Scheffers *et al.*, 2014), but has only been recently considered for endotherms (Boyles *et al.*, 2011; Long *et al.*, 2014). The influence of

climate on endothermic species distributions has been almost exclusively explored at large spatial scales (Peterson *et al.*, 2002; Mitikka *et al.*, 2008), 10^4 -fold larger than the scale at which organisms generally make habitat selection decisions (Potter *et al.*, 2013). An important advance in our study was that we directly measured air temperature at the same sites where we counted birds; we did not use elevation as a proxy for temperature (Klemp, 2003; Maggini *et al.*, 2011) or interpolate temperature from widely spaced temperature stations placed in open areas (Scherrer *et al.*, 2011). The combination of dynamic occupancy modelling and high-resolution temperature data allowed us to elucidate clear changes in intra-season distributional patterns for multiple species along a microclimate gradient.

We found that most species of forest birds examined exhibited apparent within-season distribution dynamics. Our results add to growing evidence that within-season site occupancy may be less static than traditionally assumed (Betts *et al.*, 2008; McClure & Hill, 2012). For example, McClure & Hill (2012) also found dynamic occupancy models outperformed static occupancy models in a south-eastern U.S. forest bird community suggesting birds were shifting sites within a breeding season. Radio tracking (Klemp, 2003; Gow & Stutchbury, 2013), territory mapping (Brambilla & Rubolini, 2009) and mark-recapture studies (Gilroy *et al.*, 2010) have also demonstrated within-season movements and site shifts in birds.

Within-season shifts can be the result of three main processes: (1) habitat upgrading, (2) thermoregulation and (3) resource tracking. Shifts are often thought to follow failed breeding attempts (Switzer, 1997; Hoover, 2003) or represent

Table 2 Coefficients (Est) and standard errors (SE) for apparent settlement (γ) as a function of temperature and vegetation (structure and composition) metrics by species and year for top models (see Table 1 for species code definitions and see Appendix S6 for all model selection tables).

Species	Vegetation						Temperature											
	Intercept		Structure PC1		Structure PC2		Composition		CDD > 0 J–M		CDD > 10 A–J		Max T A–J		Min T A–J		Mean T A–J	
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
2012																		
BRCR	−1.90	0.17	0.69	0.17*	−0.19	0.13												
CBCH	0.19	0.19	0.19	0.18	−0.57	0.19*									0.36	0.17*	−0.56	0.11*
GCKI	−1.13	0.11					−0.15	0.13										
HAFL	−2.67	0.29					0.40	0.19*	−0.43	0.34								
HETH	−1.31	0.21	−0.44	0.17*											0.17	0.19		
HEWA	−0.39	0.15	−0.18	0.16													−0.53	0.16*
ORJU	−1.08	0.17	−0.39	0.16*													−0.54	0.19*
PAWR	−0.43	0.12	0.64	0.14*											0.49	0.13*		
PSFL	−0.93	0.11	0.55	0.13*			0.57	0.16*							0.26	0.12*		
RBNU	−1.74	0.27													−0.33	0.29		
STJA	−1.07	0.20	−0.27	0.16†									0.23	0.13†			0.32	0.14*
SWTH	−0.93	0.15	−0.27	0.14*													−0.53	0.13*
VATH	−1.43	0.14			−0.31	0.12*												
WETA	−2.85	0.26			0.54	0.19*					0.90	0.20*						
WIWA	−2.95	0.19	−0.50	0.18*							−0.38	0.17*						
2013																		
BRCR	−1.68	0.18	0.46	0.18*	−0.23	0.14†	−0.34	0.22					−0.27	0.17				
CBCH	−0.64	0.14	0.32	0.15*	−0.37	0.13*									0.28	0.16†	−0.91	0.13*
GCKI	−1.29	0.11			−0.13	0.12											0.22	0.19
HAFL	−2.19	0.18	0.47	0.16*													−0.32	0.12*
HETH	−1.86	0.12	−0.47	0.12*	−0.25	0.12*											−0.64	0.16*
HEWA	−0.03	0.15	−0.43	0.17*			−0.38	0.17*										
ORJU	−1.08	0.13	−0.50	0.14*														
PAWR	−0.94	0.12	0.56	0.14*														
PSFL	−0.48	0.11	0.43	0.13*														
RBNU	−0.12	0.26			−0.48	0.24*	−0.46	0.23*					−0.54	0.24*				
STJA	−3.27	1.64							1.33	0.92								
SWTH	−1.13	0.12					0.19	0.11†					0.36	0.10*				
VATH	−1.52	0.13			−0.21	0.12†					−0.43	0.12*						
WETA	−2.00	0.25	−0.64	0.16*									0.21	0.15				
WIWA	−3.11	0.30			−0.65	0.26*					−0.42	0.26*						

*95% confidence interval does not overlap 0.

†90% confidence interval does not overlap 0; CDD, cumulative degree days; J–M, January–March; A–J, April–June; T, temperature; PC, principal component.

Table 3 Coefficients (Est) and standard errors (SE) for apparent vacancy (ε) as a function of temperature and vegetation (structure and composition) metrics by species and year for top models (see Table 1 for species code definitions and see Appendix S6 for all model selection tables).

Species	Vegetation						Temperature											
	Intercept		Structure PC1		Structure PC2		Composition		CDD >0 J–M		CDD >10 A–J		Max T A–J		Min T A–J		Mean T A–J	
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
2012																		
BRCR	1.13	0.47			0.28	0.28	1.22	0.86										
CBCH	−0.54	0.14	−0.24	0.13 [†]	0.15	0.12			−0.22	0.13 [†]							0.33	0.16*
GCKI	0.35	0.18			0.10	0.16												
HAFL	−0.52	0.39	−0.71	0.41 [†]														
HETH	0.64	0.30	0.11	0.26											0.69	0.29*		
HEWA	−1.01	0.16	0.18	0.13			0.19	0.21							0.54	0.21*		
ORJU	0.38	0.26													1.32	0.28*		
PAWR	−0.50	0.13	−0.31	0.14*											−0.70	0.16*		
PSFL	−0.39	0.16	−0.26	0.16	0.29	0.13*									−0.24	0.19		
RBNU	−1.22	0.49	0.28	0.36													0.69	0.46
STJA	1.04	0.31					−0.27	0.24	−0.23	0.25								
SWTH	−0.27	0.23	0.20	0.19														
VATH	0.95	0.28	−0.03	0.21										0.65	0.25*			
WETA	0.81	0.47	0.60	0.36 [†]													−0.28	0.36
WIWA	0.90	0.40	0.26	0.28									1.69	0.48*				
2013																		
BRCR	0.30	0.24			0.36	0.21 [†]											−0.32	0.18 [†]
CBCH	−0.57	0.21					−0.63	0.29*									0.55	0.17*
GCKI	0.23	0.19					0.32	0.17 [†]									−0.35	0.25
HA(SE) FL	−0.34	0.32			−0.42	0.20*											0.15	0.20
HETH	0.64	0.21	0.34	0.18 [†]													0.43	0.11*
HEWA	−0.81	0.10	−0.06	0.10														
ORJU	−0.10	0.20	0.02	0.20														
PAWR	−0.69	0.13			0.38	0.12*									0.29	0.18 [†]		
PSFL	−0.62	0.14	−0.33	0.14*											−0.52	0.16*		
RBNU	−1.05	0.17			0.14	0.15	0.19	0.18							−0.41	0.17*		
STJA (Est)	−2.68	0.63	1.00	0.41*													0.23	0.15
SWTH	−0.07	0.19			−0.36	0.16*	−0.17	0.16					−0.14	0.18	0.69	0.54		
VATH	1.05	0.26					−0.40	0.31 [†]							0.39	0.22		
WETA	1.46	0.44													0.29	0.40		
WIWA	−4.66	1.78			−1.13	0.46*	−4.62	2.34*									−1.15	0.74

*95% confidence interval does not overlap 0.

†90% confidence interval does not overlap 0; CDD, cumulative degree days; J–M, January–March; A–J, April–June; T, temperature; PC, principal component.

upgrading along gradients in habitat quality (Betts *et al.*, 2008). Models of habitat selection typically assume that when animals select a breeding site, they possess the necessary ('ideal') information about site quality and dispersal capabilities to make the best choice (Fretwell & Lucas, 1969; Pulliam & Danielson, 1991). In reality, it may not be possible to obtain dependable site quality information quickly (Stamps, 2006) and it may take time for individuals to gain personal information (Doligez *et al.*, 2002). This could result in a delay between when birds initially arrive at a location and settle at a final breeding site.

Secondly, it is likely that some portion of the shifting distribution dynamics could be due to behavioural thermoregulation (Bernardo, 2014). Mammals (Long *et al.*, 2014) and birds (Dolby & Grubb, 1999) have both been shown to alter their behaviour in response to temperature conditions. Karr & Free-mark (1983) hypothesized that tropical birds often avoided extremely wet or dry sites (depending on time of year) for physiological reasons rather than due to food resources. Other studies have documented upward shifts along elevational gradients (e.g., Klemp, 2003), which are suggested to indicate shifts towards climatically favourable sites amid seasonal warming. Shifts in distributions towards more thermally appropriate sites could also occur at finer, within-territory scales.

Finally, within-season movement may enable birds to capitalize on ephemeral resources available in spatially distinct locations either within territory boundaries or at broader scales (Diggs *et al.*, 2011). Within-season shifting could represent upgrading along ecological gradients in habitat quality to track changes in resources. Hence, motivation behind settlement, vacancy and within-territory habitat use decisions could potentially be linked to temperature-sensitive food resources – particularly arthropod abundance (Lack, 1954; Martin, 1987; Rodenhouse *et al.*, 2003). Temperature and degree days in late winter and spring are known to be strongly associated with important phenological events such as bud break (Yu *et al.*, 2010), insect emergence (Both *et al.*, 2009) and insect abundance (Kingsolver *et al.*, 2011).

It is important to note that we did not measure movement directly through methods such as telemetry (e.g., Gow & Stutchbury, 2013). In particular, we were only able to quantify distributional changes within a season based on modelled 'colonization' and 'extinction' rates (MacKenzie *et al.*, 2006). Despite the fact that our models were designed to account for imperfect detection, within-territory movements of birds into and outside of our count circle between sampling sessions could result in the settlement and vacancy patterns that we observed (Betts *et al.*, 2008). However, based on simulation studies performed by Chandler *et al.* (2011), temporary emigration from a sample location is only likely to bias parameters estimates when it is not random. Further, we did not find strong support for a home-range size effect on colonization and extinction rates (Appendix S3). However, from the most conservative standpoint, estimated rates of vacancy and settlement could also be due to within-territory shifts in resource use, or gradients in density associated with microclimate.

Implications

We have provided evidence that high-resolution temperature data are useful for species distribution modelling. Although the logistics of obtaining such data may be challenging (Bennie *et al.*, 2014), we argue that failing to incorporate local microclimate variability masks important occupancy processes. The unexpectedly high relative importance of site-level climate over local vegetation in local habitat selection versus regional scales could stem from mismatches in data quality across scales; climate data tend to be measured well at broad scales, but not fine scales. In contrast, vegetation data are often collected at high resolution (and accuracy) at fine scales, but not broad scales (Betts *et al.*, 2006). Our results indicate that lack of fine-scale temperature data may mask the relative role of temperature and could lead to the appearance of vegetation as the key driver of distributions at fine scales (Luoto *et al.*, 2007). For some temperature metrics, widely available elevation and aspect data could serve as surrogates for fine-scale temperature; however, results from Frey *et al.* (2016) indicate that vegetation structure and microtopography also have important implications for under-canopy temperature.

While most species showed apparent habitat shifts in response to site temperature conditions, the direction of these responses varied by species. Moritz & Agudo (2013) also found that many species had highly variable responses to climate. Many range-shift studies have reported high variability in both the degree and direction of range shifts (Lenoir *et al.*, 2010; Chen *et al.*, 2011). Microclimate heterogeneity and species-specific responses to local-scale temperature could explain the inconsistencies between predicted and observed responses to climate change (Buckley & Kingsolver, 2012).

Our results showing within-season distribution dynamics for most species we examined suggest that forest bird species potentially have the behavioural flexibility to track favourable microclimates within a season (Boyles *et al.*, 2011; Tuomainen & Candolin, 2011). In montane landscapes, complex terrain could create buffered 'microrefugia' (Dobrowski, 2010). Microclimate heterogeneity may be an important factor in providing options for behavioural adaptation (Bonebrake *et al.*, 2014) in the face of regional climate changes. Stable populations in heterogeneous landscapes could stem from increased options for tracking microclimate (Oliver *et al.*, 2010). Indeed, we found some evidence for population declines in species we identified as being 'cool-associated' (mean trend [95% CIs] = $-1.06\%/year$ [-1.96 to -0.16]) at the regional scale (Breeding Bird Survey 2002–2012 trends from the Pacific Northwest temperate rainforest region) relative to their warm-associated counterparts ($-0.16\%/year$ [-0.99 to 0.68], see Appendix S7). This suggests that at least regionally, buffering capacity may be insufficient to sustain stable populations for cool-associated species in the face of climate change.

Conclusions

Our results show that distributional patterns of forest birds are strongly associated with fine-scale thermal regimes in mountainous landscapes. Birds tended to both vacate and settle sites with particular microclimate conditions, even after accounting for the influence of vegetation and imperfect detection. This behavioural flexibility to adapt to changes within a breeding season appears widespread as it was demonstrated by almost all members of the forest bird community we examined. Future efforts should examine the degree to which such vagility and apparent flexibility in habitat selection might propagate to buffer such species against the impact of long-term climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details concerning placement of HOBO temperature sensors and processing of temperature data.

Appendix S2 Details concerning LiDAR-derived variables for vegetation structure and principal component analysis.

Appendix S3 Dynamic occupancy model structure and additional details.

Appendix S4 Methods for creating spatial maps of bird distributions as a function of microclimate and vegetation structure variables.

Appendix S5 Results from home range tests on assumptions of dynamic occupancy models.

Appendix S6 Dryad digital depository for AIC model selection tables.

Appendix S7 Methods for Breeding Bird Survey population trends comparison between cool- and warm-associated species.

Figure S1 Bi-plot of the first two components (PC1 on the x-axis and PC2 on the y-axis) from the principal component analysis showing how vegetation structure metrics differ between old-growth/mature forest sites (blue dots) and plantations (red dots).

Figure S2 Maps of study area showing sample points, elevational gradient, and canopy height.

Figure S3 Predicted occupancy probability maps for cool-associated species.

Figure S4 Predicted occupancy probability maps for warm-associated species.

Table S1 LiDAR-derived vegetation structure variables used in the principal component analysis.

Table S2 Results from the principal component analysis of all vegetation structure predictor variables.

Table S3 Deciduous tree and large shrub species used to quantify forest composition at our sample points.

Table S4 Pearson's correlation coefficients between all predictor variables.

Table S5 Coefficients (Est) and standard errors (SE) for initial occupancy (ψ).

Table S6 Coefficients (Est) and standard errors (SE) for detection probability (p) as a function of survey covariates.

Table S7 Coefficients (Est) and standard errors (SE) for detection probability (p) as a function of environmental covariates.

Table S8 Coefficients (Est) and standard errors (SE) for all parameters from constant models.

Table S9 Comparison of effect sizes between fine-scale temperature and vegetation on settlement and vacancy.

Table S10 Goodness-of-fit bootstrap results for top models.

Table S11 Results from tests for spatial autocorrelation in the residuals from the top models.

Table S12 Interactions between temperature and vegetation variables from the top models for occupancy, colonization and extinction.

BIOSKETCHES

Sarah J. K. Frey, Adam S. Hadley and Matthew G. Betts are based in the Forest Biodiversity Research Network in the Department of Forest Ecosystems and Society at Oregon State University (<http://www.fsl.orst.edu/flel/index.htm>). They are members of a research team directed at understanding climatic and land-use factors underlying the spatial and temporal distribution of biodiversity in forests of the Americas.

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