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*Research Article*

# Microclimate mediates the strength and direction of avian biotic interactions

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Theory predicts that the strength and direction of species interactions can shift from being competitive in benign environments toward being facilitative in stressful environments. However, the environmental context dependency of species interactions has rarely been tested in animal communities. We capitalized on a 15-year, landscape-scale dataset, collected annually in a relatively stable old-growth forest environment, to test the long-held hypothesis that the strength and direction of species interactions might be mediated by climatic conditions. It is generally accepted that competitive and facilitative interactions drive the distributions of many species, but are rarely included in climate envelope models, and may partly explain poor predictive performance of species distribution models in the face of climate change. Using multi-species dynamic occupancy models applied to long-term data, we tested whether annual settlement by bird species could affect either the persistence or settlement by other phylogenetically related species, and whether these interactions are mediated by microclimate. We found that species interactions were influenced by microclimate for a high proportion of species pairs (80%). Related species pairs more often showed settlement dynamics that were indicative of attraction rather than repulsion (55 versus 30%, respectively). In some cases, competitive interactions in colder microclimates flipped to become facilitative in warmer ones (15%) and vice versa (5%). Furthermore, species pairs that were closely related were more likely to exhibit competitive relationships along at least part of the microclimatic gradient. Our results highlight the importance of using long-term data to incorporate competitive and facilitative interactions into species distribution models, and support the notion that the strength and direction of species interactions can be dependent on microclimatic conditions.

Keywords: biotic interactions, competition, heterospecific attraction, microclimate, species distribution models



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## Introduction

It has long been hypothesized that species interactions should play a major role in governing the distributions of species (Darwin 1859, Hutchinson 1957), ecosystem processes (Loreau et al. 2001), and evolution (Thompson 1999). Nevertheless, most species distribution models to date have ignored competition, predation and, mutualisms, and instead focused on environmental drivers of distributions (Thomas et al. 2004, Elith and Leathwick 2009). The absence of biotic interactions in most estimates of biodiversity responses to climate change has been invoked as one reason for relatively poor model prediction success (Zarnetske et al. 2012, Watling et al. 2013, Betts et al. 2019). Indeed, a host of theories (Chesson 2000, Fukami 2015) and experiments (Dhondt and Eyckerman 1980, Martin and Martin 2001) have demonstrated the importance of species interactions in driving distributions. Alternatively, according to the Eltonian noise hypothesis, the 'noise' of fine-scale factors such as species interactions averages out at macroscales where abiotic factors such as climate dominate (Fraterrigo et al. 2014).

Importantly, the strength and direction of species interactions are expected to vary across environmental gradients; one of the key mechanisms facilitating the coexistence of similar species is the context-dependent competitive abilities of species (Chesson 2000). For instance, in birds, a cold-tolerant species may outcompete a warm-tolerant species under cool conditions – a property that prevents continuous up-slope or poleward range expansion by warm-tolerant species (Diamond 1973, Freeman et al. 2022). Further, competitive relationships have been hypothesized to flip to become facilitative under low productivity, harsh conditions such as alpine meadows and deserts (Bertness and Callaway 1994) due to resource acquisition taking precedence over competition. This context dependency in species interactions has been examined extensively in the plant literature, often as tests of the stress-gradient hypothesis (Barrio et al. 2013, LaManna et al. 2022), but to date, few tests have been available for animals (Fletcher 2009, Jankowski et al. 2010). Interaction dynamics could also vary depending on similarities or differences in resource use due to genetic relatedness (Darwin 1859). Phylogenetically similar species are likely to be using the same habitat type and food items, and are probably more likely to compete, compared to more distantly related species (Cahill et al. 2008, Pigot et al. 2016).

Until recently, modeling frameworks were insufficient to include both species interactions and environmental drivers. Over the past decade, there have been a number of methodological advancements that enable incorporation of species co-occurrences into predictive models (Warton et al. 2015, Dormann et al. 2018). The most common of these models are joint species distribution models (jSDMs, Pollock et al. 2014). However, most approaches do not account for the fact that species are detected imperfectly in biodiversity surveys (Tobler et al. 2019, Doser et al. 2023), which has the potential to lead to estimator bias both in the strength of environmental and biotic interaction effects by inflating, masking or confounding (Bailey et al. 2009, Beissinger et al. 2016). Further, co-occurrence models are often conducted at spatial scales that poorly reflect the scale of likely interactions among species. For instance, entire bird atlas squares (> 1 $km^2$) or North American breeding bird survey routes (39.2 km) data may be used to infer interactions among species occupying small territories (< 10 ha) and therefore interacting at much finer resolutions (Seoane et al. 2005). Perhaps most importantly, many species interaction models rely on a single time period of co-occurrence data. This renders them prone to the 'missing environmental variable problem'. That is, boosts in model performance are attributed to the direct effects of interacting species, but the inclusion of interactions simply represents one or many missing environmental variables in the analysis. Indeed, Blanchet et al. (2020) showed analytically that using only co-occurrence data from a single time period cannot be used reliably to quantify species interactions.

Experiments have the potential to provide strong inference about species interactions. For instance, reciprocal transplants have enabled testing how competitive effects vary across environmental gradients (Alexander et al. 2015). Removal (Martin and Martin 2001) and playback (Jankowski et al. 2010) experiments have demonstrated the importance of competition in limiting animal distributions. However, gains in rigor from experimental approaches necessarily trade off against range of inference across spatial and temporal scales; it would be extremely challenging to experimentally quantify the strength and direction for all potentially interacting species pairs in a community – particularly in highly species-rich regions.

Given weaknesses associated with co-occurrence models and limited generality from experiments, how should ecologists test hypotheses about the strength of biotic interactions and the degree to which these are mediated by the environment? One potential solution lies in examination of long-term occupancy dynamics of co-occurring species (Dormann et al. 2018, Blanchet et al. 2020). In relatively stable environments, if settlement of a site by one species consistently results in the local extinction of another, this could be evidence of competitive effects. Similarly, chronic patterns of occupancy by one species resulting in the settlement of another could be interpreted as evidence of facilitative effects. Although such patterns are still correlative, the 'missing environmental variable problem' is likely diminished because it is unlikely that physical environmental dynamics of the system perfectly match the dynamics of species colonizations and extinctions (Yackulic et al. 2015).

Here, we used a dynamic occupancy model to address two major questions. First, we asked: to what extent the long-term occupancy dynamics (i.e. site settlement and persistence) of forest bird species are influenced by the presence of closely related species? Second, we tested the degree to which either competitive or facilitative interactions are mediated by environmental context (vegetation and microclimate). We selected species pairs with varying phylogenetic distance values, to enable quantification of the relationship between

interaction strength and relatedness. The dominant paradigm is that competitive interactions are a driving force in the ecology and evolution of forest birds (MacArthur 1958, 1964, Sherry 1979, Dhondt and Eyckerman 1980, Jankowski et al. 2010, Dugger et al. 2015). However, to a more limited extent, experimental and correlative studies have shown that heterospecifics may use each other as cues in habitat selection, resulting in facilitation – a phenomenon known as 'habitat copying' (Thomson et al. 2003, Parejo and Avilés 2016). The use of information about the habitat gathered from conspecific and heterospecific behavior, like vocalization quality, can provide condition-dependent settlement decisions (Mönkkönen et al. 1990, Morinay et al. 2020).

We paired long-term microclimate and bird community data at 184 individual sample points across a climatic gradient in old-growth forest (Frey et al. 2016, Kim et al. 2022) to provide, to our knowledge, one of the first tests of context-dependency in species interactions among animals (Bertness and Callaway 1994). Under the stress-gradient hypothesis as conceptualized in the plant literature (Bertness and Callaway 1994), we should see competitive interactions among species in less stressful climates (in this system, lower elevations and warm microclimates), but facilitative interactions in harsh climates (cold microclimates and high elevations). Indeed, interspecific flocks of temperate birds typically occur in winter, and this is considered an adaptation to difficult conditions (Morse 1970). However, in birds it is also true that hot conditions during the breeding season can be stressful – both in terms of the direct effect of heat on thermoregulation and the increased energetic demands associated with foraging (Riddell et al. 2021). Of course, individual bird species likely have variable adaptations to handle both heat and cold, but these physiological tolerances are not well known, so the direction of context dependency within individual species pairs is challenging to predict.

## Material and methods

### Study site

We collected bird occurrence data at the watershed-scale at a long-term ecological research (LTER) site, the H. J. Andrews Experimental Forest (HJA). HJA is located in the western Cascade Range of Oregon, USA, and covers 6400 ha of young, mature and old-growth forests (44°12′N, 122°15′W; 410–1630 m a.s.l.). HJA has an extensive valley-wide dataset on forest bird populations with 184 sample points located across the watershed. We established sample points so that they spanned gradients in elevation, climate and forest vegetation (structure and composition), allowing for the comparison of relative drivers of species distributions (Fig. 1).

### Sample plot selection

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 of individual birds. 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. 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. 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 comprised 60 transect points, 68 road points, and 55 trail points.

### Bird surveys

Corresponding with the breeding period for most bird species, point counts were conducted on two to six separate occasions from May to July from 2009 to 2023 (Betts et al. 2026). Point counts were done during favorable weather conditions by trained observers. The order in which points were visited and which observer did the survey varied for each sampling session to reduce potential bias. Each round of point counts lasted between 4 and 7 days with a break of 2–10 days between sessions.

Point counts occurred between 05:00 and 10:30 h, corresponding to the period of peak activity. Each site visit consisted of a 10 min point count where all birds seen or heard were recorded and determined to be either within a 50 m radius or between 50 and 100 m. Observers monitored the location of the individual birds to reduce the possibility of double-counting individuals.

### Site-level features

#### Vegetation structure data

Fine-scale, high-resolution data on vegetation structure were obtained using LiDAR data collected in August 2008 (Spies 2016). We statistically accounted for vegetation structure in our models to isolate the influence of microclimate (a summary of the vegetation variable and effects is presented in the Supporting information). Structural characteristics included: 1) canopy height, 2) percent cover mid-canopy (2–10 m) and upper canopy (> 10 m), 3) biomass, 4) coefficient of variation in canopy height, 5) height of median return (HOME) and 6) vertical distribution ratio (VDR). The first dimension from a principal components analysis (44.7% variance explained) was used to combine these variables at the 25 m scale to represent a vegetation structure gradient from plantation to old-growth forest (PC1; Supporting information). We assumed that vegetation characteristics did not change systematically in any substantial way during our study period; however, we recognize that local-scale changes do occur (e.g. tree falls, standing dead trees). We did not consider this a concern because of the slow growth rates of mature and old-growth rain forests and the infrequency of major stand-replacing disturbances (Franklin et al. 2002) in relation to the duration of our study.

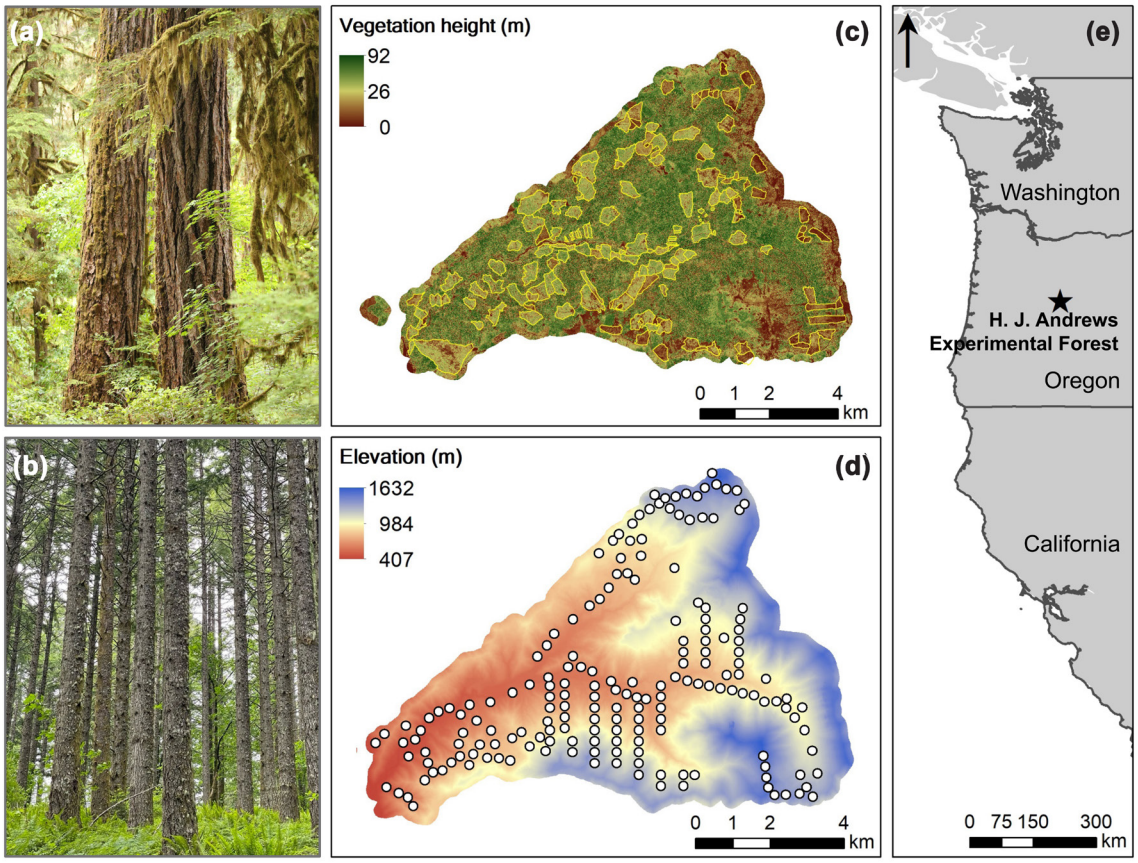


Figure 1. Study area map and photographs of typical vegetation in the study area. (a) Typical old-growth Douglas fir–western hemlock forest and (b) Douglas fir second-growth plantation in H. J. Andrews Experimental Forest (HJA). (c) Vegetation height and stands with harvest history (yellow boundaries). (d) Sampling locations (points; black circles) and altitudinal gradient of the watershed, and (e) location of the study area, HJA in Oregon, USA. Photo credits (a) and (b) Matt Betts.

### *Climate data*

To capture the local microclimate, we placed Onset HOBO pendant data loggers (UA-002-64) at each sample point, which recorded temperature every 20 min. Each data logger was placed at a height of 1.5 m using a flexible fiberglass post. An 20.3-cm long piece of PVC pipe (schedule 12, 7.6-cm diameter) cut in half was used as a solar radiation shield. Where possible, the data loggers were placed in areas without any shrubs or branches with a 1.5 m radius. On steep slopes, data loggers were placed approximately 1 m downslope from a large tree to prevent destruction from snowpack. We excluded data during periods when loggers were buried in snow. We calculated the average maximum daily June temperature for each year to coincide with the timing of the bird sampling, bird arrival, and the peak breeding period (Kim et al. 2024). June temperatures have also been most predictive of bird population trends in this study system (Kim et al. 2022). Because of the complexity of multi-species occupancy models, we sought to adopt a parsimonious approach to climate variable selection.

### *Selection of species pairs*

It has long been hypothesized that more closely related species should exhibit the strongest evidence of competition (Diamond 1975, Drury et al. 2020) unless strong character displacement occurs. For instance, in a synthesis of existing studies, Drury et al. (2020) found that most published instances of interspecific territoriality were among pairs of species in the same genus. We chose 10 pairs of species that were categorized as potential competitors (or facilitators) based on their phylogenetic relatedness (Fig. 2, Supporting information) and prevalence in HJA (Supporting information). We used the global phylogeny of birds (Jetz et al. 2012) to create the phylogenetic tree for 24 species (selected such that at least one species had a prevalence of > 5% across all years and sites), from which we selected the 10 pairs that had the shortest distance between one another (Fig. 2, Supporting information). Selected species pairs differed substantially in their relatedness (Supporting information) and we considered this in post hoc interpretations of strength of putative interspecific interactions through calculation of probability of competition and facilitation. We acknowledge that an alternative approach would be to consider all pairwise interactions across the bird community. Joint species distribution models (jSDMs) enable this flexibility but this trades off against 1) the capacity to account for imperfect detection (Tobler et al. 2019, Doser et al. 2023) and 2) careful

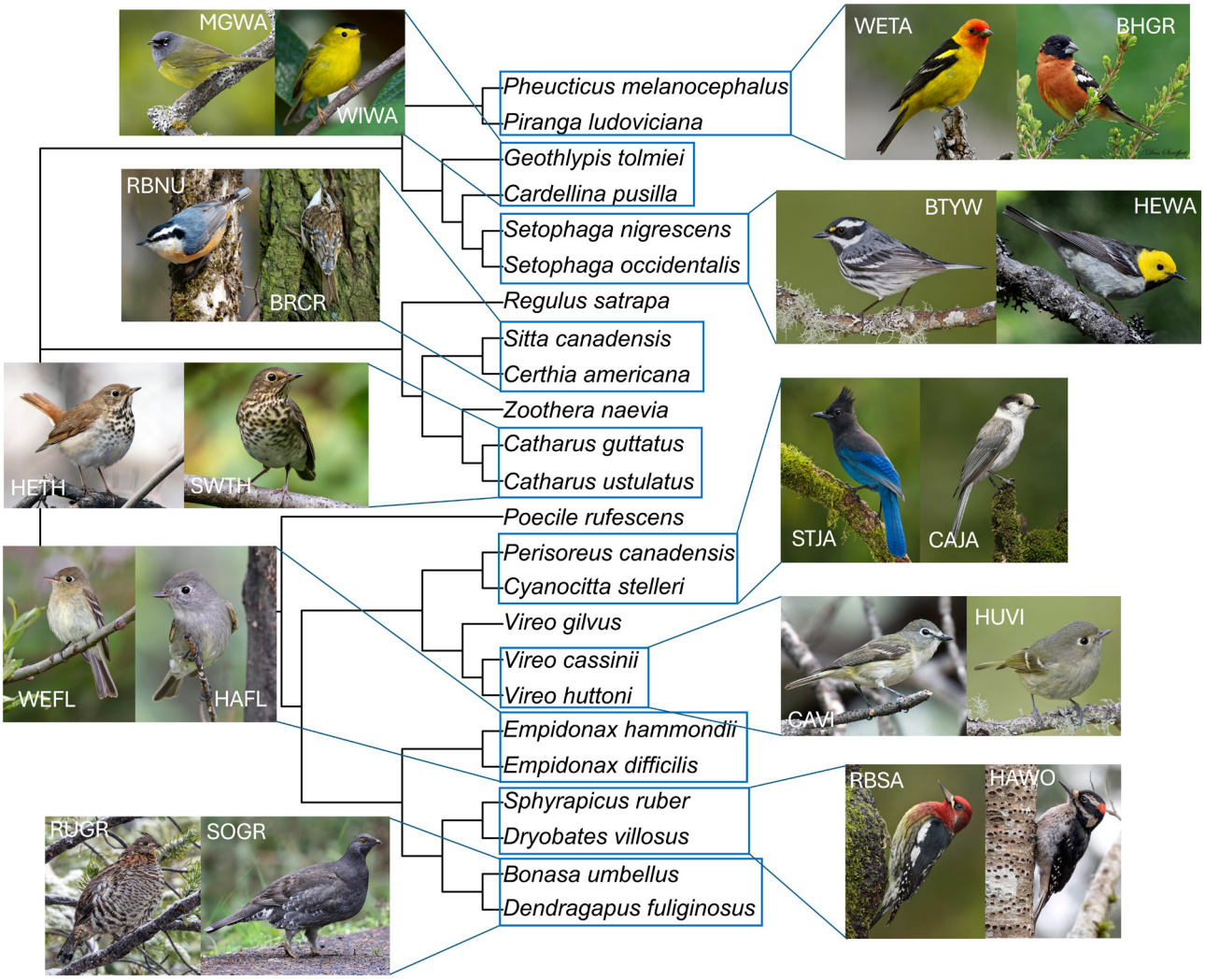


Figure 2. The 10 species' pairs (20 species total) used in this study to investigate heterospecific interactions, specifically the influence of a heterospecific on site settlement along a gradient in microclimate. Species are organized by relatedness and paired based on phylogenetic distance. The phylogenetic tree was produced using the global phylogeny of birds Jetz et al. (2012, http://birdtree.org/, Supporting information). RUGR = ruffed grouse, SOGR = sooty grouse, HAWO = hairy woodpecker, RBSA = red-breasted sapsucker, WEFL = western flycatcher, HAFL = Hammond's flycatcher, CAJA = Canada jay, STJA = Steller's jay, HUVI = Hutton's vireo, CAVI = Cassin's vireo, WETA = western tanager, BHGR = black-headed grosbeak, WIWA = Wilson's warbler, MGWA = Macgillivray's warbler, HETH = hermit thrush, SWTH = Swainson's thrush, HEWA = hermit warbler, BTYW = black-throated gray warbler, RBNU = red-breasted nuthatch, BRCR = brown creeper. Photo credits are listed in the Supporting information.

hypotheses about which species are most likely to be interacting (e.g. phylogenetically related species). The former is critical in studies such as ours because it is quite likely that heterospecifics could alter singing rates in the presence of competitors (Dugger et al. 2011).

### *Species interaction model*

For incorporation of species interactions into the modeling process, we extended the single-season co-occurrence model of Waddle et al. (2010) to estimate dynamic parameters (colonization, local extinction) for a species over multiple seasons as a function of the presence of a second species. As this co-occurrence model can be used for any nature of unidirectional, two-species interactions, we used it to examine heterospecific interactions between co-occurring forest birds. Specifically, we tested the degree to which the presence of one species affected the settlement or persistence of a second species within the same breeding season. To accomplish this, we extended the approach of Waddle et al. (2010) into a dynamic (multi-season) form and parameterized site colonization (settlement) and survival (persistence) in terms of a competitor's presence. We compared the settlement probability in both scenarios (with and without the heterospecific present). Importantly, we tested whether the strength of these interactions is mediated by environmental conditions – in this case, microclimate.

In all models, we included both vegetation (PC1) and microclimate (maximum June temperature in year one)

as covariates on initial occupancy. We addressed sources of bias in detection (e.g. observer, weather) via our experimental design. To account for additional temporal variation in detection, we included survey start time and day of year as detection covariates in all models (Supporting information).

### *Model structure*

We fit our data using a conditional co-occurrence model (Richmond et al. 2010, Waddle et al. 2010) adapted to estimate dynamic parameters of site-level settlement and persistence probabilities across multiple years (MacKenzie et al. 2017). This model treats one species as 'dominant' (A) and the other 'subordinate' (B), assuming uni-directionality of the effects between species. We fit this model to each species, switching which was dominant and subdominant, preferring the simplicity in inference over doing the same approach in a single framework (Fidino et al. 2018). As such, we estimate separate dynamic parameters depending on the dominant species, rather than jointly as in Fidino et al. (2018). The benefit is ease of coding implementation, simpler expression of our modeled hypotheses and improved posterior convergence; the cost may be a small reduction in posterior uncertainty compared to jointly modeled parameters. The data consisted of detections (1) and non-detections (0) for each species at site $i$ from 1 to 184, occasion $j$ from 1 to 6 and year $t$ from 1 to 15. We modeled the initial occupancy probability in year 1 separately for each species ($\psi^A_{i,t=1}$, $\psi^B_{i,1}$) as:

$$\text{logit}\left(\psi^A_{i,t=1}\right) = \beta^A_0 + \beta^A_1 \text{Veg}_i + \beta^A_2 \text{Clim}_{i,t=1}$$

Initial occupancy was modeled as a function of vegetation ($\text{Veg}_i$) and microclimate ($\text{Clim}_{i,1}$) for both species A and B in all model runs, such that $\beta^A_0$ is the intercept, $\beta^A_1$ represents the effect of vegetation and $\beta^A_2$ the effect of microclimate on initial occupancy ($\psi^A_{i,1}$) in year 1. The model structure was analogous for species B.

Our primary inferential focus was on the settlement probability ($\gamma$) of species A from year $t$-1 to $t$, which depends on the presence or absence of species B in year $t$. We indicated the conditional settlement probabilities as $\gamma^{A|B}_{i,t}$ given species B's presence and $\gamma^{A|\varnothing B}_{i,t}$ when species B is absent (where ⌀B denotes species B's absence) in the same year, $t$. We modeled the transition process for species A as follows:

$$z^A_{i,t} \sim \text{Bernoulli}(z^A_{i,t-1}\varphi_A + (1 - z^A_{i,t-1})\left[z^B_{i,t}\gamma^{A|B}_{i,t} + (1 - z^B_{i,t})\gamma^{A|\ B}_{i,t}\right]), t \geq 2$$

The latent occupancy state in years $t = 2,\ldots,T$ of species A at site $i$ ($z^A_{i,t}$) is determined by three possible pathways. The first ($z^A_{i,t-1}\varphi_A$) is that the site was occupied by species A in the previous year, t−1 ($z^A_{i,t-1} = 1$), and remains occupied with the persistence probability of $\varphi_A$. The next is that the site was not occupied by species A in the previous year ($z^A_{i,t-1} = 0$), is occupied by species B in the current year t ($z^B_{i,t} = 1$) and is settled by species A with the probability of $\gamma^{A|B}_{i,t}$. Finally, a site not occupied by species A in the previous year ($z^A_{i,t-1} = 0$), is not occupied by species B in the current year $t$ ($z^B_{i,t} = 0$) and is settled by species A with the probability $\gamma^{A|\varnothing B}_{i,t}$.

We modeled the settlement probabilities of species A separately depending on the presence or absence of species B, incorporating site-level measures of vegetation (Veg) and microclimate (Clim) through a random effect as:

$$\text{logit}\left(\gamma^{A|B}_{i,t}\right) = \beta_0 + \beta_1 \text{Veg}_i + \beta_{2,t}\text{Clim}_{i,t}$$

$$\text{logit}\left(\gamma^{A|\ B}_{i,t}\right) = \alpha_0 + \alpha_1 \text{Veg}_i + \alpha_{2,t}\text{Clim}_{i,t}$$

With year-specific random slopes on microclimate:

$$\beta_{2,t} \sim \text{Normal}\left(\mu_{\beta_2}, \tau_{\beta_2}\right), \alpha_{2,t} \sim \text{Normal}\left(\mu_{\alpha_2}, \tau_{\alpha_2}\right), t = 2,\ldots,T$$

where $\beta_0$ and $\alpha_0$ are intercepts, $\beta_1$ and $\alpha_1$ are the effects of vegetation on the colonization of species A in the presence and absence of species B, respectively, and $\beta_2$ and $\alpha_2$ are the effects of climate on the colonization of species A in the presence and absence of species B, respectively. The time varying effects of climate are assumed to come from a mean-regularizing process, defined as a normal distribution with mean $\mu_{\beta_2}$ and $\mu_{\alpha_2}$ and precisions $\tau_{\beta_2}$ and $\tau_{\alpha_2}$. Heterospecific effects are dependent on species B, vegetation is a static site effect and microclimate is a year-specific site effect in year $t$. Settlement and persistence for the subdominant species (B) were modeled as constant when the interaction was on settlement or persistence for the dominant species (A), respectively. When the interaction was on settlement for species A, the survival parameter was held constant and vice versa. Because initial occupancy was modeled as a function of vegetation and microclimate, this sets the stage for latent occupancy to be estimated in later years. In the interest of parsimony, we chose not to add additional covariates (e.g. on persistence and settlement of the subordinate species) into an already complex model with many parameters (Supporting information).

To account for bias from the observation process, we estimated detection probability for each species as a function of survey start time and day of year:

$$\left(y^A_{i,j,t}\right) | \left(z^A_{i,t}\right) \sim \text{Bernoulli}\left(z^A_{i,t} p^A_{i,j,t}\right)$$

$$\text{logit}\left(p^A_{i,j,t}\right) = \beta^A_0 + \beta^A_1 \text{ST}_{i,j,t} + \beta^A_2 \text{DoY}_{i,j,t}$$

For species A, $y^A_{i,j,t}$ are the detections at site i for replicate j in year $t$, $z^A_{i,t}$ is the latent occupancy for site i in year t, modeled as a Bernoulli process, and $p^A_{i,j,t}$ is the species-specific detection probability across sites and years. Using a logit link, we modeled detection with two temporal covariates (survey start time and day of year). $\beta^A_0$ represents the detection intercept,

$\beta_1^A$ the effect of start time ($ST_{i,j,t}$) on detection, $\beta_2^A$ the effect of day of year ($DoY_{i,j,t}$) on detection. The observation process was modeled independently for species B using the same structure.

This model has several key assumptions: 1) only information on species B in the current year is relevant for settlement of species A (not the prior year); 2) microclimate has a linear effect on settlement and potential interactions; 3) other environmental (i.e., vegetation) factors do not change substantially over time; 4) the microclimate effect is on settlement or persistence; and 5) only occupancy (not density) matters for interactions.

We used three consecutive chains consisting of 75 000 iterations each with a 'burn-in' period of 5000 iterations and thinned by 15 draws. This combination gave us a total of 14 001 draws. Model convergence was assessed by visually inspecting parameter traceplots and with the Gelman–Rubin diagnostic (Gelman and Rubin 1992), which was estimated at $\leq 1.1$ or all parameters using three (or four) chains. We used a Bayesian framework with diffuse prior probability distributions (Supporting information). We fit our model using Markov chain Monte Carlo methods in program R (www.r-project.org) calling JAGS with the packages 'rjags' (Plummer 2025) and 'R2jags' (Su and Yajima 2024). We derived the difference in the posterior distributions in settlement and persistence with and without the heterospecific present to calculate the probabilities of facilitation and competition. Interaction effects were considered positive when this difference was larger with the heterospecific than without. Conversely, we considered negative interactions to have occurred when the difference in posterior distributions was larger without the heterospecific. We considered statistically supported responses to be competitive (repulsion) or facilitative (attraction) when the posterior probabilities were $> 0.8$. We then tested whether this metric of interaction strength was correlated with the relatedness values (phylogenetic distance) between species pairs.

We also explored the interaction on the site-level 'persistence' parameter as a means of testing whether the presence of heterospecific influenced a species persistence at a site. We tested whether the presence of species B affected the likelihood of species A persisting at a site (i.e. not going locally extinct). Model structure was identical to that used in settlement, but with persistence as the focal response variable.

Our models enable accounting for imperfect detection for both species in a pair independently which, given that species may vocalize less or more in the presence of heterospecifics, is essential when testing for biotic interactions (Bailey et al. 2009, Dugger et al. 2015). Importantly, the fine resolution of our microclimate–bird data and analysis (0.78 ha) is similar to the scale of individual bird territories. Overall, this model structure enabled us to test the hypothesis that the strength of species interactive effects was contingent on environmental context – in this case microclimate. Under the stress-gradient hypothesis, we should see stronger competitive interactions in warm, moderate microclimates but facilitative effects in cold, harsher microclimates.

## Results

### Settlement

We found clear evidence for the role of biotic interactions on settlement dynamics in eight of 10 species pairs; in these instances, posterior probabilities for either competitive or facilitative effects were $> 0.8$ (Fig. 3, Table 1). Overall, competitive effects were less common than facilitative relationships; the presence of one species reduced the settlement probability of another in six out of 20 pairings: 1) sooty grouse *Dendragapus fuliginosus*–ruffed grouse *Bonasa umbellus*, 2) MacGillivray's warbler *Geothlypis tolmiei*–Wilson's warbler *Cardellina pusilla*, 3) hermit warbler *Setophaga occidentalis*–black-throated gray warbler *Setophaga nigrescens*, 4) hairy woodpecker *Dryobates villosus*– red-breasted sapsucker *Sphyrapicus ruber*, 5) Canada jay *Perisoreus canadensis*–Steller's jay *Cyanocitta stelleri*, 6) western tanager *Piranga ludoviciana*–black-headed grosbeak *Pheucticus melanocephalus*. This suggests competitive relationships across at least part of the microclimate gradient for these species.

Eleven of 20 pairings displayed facilitative interactions indicating strong support for attraction along a portion of the microclimate range (Fig. 3, Table 1). For four species pairs, whether heterospecific effects were positive or negative depended on the microclimate gradient (Table 1). For example, hermit warblers appeared to be repelled in locations with black-throated gray warblers where microclimates are cool, but there was evidence for attraction in locations with warm temperatures (Fig. 4, Table 1, posterior probability of attraction = 0.85). For instance, MacGillivray's warblers were more likely to settle warmer sites when Wilson's warblers were present (Supporting information, Table 1, posterior probability of attraction = 1.0), but less likely to colonize cool sites in the presence of Wilson's warblers (Supporting information, Table 1, posterior probability of competition = 0.96). Red-breasted nuthatch *Sitta canadensis* and brown creeper *Certhia americana* displayed a strong facilitative relationship across the microclimate gradient (Fig. 5, Table 1; posterior probability of attraction = 1.0).

Overall, although competition versus facilitation was mediated by microclimate (our hypothesized proxy for stress), these effects were not consistently in the direction that might be expected. Attraction appeared to occur more frequently under warmer, rather than colder microclimates for MacGillivray's warblers and Wilson's warblers, as well as for western tanager and black-headed grosbeak. This was also the pattern for sooty grouse in the presence of ruffed grouse, and red-breasted nuthatch in the presence of brown creepers (Table 1, Fig. 5). Alternatively, hermit warblers showed attraction to black-throated gray warblers under colder temperatures (Fig. 4).

### Local persistence

Overall, results for site-level persistence parallelled those for settlement (Supporting information). We found evidence for species interactions for seven of ten species pairs. Again, facilitative relationships tended to be more common than

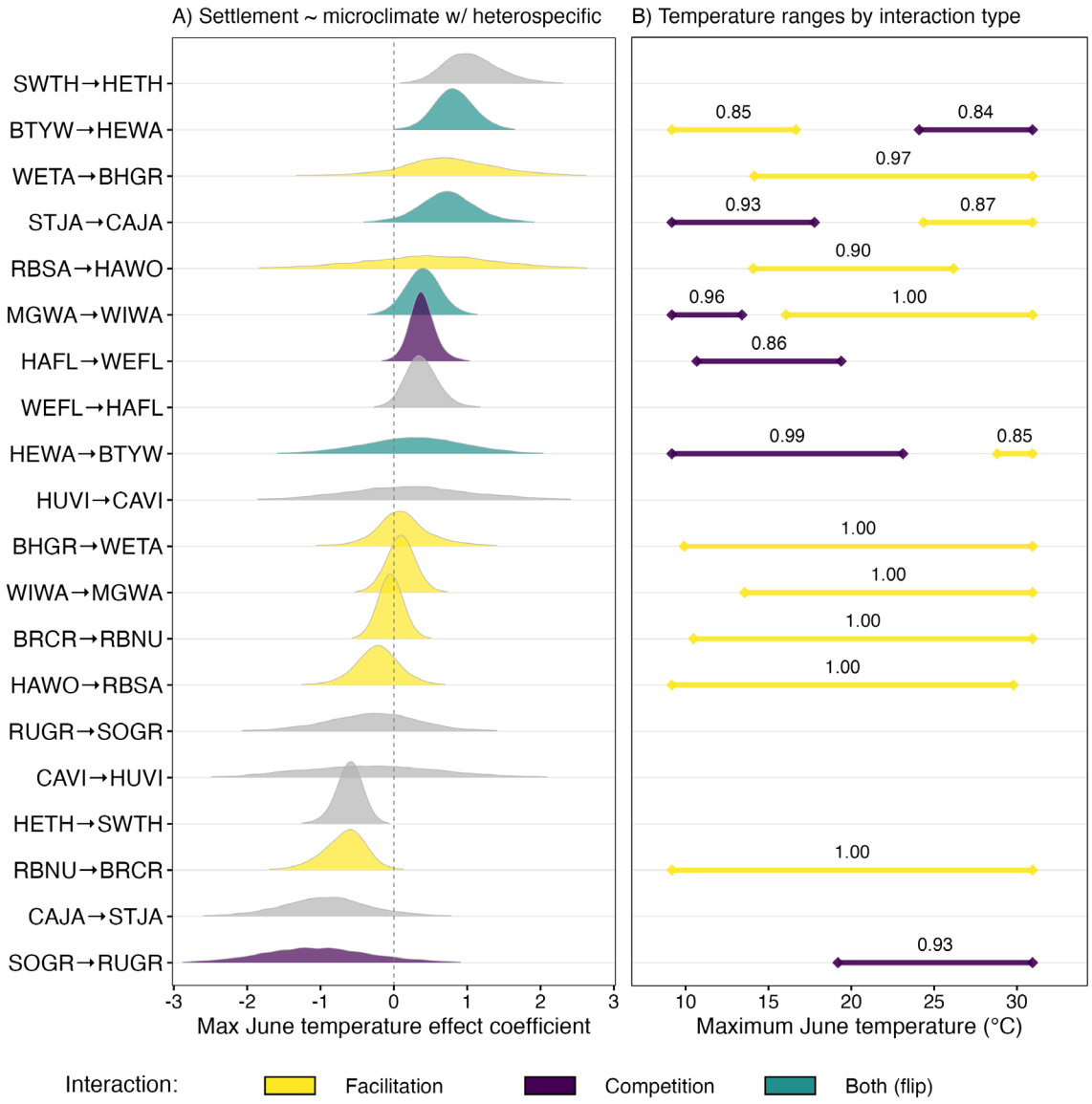


Figure 3. Microclimate effects on settlement when a heterospecific is present (A) and the temperature ranges where statistically supported interactions occur (B). (A) Posterior distributions of the effect coefficient of maximum June temperature on settlement for each species pair in each direction (A→B and B→A) when a heterospecific is present. Distribution colors reflect the overall interaction type: yellow = facilitation, purple = competition, teal = both (flip), and gray = no supported interaction (posterior probability < 0.8). Distributions are ordered by effect size (largest positive at top to largest negative at bottom). The dashed vertical line at zero indicates no effect. (B) The temperature ranges where supported interactions occur. The colored bars show the temperature ranges (from Table 1) where competition (purple) and facilitation (yellow) are significant (posterior probability > 0.8). The numbers above the bars are the posterior probabilities of the interaction type. No bars present for a species pair reflects no supported species interaction. See Fig. 2 caption for species common names.

competitive ones. The presence of one species increased probability of another going locally extinct in only four out of 20 pairings (1) western flycatcher–Hammond's flycatcher, 2) Steller's jay–Canada jay, 3) hermit thrush–Swainson's thrush, 4) hermit warbler–black-throated gray warbler; Supporting information). Eight species pairs showed strong support for attraction along at least part of the microclimate gradient; that is, the presence of one species reduced the likelihood that the second species would vacate a site across years (Supporting information). For example, the probability of brown creepers persisting across years at sites with warm microclimates was higher when red-breasted nuthatches were present (posterior probability of attraction = 1.0), but this heterospecific effect dissipated in cool microclimates (Supporting information).

Models for local persistence did not consistently support the hypothesis that colder microclimates should show greater evidence for facilitative effects. For several species' pairs (e.g. hermit warbler: black-throated gray warbler, Canada jay: Steller's jay, brown creeper: red-breasted nuthatch, Supporting information), persistence was enhanced by the presence of

Table 1. Posterior probability of species interaction effects (competition or facilitation) on settlement in differing microclimatic contexts. Bold indicates that the probability of either competition or facilitation is greater than 0.8. In instances where posterior probabilities of attraction or competition occur, we report the range of microclimatic temperatures (Min, Max in °C) over which these behaviors occurred. A posterior probability of competition or attraction greater than 0.80 (in bold) was considered evidence of repulsion or attraction, respectively, and will have a corresponding temperature range, otherwise NA for not applicable. Prob = probability, Max T = maximum temperature in °C, Min T = minimum temperature in °C. See Fig. 2 caption for species common names.

| Species pair | Prob of competition | Min T competition | Max T competition | Prob of facilitation | Min T facilitation | Max T facilitation |
|---|---|---|---|---|---|---|
| RUGR_SOGR | 0.628 | NA | NA | 0.701 | NA | NA |
| **SOGR_RUGR** | **0.929** | **19.195** | **30.938** | 0.755 | NA | NA |
| **HAWO_RBSA** | 0.226 | NA | NA | **1.000** | **9.173** | **29.783** |
| **RBSA_HAWO** | 0.332 | NA | NA | **0.898** | **14.075** | **26.166** |
| WEFL_HAFL | 0.630 | NA | NA | 0.477 | NA | NA |
| **HAFL_WEFL** | **0.859** | **10.676** | **19.391** | 0.489 | NA | NA |
| CAJA_STJA | 0.800 | NA | NA | 0.459 | NA | NA |
| **STJA_CAJA** | **0.925** | **9.173** | **17.779** | **0.868** | **24.358** | **30.938** |
| HUVI_CAVI | 0.507 | NA | NA | 0.657 | NA | NA |
| CAVI_HUVI | 0.582 | NA | NA | 0.712 | NA | NA |
| WETA_BHGR | 0.413 | NA | NA | **0.971** | **14.140** | **30.938** |
| **BHGR_WETA** | 0.221 | NA | NA | **0.999** | **9.914** | **30.938** |
| **WIWA_MGWA** | 0.556 | NA | NA | **1.000** | **13.552** | **30.938** |
| **MGWA_WIWA** | **0.960** | **9.173** | **13.400** | **1.000** | **16.058** | **30.938** |
| HETH_SWTH | 0.451 | NA | NA | 0.784 | NA | NA |
| SWTH_HETH | 0.568 | NA | NA | 0.505 | NA | NA |
| **HEWA_BTYW** | **0.994** | **9.173** | **23.116** | **0.847** | **28.803** | **30.938** |
| **BTYW_HEWA** | **0.839** | **24.097** | **30.938** | **0.853** | **9.173** | **16.646** |
| **RBNU_BRCR** | 0.125 | NA | NA | **1.000** | **9.173** | **30.938** |
| **BRCR_RBNU** | 0.254 | NA | NA | **1.000** | **10.480** | **30.938** |

a heterospecific – but at warm rather than cold sites. On the other hand, under cool temperatures, brown creepers were more likely to persist in the presence of red-breasted nuthatches, and western tanagers were more likely to persist when black-headed trosbeaks were present (Supporting information).

Species that were more closely related were more likely to display competitive interactions; the phylogenetic distance values describing the relatedness between species pairs was significantly negatively correlated with the probability of competition in both the settlement ($r = -0.58$, $p = 0.008$) and persistence models ($r = -0.51$, $p = 0.021$; Fig. 6A). We detected a non-significant, positive correlation between the probability of facilitation and relatedness for both processes we modeled (settlement $r = 0.39$, $p = 0.093$; persistence $r = 0.26$, $p = 0.263$, Fig. 6B), suggesting that species that are more distantly related are more likely to show facilitative relationships.

## Discussion

We used multi-species dynamic occupancy models and long-term, landscape-scale avian data to test whether the strength and direction of interspecific interactions are dependent upon environmental context. We found that species interactions were mediated by microclimate for some, but not all species pairs. Species pairs more often showed settlement dynamics that were indicative of attraction rather than repulsion. In some cases, competitive interactions at warmer climates flipped to become facilitative interactions in colder microclimates – support for the traditional stress gradient hypothesis as envisioned in plant ecology. However, in birds, the reverse was also often true: facilitative interactions amplified for some species under warm conditions. Furthermore, the strength of species interactions detected varied depending on the phylogenetic distance between pairs, with more closely related species tending toward more competitive interactions.

Overall, our results highlight the long-held assertion that species interactions exert a strong influence on realized species distributions (Hutchinson 1957, Diamond 1973). These interactions are still rarely taken into account when building species distribution models and predicting the future of biodiversity under climate change (Zarnetske et al. 2012). We argue that the methods we present are more rigorous than jSDMs which can be highly prone to type 1 error when it comes to identifying species interactions (Blanchet et al. 2020). Missing variables are more likely to cause issues in jSDMs because usually such models use data from a single time period and there is a high likelihood that the presence or absence of a heterospecific might simply signal the presence or absence of a critical habitat feature for the focal species. Of course, there is still the risk of a missing variable in our dynamic occupancy approach (Twining and Kellner 2025), but in stable environments (such as mature forest) this is less likely. Spurious detection of interspecific interactions would likely require that the missing variable be something dynamic (e.g. arrival of insect populations, sudden arrival of cold weather), but that these events coincide systematically in time with the arrival of competitor or facilitator species. One mechanism for such cross-species correlated

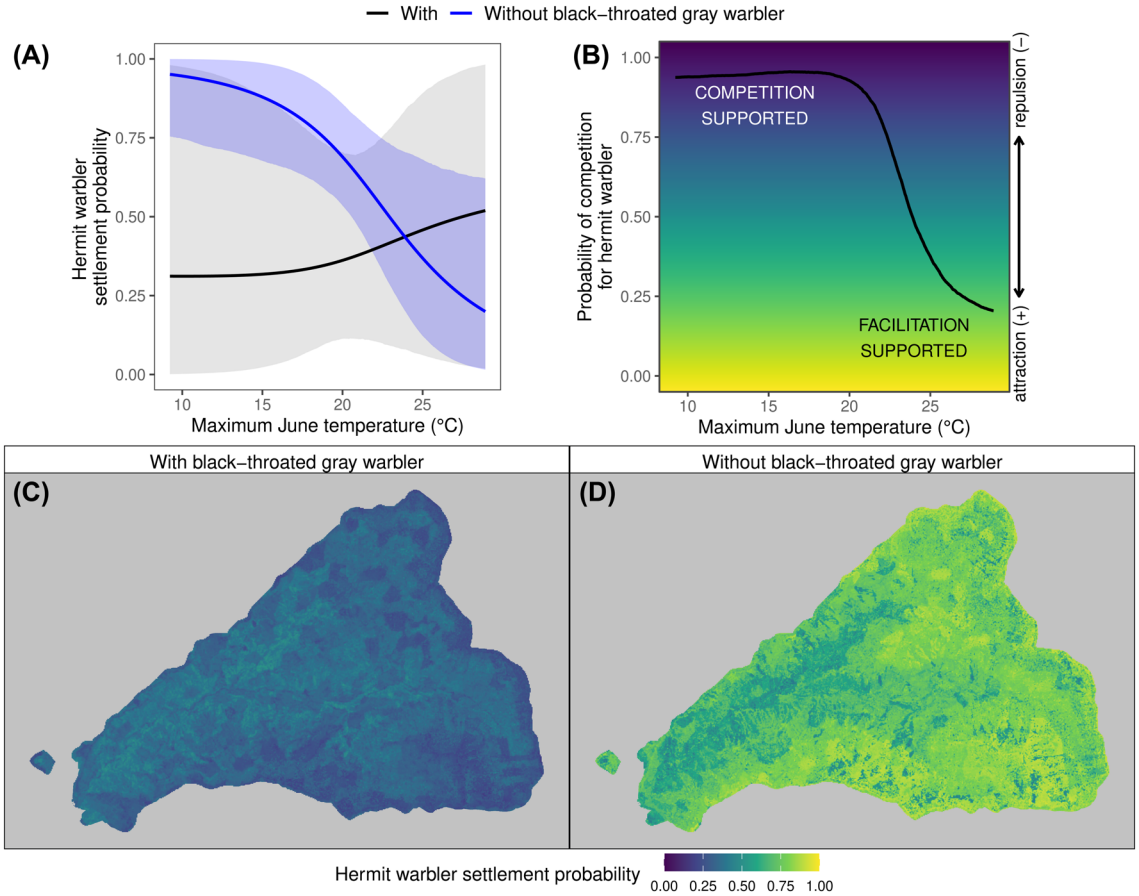


Figure 4. An example of a species in which the direction of interspecific interactions (competitive, facilitative) is contingent on environmental context. (A) Hermit warbler settlement is positively associated with cool microclimates but is reduced in the presence of black-throated gray warblers. Hermit warblers are much less likely to settle sites with warm microclimates if black-throated gray warblers are present. Blue lines represent the effect of microclimate on settlement in the absence of heterospecifics, and black lines show the effect in the presence of heterospecifics (shading represents 95% credible intervals). (B) Hermit warbler probability of competition across a gradient in maximum June temperature. Facilitation is supported in warmer locations and competition at cooler sites. Hermit warbler probability of competition across a gradient in maximum June temperature. Hermit warbler probability of settlement (low = purple, high = yellow) across the HJ Andrews landscape with (C) and without (D) black-throated gray warbler. Sites with lower max June temperatures show higher settlement (areas in green and yellow).

effects could be if both members of a species pair overwintered in similar locations, and habitat or climate in those locations changed, resulting in correlated persistence/settlement patterns. As our study is correlative, we cannot rule out the possibility that this occurred. Only true experiments with controls – in which species are experimentally removed (Martin and Martin 2001) or added (Betts et al. 2010) can unambiguously detect interaction effects, but such experiments can be extremely challenging logistically, especially at broad scales, and may be ethically fraught (Vucetich and Nelson 2007).

Tests of future projections from species distribution models often reveal quite poor prediction success (Betts et al. 2019, Briscoe et al. 2023). A next step, given the species interactions we observed, is to develop new models that incorporate interactions into estimates about the future of biodiversity under global change. The most effective way to do this may be via process-based models, that incorporate data on dispersal, species interactions and demography into future projections (Evans et al. 2016). An additional avenue might be to develop statistical approaches that iteratively estimate the distributions of one species based on the predicted distribution of another in each time step. This approach has an existing analogue in spatial ecology in which spatial clustering of species is estimated for unmeasured parts of the landscape in a spatially iterative fashion via Gibbs sampling (Augustin et al. 1996).

In the absence of quantitative predictions, species interaction models may nevertheless inform hypotheses about the fate of species under global change. For instance, hermit warblers are on the decline at HJA, particularly in warm microclimates (Kim et al. 2022). According to our findings, this should competitively release black-throated gray warblers at warm, low-elevation, second growth sites, but continued presence of hermit warblers at cool, higher elevations and in old growth may hinder settlement of these areas. In another

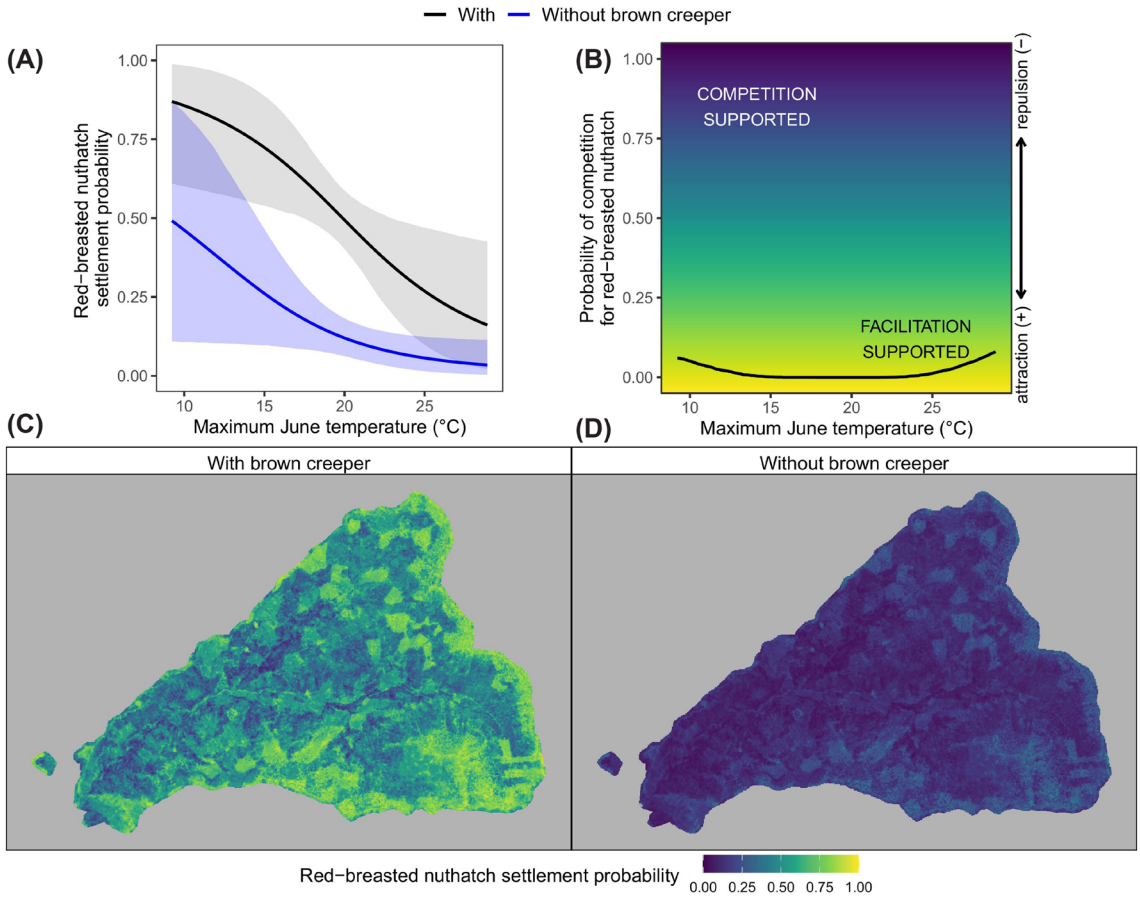


Figure 5. An example of a purely facilitative interaction occurs between red-breasted nuthatch and brown creeper. (A) Red-breasted nuthatches are likely to settle any site in the presence of brown creepers, although settlement decreases for both species at warmer temperatures. (B) Probability of competition is low across the entire microclimate gradient displaying high attraction. Red-breasted nuthatch settlement probability (low = purple, high = yellow) across the HJ Andrews landscape with (C) and without (D) brown creeper. All sites show higher settlement with the heterospecific present, but particularly so for cool microclimates.

example, Wilson's warblers are exhibiting long-term declines at the HJA (Kim et al. 2022) which, given an apparent facilitative relationship with MacGillivray's warbler (Fig. 3, Supporting information), could hinder future colonization of the latter species at warmer, lower elevation sites. If the species interactions we report in this study persist over the long term, we expect coinciding declines in facilitative species pairs.

It is commonly believed that competitive interactions are a key driving force in species distributions (Diamond 1973). Following this theory, it is therefore surprising that most of the interactions that we observed tended to be facilitative and indicate attraction between species pairs. Nevertheless, there are several instances when the presence of other species may increase fitness. For instance, Forsman et al. (1998) showed experimentally that migrant bird species (e.g. redwings *Turdus iliacus*) were more likely to settle in locations with high resident activity (willow tits *Poecile montanus*, Siberian tits *Poecile cinctus* and great tits *Parus major*). One species may use the presence of another as a signal that a site is high in food resources, or that predators are comparatively less risky. Indeed, the tendency for both tropical and temperate bird species to join mixed-species flocks in the interest of foraging efficiency is well established (Graves and Gotelli 1993), as are the benefits of multi-species anti-predatory behavior (Curio et al. 1978). Such habitat copying is becoming well studied within species (Nocera et al. 2006, Betts et al. 2008, Fletcher 2009), but relatively little experimental work has tested for interspecific effects. One of the few experimental studies of long-term heterospecific interactions (Dhondt 2023) found that when blue tit *Poecile caeruleus* density was boosted, breeding dispersal from sites by great tits declined and juvenile dispersal into sites increased. This was taken as an indication of heterospecific attraction.

How might two migrant species use each other as cues in habitat selection? One possibility is that a later arriving species might use an early arriving species as an indicator of high food availability or low predation pressure. But this would not explain the sometimes relatively symmetrical positive interactions we observed in species pairs (e.g. MacGillivray's warbler, Wilson's warbler). We speculate that these symmetrical positive interaction cases are driven by differences in arrival times among age classes of each species (Woodrey and Chandler

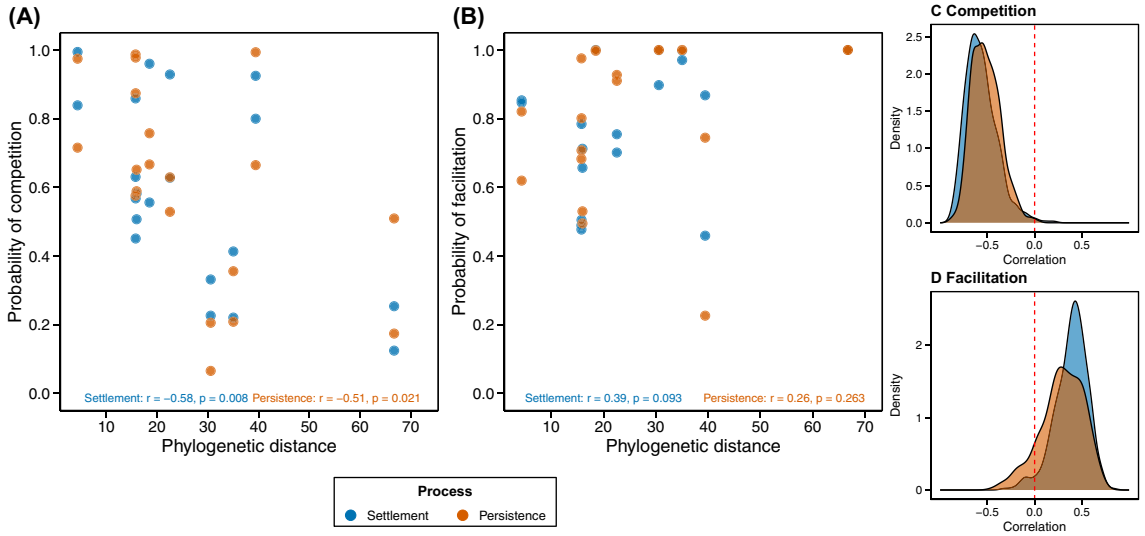


Figure 6. Relationship between interaction strength (as measured by probability of competition (A) and facilitation (B)) and phylogenetic relatedness (distance) between all 20 combinations of the 10 species pairs. Points represent pair probabilities for settlement (blue) and persistence (orange) processes. Bootstrapped distributions of Pearson's correlation coefficients (r) are displayed for competition (C) and facilitation (D). Correlation coefficients (r) and p values are displayed on each panel. Competition tends to increase for more related species, but facilitation tends to decrease with relatedness.

1997). Younger, late-arriving birds may use cues from earlier arriving heterospecific adults in settlement. Playback studies, which use recordings of one species to attract another, could be implemented during the early migration period to enable experimental testing of this hypothesis (Fletcher 2009, Forsman and Martin 2009).

Although we found support for the strength and direction of species interactions to vary across a microclimate gradient, the environmental context for competitive versus attractive effects were not consistent across species pairs. As mentioned above, in plants, the 'stress' in the stress-gradient hypothesis generally refers to geographic locations that are particularly cold, or dry. Most work to date on plants has therefore shown greater facilitation at higher elevations and latitudes, with greater degrees of competition in low elevation and equatorial regions (LaManna et al. 2022). This might not be the case for birds, however, as they are highly vagile. As is clear from the wide range of species' settlement and persistence responses to microclimate in our study, for many northern distributed species, colder may not necessarily be more stressful than warm temperatures. We argue that the stress-gradient hypothesis likely needs to consider individual species' thermal tolerances and the distribution within their native ranges. Unfortunately, such physiological thermal tolerances are not well known in most endotherms, including birds (Londoño et al. 2016). However, it is intuitive that in a temperate Mediterranean environment such as in the western Cascade Range of the Pacific Northwest USA, where moisture may be limiting in the post-breeding period, that aridity and heat could comprise the most stressful conditions. When rainfall is low and conditions hot, food likely becomes limiting (Schowalter 1995, Finn et al. 2022) and facilitation (in this case, driven by habitat selection or foraging) may be most adaptive.

In conclusion, our long-term data provide correlative evidence for the importance of heterospecific interactions in driving colonization and persistence dynamics in a forest bird community. Apparent facilitative interactions were generally more common than competitive ones, but interaction direction tended to be dependent on forest microclimate. Species' ecological traits likely play a role in determining the nature of these interactions through the degree of overlap in resources and timing, particularly if they are more closely related. Next steps in this work will be to assemble multiple long-term distributional datasets for animals, to enable testing the degree to which the patterns we observed are more general, and to uncover whether life history traits can predict the direction of species interactions.

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*Conflict of interest* – The authors declare no conflict of interest.

### Author contributions

**Sarah J. K. Frey**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Brian D. Gerber**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Adam S. Hadley**: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Hankyu Kim**: Data curation (equal); Project administration (equal); Writing – review and editing (supporting). **Madison Sutton**: Data curation (equal); Project administration (equal); Writing – review and editing (supporting). **Nina C. Ferrari**: Data curation (equal); Project administration (equal); Writing – review and editing (supporting). **Matthew G. Betts**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/ecog.08313.

### Data availability statement

Data are available from: https://portal.edirepository.org/nis/mapbrowse?packageid=edi.359.3 (Betts et al 2026). Stastical code and data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pg4f4qs58 (Frey et al. 2026).

### Supporting information

The Supporting information associated with this article is available with the online version.

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