

# Direct and indirect effects of climate on bird abundance along elevation gradients in the Northern Appalachian mountains

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## Funding information

Northern States Research Cooperative, Grant/Award Number: 16-CO-11242307-009; US Forest Service Northern Forest Research Station; Department of Interior's Northeast Climate Adaptation Science Center

Editor: Jose Lahoz-Monfort

## Abstract

**Aim:** The stratification of organisms along elevational gradients is widely reported, with montane communities characterized by species occurring in relatively small and isolated populations; these species are of considerable interest to ecologists and conservationists. This stratification is generally attributed to climatic zonation. Evidence that species are shifting upward in elevation has fuelled speculation that species are tracking their climatic niches in response to climate change. Uncertainty regarding the degree to which climate directly influences species abundance versus the degree to which climate has an indirect influence via vegetation represents a key impediment to understanding the ecology of montane species; here, we evaluate these direct and indirect effects.

**Location:** White Mountains, New Hampshire, USA.

**Methods:** We used N-mixture models to correct for imperfect detection of species, principal component analysis to represent gradients in vegetation structure and composition and structural equation models to assign variation to the direct and indirect effects of climate upon birds.

**Results:** Analysis of 13 species revealed that climate exerts direct influences on bird abundance and indirect influences mediated by vegetation composition and structure. All species exhibited indirect effects of climate via forest habitat, with 77% exhibiting both direct and indirect effects and 53% exhibiting stronger indirect effects.

**Main conclusions:** We provide insight into the mechanistic pathways of how climate influences the distribution of species along elevational gradients, underscoring the complex vulnerability of species to climate change. Our results reveal that the majority of species experience both direct and indirect effects of climate, implying that forests play a key role in mediating climate effects. For species that are primarily influenced by climate directly, typical climate envelope models may continue to be informative, but for the majority of the species included in this study, we show that distribution models should also include measures of habitat.

## KEYWORDS

climate change, climate effects, montane bird abundance, spruce-fir ecosystems, structural equation modelling

## 1 | INTRODUCTION

The stratification of species across elevation gradients is a well-documented phenomenon in montane systems around the world (Cadena et al., 2012) and has been widely reported in birds (Kendeigh & Fawver, 1981; Londoño, Chappell, Jankowski, & Robinson, 2016; Price et al., 2014; Remsen, 1985; Ruggiero & Hawkins, 2008; Tingley, Koo, Moritz, Rush, & Beissinger, 2012). The Northern Appalachians, which extend (North to South) along Maritime Canada to Maine, the White Mountains of New Hampshire, the Green Mountains of Vermont, and Tug Hill and Adirondack ranges of New York, also present a well-documented elevational stratification of avian species (Able & Noon, 1976; DeLuca, 2013; Sabo, 1980). This stratification often involves the relegation of species to spatially limited and geographically isolated areas (Cadena et al., 2012). The resulting high levels of specialization and endemism contributes greatly to regional biodiversity (Cadena et al., 2012; Rahbek, 1997; Rahbek et al., 2007; Ruggiero & Hawkins, 2008); subsequently, montane systems have high conservation value (Boyle & Martin, 2015). Although previous work suggests that climate and habitat drive species distributions along elevation gradients (Able & Noon, 1976; Elsen, Tingley, Kalyanaraman, Ramesh, & Wilcove, 2017; Terborgh & Weske, 1975; Tingley et al., 2012), the interplay between these causative factors has not yet been quantified.

Recent changes in passerine distributions and abundances have been observed occurring across latitude and elevation gradients across the world (Auer & King, 2014; Hickling, Roy, Hill, Fox, & Thomas, 2006; Parmesan, 2006; Parmesan & Yohe, 2003; Tingley, Monahan, Beissinger, & Moritz, 2009). In the Northeastern United States, there is evidence that populations of high-elevation montane bird species have been declining for decades (Hill & Lloyd, 2017; King, Lambert, Buonaccorsi, & Prout, 2008; Lambert, King, Buonaccorsi, & Prout, 2008; Studds, McFarland, et al., 2012), including state-level extirpation of high-elevation endemic species (Rimmer & McFarland, 2013). Moreover, in the White Mountains of New Hampshire, low-elevation birds have been shown to have shifted their range over 100 m upslope while high-elevation birds have shifted their ranges downslope over the same 19 year period (DeLuca & King, 2017).

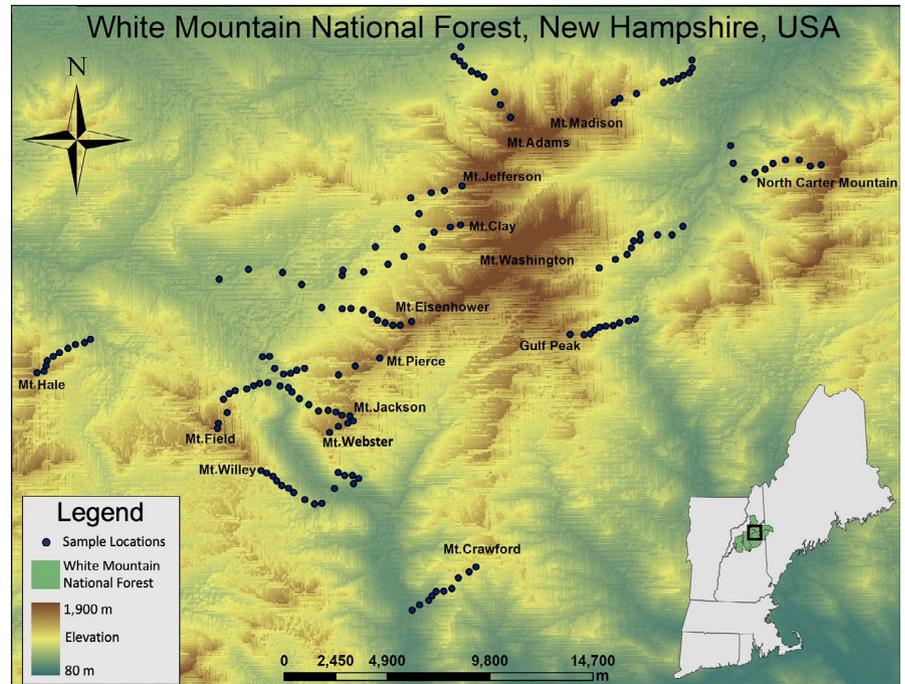
These changes in bird populations occur alongside decades of increasing temperature and precipitation associated with the regional effects of global climate change (Grant, Pszenny, & Fischer, 2005; Hamburg, Vadeboncoeur, Richardson, & Bailey, 2013; IPCC, 2014; Seidel et al., 2009; Wright, 2009). Since climate is known to be a key correlate of the geographic distribution of birds (Root, 1988), climate change is suspected as a major driver underlying observed changes in bird populations across North America (Leech & Crick, 2007; Parmesan & Yohe, 2003; Tingley & Beissinger, 2013; Tingley et al., 2012; Walther et al., 2009), including the Northern Appalachians (Rodenhouse, 1992; Rodenhouse et al., 2007). However, there is also indication that the forest community is changing in this region (Beckage et al., 2008; Foster & D'Amato, 2015), with evidence that the low-elevation northern hardwood forests are moving up

in elevation in many areas and high-elevation spruce-fir forests are moving down in others (Foster & D'Amato, 2015). Given that the composition and structure of forests are also known to exert a fundamental influence on bird communities (DeGraaf, Hestbeck, & Yamasaki, 1998; Holmes & Sherry, 2001; MacFaden & Capen, 2002), such phenomena presents the possibility that the elevational shift of bird species may be partially or wholly attributable to an indirect response to climate change as birds track shifts in favourable habitat conditions that are in turn influenced by changing climate.

Disentangling direct and indirect influences of climate on forest species is important given the strong potential for the future decoupling of current climate/forest conditions, with forest processes predicted to lag behind projected rapid changes in climate (Iverson, Prasad, & Matthews, 2008; Iverson, Schwartz, & Prasad, 2004; Rustad et al., 2012; Stralberg et al., 2015; Wang, He, Thompson, Fraser, & Dijak, 2002). Additionally, bird distributions have also been found to lag behind their measured climate niche (Devictor, Julliard, Couvet, & Jiguet, 2008). Such a decoupling would likely have negative effects upon forest birds due to differential changes in niche parameters (Leech & Crick, 2007; Stralberg et al., 2015); this decoupling would also undermine the assumptions underpinning many species distribution models (Araújo & Peterson, 2012; Guisan & Thuiller, 2005). While recent efforts have focused on describing the effects of climate and habitat upon bird occupancy (Frey, Hadley, & Betts, 2016) and abundance (Elsen et al., 2017) along elevation gradients, the statistical methods employed in these studies do not account for indirect effects stemming from the causal relationship between climate and forests. As such, this work does not effectively isolate the concurrent roles that climate and habitat have in affecting species abundance, instead relying on the assumption of independence between these predictors. Studies explicitly distinguishing the mode and degree of influence of climate upon species abundance, both directly as well as indirectly via effects of climate on the forest community, provide information critical to reducing the uncertainty associated with predictive models used to prescribe actions to conserve priority species in a changing climate.

Given the regionally observed changes in climate, forests and bird abundance and distribution, we examined the degree to which the abundance of birds within Northern Appalachian montane forests are driven by the direct effect of climate (i.e., temperature and/or precipitation) as well as concurrent indirect effect of these climate variables mediated by gradients of forest structure and composition. We hypothesized that precipitation (Martin, 2001; McCain & Colwell, 2011; Tingley et al., 2012) and mean temperature (Tingley et al., 2012) as well as forest structure and composition (DeGraaf et al., 1998; Holmes & Sherry, 2001; MacFaden & Capen, 2002) are important predictors of bird abundance along environmental gradients. Forest processes are also known to be, in part, determined by climate (Iverson et al., 2008; Matthews, Iverson, Prasad, & Peters, 2011; Rustad et al., 2012). Here, we develop and test a standard causal model (Grace, 2006; Shipley, 2016) for 13 avian species describing the relative influence of climate via these direct and indirect pathways on montane bird abundance.

**FIGURE 1** Map of 15 elevational transects comprising 150 sample points located within the Presidential region of the White Mountain National Forest, New Hampshire, USA. A subset of 100 points were sampled in 2014 and subsequently resampled in 2015 with the addition of 5 new transects representing 50 additional locations sampled only in 2015



## 2 | METHODS

### 2.1 | Site selection

We quantified bird abundance, ambient temperature and forest structure and composition along elevational transects in the Presidential Range of the White Mountains, New Hampshire, USA (N44°7' to N44°21' W71°27' to W71°14'; Figure 1) at 100 points in 2014 and these same locations plus 50 additional points in 2015. Sample locations ranged in elevation from 319 m to 1,412 m and were systematically stratified across the transition from low-elevation northern hardwood forest into high-elevation boreal forest such that points were located at least 250 m apart along transects, and when possible, no greater than 100 m apart in elevation (Figure 1). Located within the White Mountain National Forest, which is 303,930 ha in extent and is 97% forested, the region of our study is primarily used for non-motorized recreational activities (USDA Forest Service, 1986); most points ( $n = 137$ ) were located along recreational hiking trails. Previous research has shown birds in the study area to be unaffected by trails, and thus, trailside point counts are an effective means of sampling the bird community (DeLuca & King, 2014). To sample the full elevation gradient, some transects extended to areas with no trails; these sample locations ( $n = 13$ ) were placed >75 m from the nearest road.

### 2.2 | Bird surveys

Bird abundance was quantified at each point by experienced observers using 10-min point counts during which all birds seen or heard within 50 m were recorded, with detections divided into 2.5 min time intervals (Chandler, Royle, & King, 2011). Surveys began 30 min before dawn and concluded within 5 hr. Time of day, date, ambient temperature, observer, wind speed, cloud cover and amount of

ambient stream noise were recorded by the observer at the start of each survey. Surveys were conducted neither during precipitation events nor during high wind. The original 100 points were surveyed three times during the peak of the avian breeding season between 1 June and 11 July 2014. In 2015, the original 100 sites, plus the 50 additional locations were surveyed three times between 3 June and 27 June. The direction in which points were surveyed along each transect were alternated to control for time of day (DeLuca & King, 2014).

### 2.3 | Vegetation measurements

We measured vegetation structure and composition within each 50 m radius point count plot using two overlapping plots of 11.3 m and 5 m. Within the 11.3 m plot, centred on the point count location, we recorded species and diameter at breast height (DBH; 1.37 m) of all individual trees with stems  $\geq 8$  cm DBH. Within the 5 m radius plot, we recorded counts of live woody stems by two size classes; “regenerating” sized stems ( $\leq 2.5$  cm diameter at 10 cm high) and “sapling” sized stems ( $> 2.5$  cm and  $< 8$  cm diameter at 10 cm high); stems  $> 8$  cm diameter at 10 cm high in the 5 m plot were measured as part of the 11.3 m plot. Using measures from the 11.3 m plot, we then calculated species importance values, a continuous variable, describing the relative dominance of each species at each site  $\geq 8$  cm DBH as well as counts of stems binned into size classes previously established as standard for wildlife investigations in the Northeast (DeGraaf & Yamasaki, 2001). Species importance values and counts of stems by size class were then used in subsequent analysis.

### 2.4 | Climate

We used Thermocron® iButton temperature loggers (Maxim Integrated) to record ambient temperature at a synchronized hourly

frequency at each point count location for both years. Instruments were placed within a shielding apparatus affixed atop 1 m tall posts, oriented to the North, and located within 5 m of the plot centre (Brooks & Kyker-Snowman, 2008; Lumpkin & Pearson, 2013). We then calculated the mean hourly temperature at each sample location between 16 June and 31 July in 2014 and 2015; the period of peak breeding activity for songbirds in the study area, ensuring that  $\geq 2$  bird surveys were conducted while temperature measures were being collected in each year. Mean temperature values calculated for each site by year were then used in subsequent analysis.

To capture the broad pattern of increasing precipitation along elevation due to orographic cooling (Sugg & Konrad, 2017), a phenomena often cited as a driver of species distributions (Tingley et al., 2012), we used a spatial dataset developed by McGarigal, Compton, Plunkett, Deluca, and Grand (2016). These data are derived from PRISM (Daly, Gibson, Taylor, Johnson, & Pasteris, 2002) and are a 30 year mean (centred on 1995) of cumulative growing season (May to September) precipitation values statistically downscaled to 800 m cells and resampled to a 30 m grid (see Appendix S1). We then z-score standardized these values, serving to relativize values across sample locations, prior to further analysis. By taking into account topography and elevation, the 800 m PRISM data effectively predict broad spatial patterns of precipitation and have been shown to perform well, even in mountainous regions (Daly, 2006). The 30 m resampling allows for a finer resolution of the increase in precipitation known to occur along elevation within each 800 m cell. These data have been independently validated from 174 weather stations, 53 of which are in New Hampshire, and found to have strong agreement ( $R_c = 0.92$ ) with on-the-ground observations of precipitation, performing better than any data product or measure available for this region (McGarigal et al., 2016). Due to the strong relationship between elevation and precipitation in our study region (as noted above), we tested the relationship that the downscaled and interpolated precipitation values increase with elevation across our bird sampling locations with a linear regression model. These precipitation data are incorporated in fine-scale wildlife species distribution models and have been evaluated and used by the US Fish and Wildlife Service to inform landscape conservation design (Loman et al., 2017, 2018).

## 2.5 | N-mixture modelling

From among 59 species detected within a 50 m radius of the plot centre (Appendix S2), 13 passerine species were selected for analysis based on the criteria of being detected on  $\geq 25\%$  of sites sampled in 2014 and 2015 (Appendix S3). We chose this conservative measure of sample sufficiency in order to avoid making incomplete inferences regarding habitat/climate relationships for species that were relatively rare across the sample area, and thus, least likely to produce dependable results in subsequent analysis. However, the remaining 13 species reflect a broad sample of species from across the elevation gradient, including species associated with each major forest type and reflecting many foraging and nesting guilds. Because field-estimated bird abundance measures are known to be inaccurate due

to imperfect detection, we first accounted for detectability by estimating abundance ( $\lambda$ ), taking into account detection probability ( $p$ ) using generalized multinomial-mixture models (Chandler et al., 2011; Kery & Royle, 2015). A year term was specified on the state side of all candidate models to account for inter-year variation in population abundance. The availability parameter ( $\Phi$ ) was set at the model intercept for all candidate models, utilizing counts of new individuals detected across sub-intervals within primary survey periods to account for variation in detectability that stems from temporary immigration and emigration (Chandler et al., 2011). We used Akaike's information criterion (AIC; Burnham & Anderson, 2002) to evaluate the most relevant and parsimonious combination of covariates affecting the probability of detection ( $p$ ) for each species. Detection covariates, representing data limited to those recorded by the observer at the time of each survey, were as follows: time of day (time), date of survey (date), individual surveyor (observer), cloud cover (sky), wind speed (wind), ambient temperature (temp\_c) and ambient stream noise (stream). In order to avoid confounding the two stages of the analysis, we chose to only include variables likely affecting detectability in the N-mixture models. We chose to reserve variables or measures we posited as affecting abundance (i.e., climate and forests) for later inclusion as explanatory variables in the structural equation models. Top models were identified as those with the lowest AIC value relative to all other possible combinations of detection covariates, including a null; adhering to convention set forth by Burnham and Anderson (2002) we further identified models with approximately equal support as those within  $2 \Delta AIC$  of the top model. The goodness-of-fit (GOF) of the top models for each species were evaluated by comparing the calculated summed square of residuals (SSE) of the top models to those calculated from 500 bootstrap iterations. Top models whose SSE fell within the distribution of bootstrapped SSE values were deemed appropriately fit (Kery & Royle, 2015). A Poisson distribution was initially considered for the abundance parameter ( $\lambda$ ) for all species. If a top model did not fit the data based upon the bootstrapping procedure, the model selection process was re-run for that species using a negative binomial distribution and GOF of resulting top models reevaluated as before. Each of the models falling within  $2 \Delta AIC$  of the top model were then applied to the original observation data to predict a single corrected abundance estimate for each species, sample location and year. We then performed model averaging of values predicted from top models in order to minimize uncertainty associated with the model selection process and used these averaged values in subsequent analysis. This procedure ensures estimates of bird abundance used in subsequent analysis were unbiased by imperfect detectability due to survey-specific conditions or the model selection process. Generalized multinomial-mixture models were fit using the *gmultmix* function from the "unmarked" package (Fiske & Chandler, 2011) in R version 3.2.2 (R Core Team, 2015).

## 2.6 | Principal component analysis

We used principal component analysis (PCA) to describe gradients of forest structure and composition from a set of 12 forest variables

(Appendix S4; McGarigal, Cushman, & Stafford, 2013). We selected forest variables for inclusion in the PCA on the basis that (a) species had respective importance values of  $>0.25$  at a frequency of  $>0.05$  among the 150 sample sites and (b) size class variables represented  $>0.25$  relative proportion of the size classes occurring on a plot at a frequency of  $>0.05$  among 150 sample sites. We adopted these criteria on the basis that rare values stand to add little to the PCA (McGarigal et al., 2013). We used Monte Carlo randomization with 1,000 permutations to evaluate the significance of the eigenvalues of the first two principal component axis compared to those calculated under a null hypothesis. We then interpreted the biological meaning of the first two principal component axis based upon factor loadings of  $<-0.3$  and  $>0.3$  (McGarigal et al., 2013). The two principal component gradients produced by the PCA were then used in subsequent analysis. The PCA was conducted using the *prcomp* function in the base package of R version 3.2.2 (R Core Team, 2015) and the Monte Carlo randomization using the *ordi.monte* function from the “biostats” package (McGarigal, 2016), also in R.

## 2.7 | Structural equation modelling

We used a structural equation modelling (SEM) framework to distinguish between direct effects of climate (temperature and precipitation) on the corrected abundance estimates of the 13 forest birds and indirect effects of climate via gradients of forest structure and composition represented by the two principal components. Structural equation modelling, a multivariate form of linear regression, allows for the simultaneous parameterization of univariate relationships comprising direct effects as well as indirect effects comprised of multiple univariate relationships linked by mediating variables. These mediating variables serve as both response variables in one univariate relationship and predictors in another, serving to evaluate the covariance structure comprising a hypothesized causal system while teasing apart and isolating direct and indirect effects (Shipley, 2016).

We used a multi-group form of SEM to test for significant differences in the system between the two years as well as produce estimates of direct and indirect effects constrained to equality between both years of data and from all sites (Studds, DeLuca, Baker, King, & Marra, 2012). Prior to model fitting, we visually assessed linearity among variables comprising the SEM using scatterplot matrixes. This revealed the need for a quadratic term to be added to the two climate predictors of the second principal component. This resulted in an improvement in significance of path values associated with the quadratic PC2 component, indicating the addition of the quadratic term was supported. We specified correlations between the two exogenous measures of climate to account for possible collinearity between these variables (Shipley, 2016). Models were then fit using the Satorra-Bentler maximum likelihood test statistic, yielding scaled measures of model fit that are robust to deviations from multivariate normality (Satorra & Bentler, 1994). We used chi-square goodness-of-fit to assess the probability that the model fits the data given the hypothesized causal structure; with a significant probability ( $p \leq .05$ ) indicating a model poorly

supported by the data. We used additional and commonly adopted measures to further assess the fit of each model; Comparative Fit Index (CFI) and Tucker-Lewis Index (TLI) values  $>0.95$  indicate a good fit; Root Means Square Error of Approximation (RMSEA) values  $<0.07$  also indicate a good fit with values close to/at zero indicating an excellent fit (Hooper, Coughlan, & Mullen, 2008). These fit measures serve to evaluate the fit of models with minimized sensitivity to possible deviations from linear regression assumptions (Shipley, 2016). Standardized path coefficients calculated from appropriately fit models were deemed significant at an alpha of  $p \leq .1$ . Indirect effect values were deemed significant if all path coefficients comprising an indirect pathway were individually significant at an alpha of  $p \leq .1$ . We chose a 5% higher alpha than convention in order to mitigate risk of type II error stemming from known sensitivities of the SEM model framework (Shipley, 2016). Collectively, it is with these criteria that we base the final determination of our strictly confirmatory model as adequately representative of the system under investigation. Structural equation modellings were fit using the “lavaan” package in R version 3.2.2 (R Core Team, 2015; Rosseel, 2012).

For each species, we used an ANOVA test of invariance to evaluate the appropriateness of interpreting the path values calculated from a multi-group model solution where paths are constrained to equality between years (effectively evaluating a “year effect”). We also used ANOVA to evaluate the degree to which the addition of the 50 new sites the second year influenced the level of variability in path values calculated between years (effectively evaluating an additional “site effect”). For this test, a  $p$ -value  $>.05$  indicates a negligible level of variation in relationships (i.e., effects) of interest between each of the 2 years. Finally, for each species we evaluated the relative importance of direct and indirect effects by comparing absolute values of significant path coefficients comprising direct and indirect pathways.

## 3 | RESULTS

Generalized multinomial mixture models using a Poisson distribution fit adequately for 12 species with a negative binomial distribution fit for black-throated green warbler (*Setophaga virens*; Table 1). The year term was significant for all species except dark-eyed junco (*Junco hyemalis*). Of the eight detection covariates considered, all appeared in top models for one or more species (Table 1) with mean detection probability varying by species and year. The number of model formulations with approximately equal support to top models varied by species (see Appendix S5) however, model averaged values from these top models were nearly identical to values predicted from the most parsimonious model, indicating a high degree of agreement between top-ranked models (see Appendix S6).

Eigenvalues for the first two principal components were significant ( $p \leq .001$ ), explaining 41% of variation in the data. The first principal component represents a gradient from high-elevation forest of medium DBH balsam fir (*Abies balsamea*) mixed with paper

**TABLE 1** Results of generalized multinomial mixture model selection; displaying top models based upon AIC considering all possible combinations of 8 detection covariates including a null model where the detection parameter ( $p$ ) was set at its intercept;  $p$  describes the probability of detection of a species

Common name (Scientific name)	Code	Model	$K$	$\Delta AIC$	$W_i$	$R^2$
Blackburnian Warbler ( <i>Setophaga fusca</i> )	BLBW	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{observer} + \text{temp}_c + \text{time} + \text{wind})$	10	1.82	0.44	0.14
Blackpoll Warbler ( <i>Setophaga striata</i> )	BLPW	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date})$	5	0.66	0.09	0.03
Black-throated Blue Warbler ( <i>Setophaga caerulescens</i> )	BTBW	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{temp}_c + \text{time} + \text{wind})$	8	0.77	0.20	0.11
Black-throated Green Warbler ( <i>Setophaga virens</i> )	BTNW	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{observer} + \text{wind})$	9	0.27	0.04	0.03
Dark-eyed Junco ( <i>Junco hyemalis</i> )	DEJU	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{stream})$	5	0.06	0.04	0.11
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	GCKI	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{observer} + \text{sky} + \text{stream} + \text{time} + \text{wind})$	11	1.29	0.36	0.18
Magnolia Warbler ( <i>Setophaga magnolia</i> )	MAWA	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{stream} + \text{time} + \text{wind})$	8	1.69	0.19	0.08
Yellow-rumped Warbler ( <i>Setophaga coronata</i> )	MYWA	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{observer} + \text{sky} + \text{stream} + \text{temp}_c + \text{time})$	10	0.99	0.13	0.11
Ovenbird ( <i>Seiurus aurocapilla</i> )	OVEN	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{stream} + \text{wind})$	7	0.50	0.09	0.11
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{stream} + \text{temp}_c + \text{wind})$	8	1.71	0.33	0.13
Swainson's Thrush ( <i>Catharus ustulatus</i> )	SWTH	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{observer} + \text{stream} + \text{temp}_c + \text{time})$	10	1.65	0.34	0.28
Winter Wren ( <i>Troglodytes hiemalis</i> )	WIWR	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{date} + \text{time} + \text{wind})$	7	1.30	0.12	0.06
Yellow-bellied Flycatcher ( <i>Empidonax flaviventris</i> )	YBFL	$\lambda(\text{year}) \sim \Phi(1) \sim p(\text{observer} + \text{stream} + \text{time} + \text{wind})$	9	0.24	0.09	0.11

A year term, describing the state of the superpopulation, was included for  $\lambda$  in all models with the availability term ( $\Phi$ ), describing the subset of the superpopulation available for detection during a given survey, set at the model intercept. Results for all models within  $2 \Delta AIC$  of top models can be found in Appendix S5; model averaged values from top-ranked models were used in subsequent analysis. Avian abundance data for 13 species from 150 survey sites sampled during 2014 and 2015 along elevational gradients in the White Mountains, New Hampshire.

birch (*Betula cordifolia*) to lower elevation forests characterized by small and large DBH red spruce (*Picea rubens*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*; Appendix S7). The second principal component describes a gradient between red spruce dominated forest, intermixed with regenerating stems and larger DBH trees, transitioning into a hardwood-dominated forest comprised of sugar maple and American beech (Appendix S7).

Pairwise tests of temperature for the 100 locations sampled both years revealed no difference ( $t = -2.29^{-15}$ ,  $df = 99$ ,  $p = 1.00$ ) between years. The mean seasonal temperature recorded for the lowest elevation sites of each transect across both years was 16.4°C ( $\pm 0.52$  SD). The mean seasonal temperature recorded for the highest elevation sites across both years was 13.4°C ( $\pm 0.85$  SD). Across all bird sampling locations, interpolated precipitation values increased significantly with increasing elevation ( $r = -.99$ ,  $p\text{-value} = <.0001$ , adjusted  $R^2 = 0.832$ ).

For the majority of species (10 of 13), multi-group SEMs fit the data well across all GOF measures considered ( $df = 18$ ,  $p > .05$ ,

CFI > 0.95, TLI > 0.95, RMSEA < 0.07; Hooper et al., 2008); for two species (yellow-rumped warbler [*Setophaga coronate*] and black-throated green warbler [*S. virens*]) models provided reduced but adequate fit when considering all GOF measures alongside path significance ( $p\text{-value} \leq .1$ ; Grace, Anderson, Olff, & Scheiner, 2010). The ANOVA test of invariance revealed no difference between years ( $p\text{-value} \geq .05$ ) when considering the full dataset for all species except winter wren (*Troglodytes hiemalis*) and yellow-rumped warbler (Appendix S8). However, for these two species, this variation was non-significant when models were run with data from just the 100 replicate sites (Appendix S8)—indicating these results may not be due to variation in relationships of interest between years (i.e., a year effect) but rather an artefact of the addition of data from the 50 new sites in 2015 to the model (i.e., a site effect). Therefore, we deemed it appropriate to interpret the constrained SEM model results for all 13 species utilizing the full dataset.

Among all species, model solutions explained 8%–57% of variation in avian abundance in 2014 and 8%–61% in 2015 (Table 2). Interpretation of SEM path coefficients, representing the direct and

**TABLE 2** Results of multi-group SEM constraining factor loading (path coefficients) to equality between year 1 (2014; 100 sample sites) and year 2 (2015; 100 replicates, 50 new)

Species	Effects	Direct effect of precipitation	Direct effect of temperature	Indirect effect of temperature via PC1	Indirect effect of precipitation via PC2	R <sup>2</sup> 14	R <sup>2</sup> 15
BLBW	I	–	–	0.27 (0.000)	0.05 (0.127)	0.32	0.33
BLPW	D, I	0.38 (0.000)	–	–0.32 (0.000)	–	0.57	0.61
BTBW	I	–	–	0.23 (0.000)	–	0.30	0.29
BTNW	D, I	0.25 (0.033)	–	0.21 (0.002)	0.03 (0.205)	0.08	0.08
DEJU	I	–	–	–	0.02 (0.13)	0.15	0.15
GCKI	D, I	–0.18 (0.086)	–	–	0.09 (0.079)	0.19	0.22
MAWA	D, I	–	0.31 (0.017)	–0.29 (0.000)	0.07 (0.069)	0.18	0.16
MYWA	D, I	0.33 (0.012)	0.39 (0.006)	–0.32 (0.000)	0.04 (0.066)	0.19	0.15
OVEN	D, I	–0.21 (0.006)	–	0.23 (0.001)	–0.07 (0.088)	0.41	0.38
REVI	D, I	–0.16 (0.067)	–	0.38 (0.000)	–0.08 (0.08)	0.46	0.50
SWTH	D, I	0.26 (0.036)	–	–0.15 (0.02)	–	0.20	0.19
WIWR	D, I	–0.29 (0.015)	–0.22 (0.08)	–	0.07 (0.085)	0.13	0.12
YBFL	D, I	0.24 (0.029)	–	–0.31 (0.000)	–	0.41	0.37

Path coefficient values have been standardized and represent the strength and sign of the effect (Effects) of climate variables upon species abundances' either directly (D) and/or indirectly (I) via one or both of the forest gradients (PC1, PC2). Values in cells are path coefficients alongside associated *p*-values in parentheses. Note that indirect effects are considered significant if all path coefficients comprising the indirect pathway are individually significant at the set alpha of ( $p \leq .1$ ). Dashes (–) indicate a non-significant effect found for a given pathway at the set alpha. Pathways without significance at set alpha for any species are not shown. Variance in species abundance explained for 2014 and 2015 appear under R<sup>2</sup>14 and R<sup>2</sup>15, respectively. Common names associated with species codes (Species) can be found in Table 1. Data from 150 survey sites sampled during 2014 and 2015 along elevational gradients in the White Mountains, New Hampshire.

indirect effects of climate, revealed that for all species, climate has a significant ( $p \leq 0.1$ ) effect on abundance, via either indirect paths only or both direct and indirect pathways (Table 2). None of the species experienced only direct effects while 77% of species experience both direct and indirect effects of climate (e.g., Figure 2a) and 23% experience only indirect effects (e.g., Figure 2b). Precipitation and temperature were found to affect ten species in combination, via indirect or both direct and indirect paths, whereas for the remaining three species, temperature or precipitation worked exclusively to affect species abundance via these paths (Figure 3). For species experiencing direct effects, precipitation had a greater direct effect than temperature for the majority of species (8 of 10). For indirect paths, the majority of species experienced greater effects of temperature than precipitation (10 of 13; Table 2). Overall, for 53% of species, the primary influence of climate on abundance was through indirect pathways via forest characteristics (Figure 4).

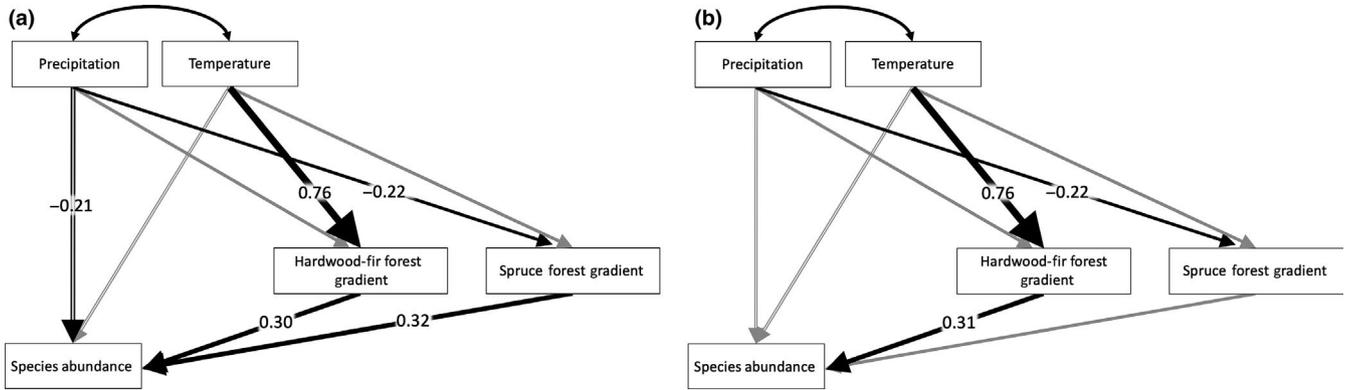
## 4 | DISCUSSION

By using a novel SEM approach, we have begun to unravel the mechanistic pathways by which climate determines patterns of species abundance and distribution. We provide evidence that for a suite of 13 forest bird species examined along an elevation gradient in the Northeastern United States, climate influences their abundance both directly and indirectly via forest habitat characteristics. Furthermore, for most species, the primary mechanism by which

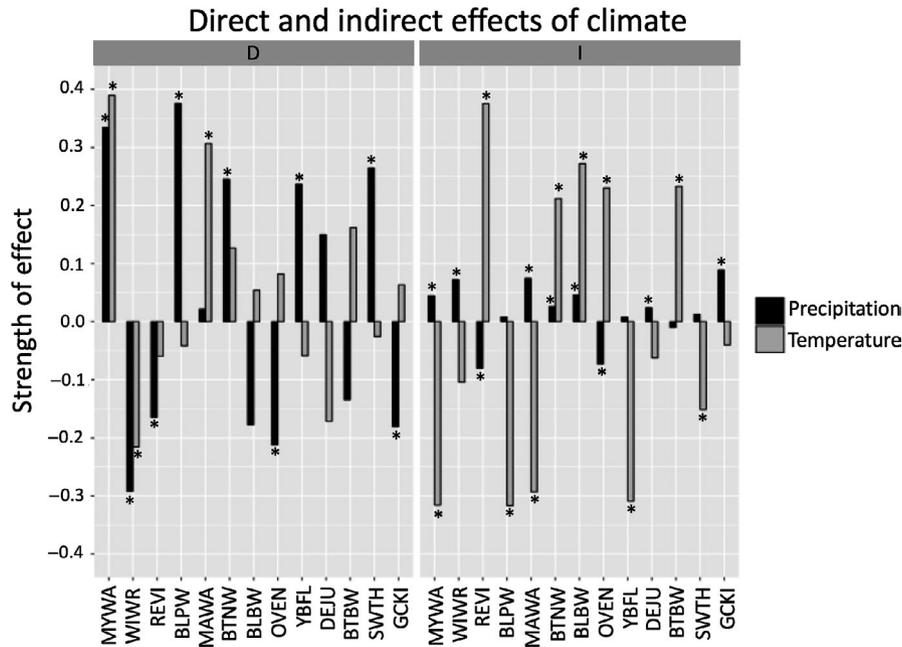
climate influences their abundance across the elevational gradient is via an indirect pathway, mediated by forest habitat. As such, these findings lend a new perspective on ways in which such species may be vulnerable to the effects of climate change as well as present a methodological framework applicable to future investigations of complex causal ecological processes underpinning patterns of species abundance and distribution.

Other researchers have also addressed the effects of climate and vegetation on bird distribution. For instance, Frey, Hadley, and Betts (2016) from the Pacific Northwest, demonstrated that gradients of vegetation structure and composition significantly correlate with within-season breeding occupancy of forest birds after statistically accounting for the role of forest microclimate. Similarly, the recent work of Elsen et al. (2017) demonstrates that gradients of temperature and forests, when modelled separately, each account for significant levels of variation in bird abundance along elevation in the Himalayas. These investigations, along with large-scale studies in the Northeastern United States (i.e., Matthews et al., 2011; Rodenhouse et al., 2007), describe the role of climate and vegetation as predictors of bird distribution; however, these investigations do not account for the potential for climate to indirectly influence birds through its influence on vegetation. As such, the findings and methodological framework presented here builds upon these prior investigations, promising to reduce uncertainty associated with inferences of avian vulnerability to future changes in forests and climate.

Our findings that temperature exerts a direct effect upon the abundance of montane species are consistent with established evidence



**FIGURE 2** Results of multi-group SEM for ovenbird (a), found to experience both a direct effect (hollow lines) of precipitation as well as concurrent indirect effect (solid lines) of temperature, via an association with the fir-mixed forest gradient, as well as an indirect effect of precipitation, via an association with the spruce-hardwood forest gradient, at the set alpha ( $p \leq .1$ ). Results for black-throated blue warbler (b), found to only experience the indirect effect of temperature via an association with the fir-mixed forest gradient at the set alpha ( $p \leq .1$ ). Values appearing in pathways are standardized regression coefficients representing the effect of a predictor on a response, with arrows pointing from predictor to response. Double headed arrows indicate covariance accounted for in the model. Non-significant pathways appear grey. Data from 150 survey sites sampled during 2014 and 2015 along elevational gradients in the White Mountains, New Hampshire

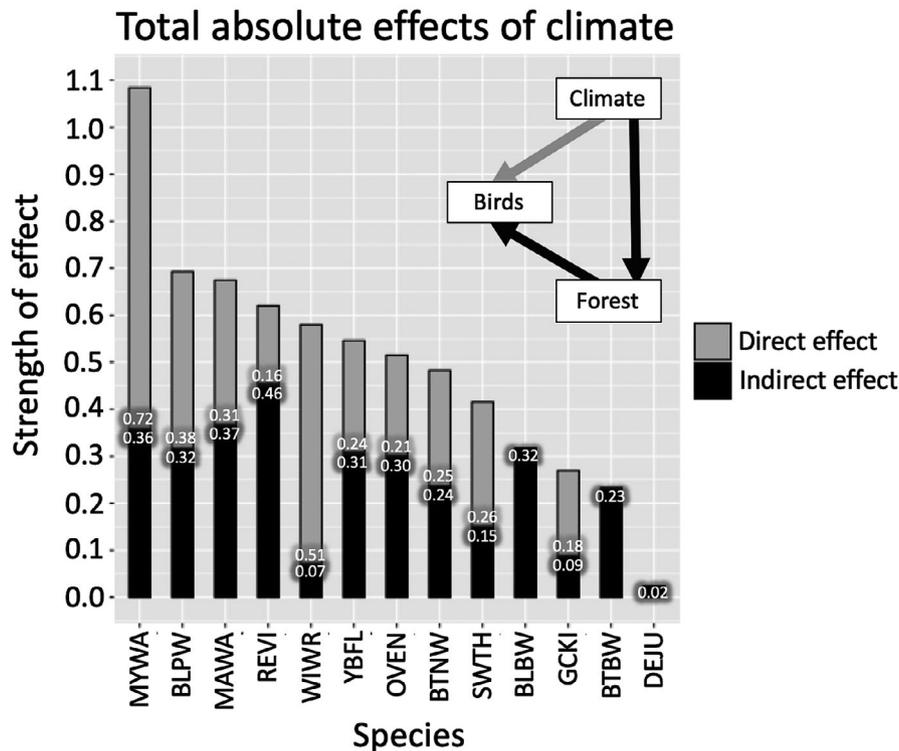


**FIGURE 3** Direct (D) and indirect (I) effects (standardized regression coefficients of respective pathways; Strength of Effect) of precipitation (black bars) and temperature (grey bars) for 13 passerine species along an environmental gradient. Asterisks indicate pathways deemed significant at set alpha ( $p \leq .1$ ). Common names associated with species codes (Species) can be found in Table 1. Data from 150 survey sites sampled during 2014 and 2015 along elevational gradients in the White Mountains, New Hampshire. Note: Theoretically, strength of these effects upon bird abundance could range in value from -1 (strongest possible negative effect) to 1 (strongest possible positive effect) of the respective direct (D) and indirect (I) effects of precipitation (black bars) and temperature (grey bars)

of the direct effects of temperature upon birds. Temperature has been described as a significant predictor of breeding bird abundance (Elsen et al., 2017) and site occupancy (Frey, Hadley, & Betts, 2016), as well as elevational shifts in avian distribution (Tingley et al., 2012) and abundance (Townsend et al., 2016). Mechanisms by which temperature influences such patterns include nest site selection (Martin, 2001), nesting behaviour (Conway & Martin, 2000; Townsend et al., 2013; Visser, Holleman, & Caro, 1986) and reproductive success

(Sherry, Wilson, Hunter, & Holmes, 2015; Townsend et al., 2013). All these factors individually, and in combination, directly affect population demographics through energetic constraints (Leech & Crick, 2007).

Similarly, our findings that precipitation imposed a direct effect upon the abundance of montane species align with established evidence of the effects of precipitation on forest birds. Changes in precipitation have been shown to correlate closely with downslope



**FIGURE 4** Total absolute effects of climate via direct (grey bars) and indirect (black bars) pathways. Values appearing in bars are the associated absolute effect value (standardized regression coefficients/path values; Strength of Effect) of respective pathway. Strength of Effect could range to a value of 6 if a species was affected to the greatest extent possible via all direct and indirect pathways evaluated here. Common names associated with species codes (Species) can be found in Table 1. Data from 150 survey sites sampled during 2014 and 2015 along elevational gradients in the White Mountains, New Hampshire. Note: Theoretically, the cumulative strength of absolute effects upon bird abundance could range as high as 4 if a species abundance was perfectly correlated with each of the four direct and indirect paths found significant for one or more of these 13 species (i.e., direct effect of temperature, direct effect of precipitation, indirect effect of temperature via PC1, and indirect effect of precipitation via PC2)

elevational shifts in avian populations in the Sierra Nevada mountains (Tingley et al., 2012) and possibly New Hampshire (DeLuca & King, 2017). Likewise, changes in precipitation patterns have been described as increasing the chances of population extirpation along elevation, especially for high-elevation species (McCain & Colwell, 2011), including those specific to the Northern Appalachians (Rodenhouse, 1992). Precipitation has direct effects upon nest site selection along environmental gradients (Martin, 2001), nest success and juvenile survival (Sherry et al., 2015) and in total affects population demographics by imposing energetic constraints associated with thermoregulation (Leech & Crick, 2007). While the precipitation data used in this study reflect broad spatial and temporal processes, for the purposes of serving as a proxy for patterns of precipitation along elevation, our results clearly indicate that bird distributions respond to precipitation patterns at this scale.

Although it was important to include precipitation in our analysis, the downscaling and subsequent bi-linear interpolation of the 800 m PRISM data should be interpreted cautiously. While the interpolation produces a dataset reflective of the original, statistically validated, values at 800 m cell centres, the interpolation of values at a 30 m resolution between cell centres results in an artificial smoothing of these values and does not consider factors affecting precipitation at

finer resolutions (See Appendix S9; McGarigal et al., 2016). For example, if two adjacent 800 m cells have similar values but, in reality, there are finer-scaled changes in precipitation between the two cell centres, possibly due to micro-topographic changes, the interpolated precipitation values, although represented at the 30 m scale, would not reflect this heterogeneity. Rather, it would reflect the more homogeneous surface of the 800 m resolution data. However, for the purposes of our investigation, we feel that the interpolation process results in a more reasonable representation of the linear change in precipitation known to occur along elevation gradients at resolutions finer than 800 m; this is supported by the strong linear relationship we found between the interpolated values and elevation (See Appendix S9). Therefore, we do not believe that the interpolation process introduced spurious sources of variation that were not already present in the 800 m data. To confirm that our biological response to precipitation was not a spurious artefact of the interpolation process, we repeated our modelling approach using the 800 m data in place of the 30 m data (See Appendices S10–S13). Irrespective to the approach, we found robust evidence that climate (temperature and/or precipitation) influences the abundance of the 13 species both directly and indirectly via forest habitat characteristics and that the primary mechanism by which climate influences their abundance is

via an indirect pathway (Figure 4, Appendix S12). The same proportion of species was found to be more strongly affected by these indirect effects of climate. However, using the coarser-level 800 m data, indirect effects of climate are entirely concentrated via an effect of temperature mediated by the hardwood-fir gradient (Appendix S10); we believe this was due to the artificial reduction in variation of precipitation when considering the 800 m cell data. While the high level of concurrence between the 30-m- and 800-m-based results signify robust conclusions, future efforts should look toward acquiring finer scale, directly measured, precipitation data.

Given the close association found between forest birds and habitat characteristics, our findings that climate imposes indirect effects upon the abundance of all species via forest conditions concur with established evidence of the relationship between climate and forests (Siccama, 1974). While the spatiotemporal scale at which forests respond to changes in climate is much greater than this 2-year study, these results suggest that our measures reflect the variation in climate across the elevation gradient that in part affects forest composition and structure (Cogbill & White, 1991). The stratification of forest communities across elevation is partially attributed to temperature (Cogbill & White, 1991) with bioclimatic model projections suggesting that high-elevation spruce-fir forest communities are vulnerable to changes in mean growing season temperature (Iverson et al., 2008). Likewise, precipitation has been described as a significant factor defining the transition between hardwoods and mid-elevation red spruce dominated forest in the Northern Appalachians (Blum, 1990; Cogbill & White, 1991).

While we found evidence of significant direct and/or indirect effects of climate upon the abundance of all the species tested, the varying reduced SEM  $R^2$  values reflect additional ecological processes that very well may further contribute toward explaining the patterns of abundance of these species (Shiple, 2016), as well as, perhaps, the relative rarity of the 46 other species observed during the study. For example, prey availability determines patterns of avian abundance (Holmes, 2011; Jones, Doran, & Holmes, 2003) as do predators (DeGregorio, Westervelt, Weatherhead, & Sperry, 2015; Sherry et al., 2015; Thompson, 2007). Competition is also a well-known determinant of species distributions (Freeman & Montgomery, 2016; Martin, 1996, 2001), especially along environmental gradients (Jankowski, Robinson, & Levey, 2010; Terborgh, 1971) and among conspecifics (Able & Noon, 1976; Srinivasan, Elsen, Tingley, & Wilcove, 2018). Considering individualistic responses of avian species to a changing climate (Tingley et al., 2012), alterations in the propensity of such interactions will likely further affect patterns of species distribution and abundance (Brodie, Post, & Doak, 2013).

Unaccounted variability within the SEM could also reflect additional constraints/processes influencing the two forest gradients. For example, soil conditions play a key role in determining tree species distributions along elevation in the WMNF (Lee, Barrett, & Hartman, 2005), especially that of red spruce (Leak, 1987). Other factors such as competition (Lenoir et al., 2010), disease (Castello, Leopold, & Smallidge, 1995), atmospheric deposition (Battles, Fahey, Siccama, & Johnson, 2003; Schaberg & DeHayes, 2000) and

recovery from past land use/timber harvest (Kelty & D'Amato, 2006) all interplay to impose varying influence upon forest dynamics in the Northern Appalachians (Rustad et al., 2012).

## 4.1 | Implications

Bioclimatic model projections, predicting the response of species to climate change based upon a shift in climatic conditions characterizing currently occupied sites (Langham et al., 2015) illustrate the potentially dramatic effects of climate change on species distributions. These model projections hinge upon the central assumption that species are influenced only by the direct effect of climate, yet do not account for the concurrent, and potentially interactive, effects of climate and habitat on the abundance and distribution of species (Langham et al., 2015). Our findings that climate does not simply exert only a direct influence upon these species suggests such bioclimatic models should be applied with caution. Furthermore, our findings of indirect effects of climate for all species provide evidence that the role of climate in altering habitat must also be accounted for when estimating future abundance and distribution of species. This is of importance to both broad-scale predictive modelling efforts (e.g., Rodenhouse et al., 2007) and finer-resolution investigations (e.g., Elsen et al., 2017; Frey, Hadley, & Betts, 2016) seeking to describe such relationships. While these approaches contribute significantly to our understanding of where species might be distributed given climate change, further research should attempt to incorporate both the direct effects of climate as well as the role of climate in altering habitat.

Although climate conditions are predicted to change rapidly in the Northern Appalachians with temperature increases of as much as 5°C over the next century and increased variability and magnitude of precipitation events and drought (IPCC, 2014), the forest habitat occupied by the species in our study are comprised of relatively long-lived tree species with average life spans on the order of centuries (Pan et al., 2011). Thus, forests have an inherent inertia with respect to the rate at which they are projected to respond to climate change, making a future decoupling of current forest-climate conditions in the northeast highly likely (Iverson et al., 2008; Rustad et al., 2012; Stralberg et al., 2009, 2015), with recent findings suggesting the response could occur on the order of several centuries (Wang et al., 2002). Such predictions align with historical records from the Northern Appalachians indicating that montane forests did not respond in sync to past changes in climate (Spear, Davis, & Shane, 1994) as well as recent evidence suggesting a differential change is already underway (Foster & D'Amato, 2015). For species sensitive to both climate and forest conditions, such a decoupling could have serious implications, potentially forcing species to occupy either marginal habitat or climatic conditions (Leech & Crick, 2007; Rustad et al., 2012; Stralberg et al., 2015). Notably, 77% of the species in our study fit this criteria, supporting previous reports that montane birds in the region are threatened by climate change (King et al., 2008; Lambert et al., 2008; Rodenhouse et al., 2007; Rodenhouse, 1992).

Our results highlight the importance of forest habitat management for the persistence of species—indicating that by promoting favourable forest conditions, managers have the opportunity to increase the capacity for species to adapt to the effects of climate change. Given our findings that climate effects are mediated by forest conditions for all species examined here, with 53% of these species more strongly affected by climate via forests, the long-lived nature of forests may provide a buffer for these species from the projected rapid changes of climate. For these species, forests management and protection efforts may support these species in the form of climate refugia; areas where species are buffered from the effects of climate change (Morelli et al., 2016). Recent findings by Frey, Hadley, Johnson, et al. (2016) provides evidence in support of this concept, suggesting that by promoting complex forest structure, some forests may provide thermal refugia to species. By protecting and maintaining such refugia, species may be able to “adapt in place” (Brodie et al., 2013). Alternatively, forest management strategies anticipating the long-term response of forests to changing climate, such as adaptive silviculture, offer the potential to allow species the opportunity to adapt over time by promoting the growth of future forest habitats into which species can move as they track their suitable climate niche. For the minority of species found here to experience stronger direct effects of climate, these results suggest such species may have a reduced capacity for resisting the effects of climate change (i.e., “adapt in place”) and thus may be more likely to undergo more immediate changes in abundance and distribution as they track their suitable climate niche.

## DATA ACCESSIBILITY

Data are available from the authors upon request.

## ACKNOWLEDGMENTS

This research was possible with support from a grant from the Northern States Research Cooperative (agreement# 16-CO-11242307-009) in addition to funding and support from the US Forest Service Northern Forest Research Station. Additional funding for this work was provided by a Department of Interior's Northeast Climate Adaptation Science Center graduate fellowship awarded to Tim Duclos. We would like to thank staff at the USFS White Mountain National Forest and the Mt. Washington Auto Road. Lastly, we would like to thank the great field assistants that made this project possible (Aaron Hulsey, Sarah Deckel, Meredith Lewis and Adam Ells).

## CONFLICT OF INTEREST

The authors have no interest or relationship, financial or otherwise that might be perceived as influencing the author's objectivity with this work and thus have no conflicts of interest to declare.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Duclos TR, DeLuca WV, King DI.

Direct and indirect effects of climate on bird abundance along elevation gradients in the Northern Appalachian mountains. *Divers Distrib*. 2019;00:1–14. <https://doi.org/10.1111/ddi.12968>