

Montane birds shift downslope despite recent warming in the northern Appalachian Mountains

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Abstract Montane regions support distinct animal and plant communities that are widely viewed as communities of high conservation concern due to their significant contribution to regional biodiversity. These communities are also thought to be particularly vulnerable to anthropogenically caused stressors such as climate change, which is generally expected to cause upward shifts and potential range restrictions in montane plant and animal distributions. In the northern Appalachian Mountains of North America, not only is it becoming warmer at mid-elevations but the ecotone between the northern hardwood and the montane coniferous forests is also shifting. Therefore, species that are limited by climate or habitat along the elevational gradient of mountains may also be experiencing distributional shifts. We studied birds along replicate elevational gradients in the White Mountains of New Hampshire, USA, from 1993 to 2009 and used mixed effects models to estimate the rate of elevational change to test the hypothesis that northern hardwood forest- and montane forest-dependent birds are shifting upslope, consistent with climate change predictions. As predicted, the upper elevational boundary of 9 out of 16 low-elevation species

showed evidence of shifting upslope an average of 99 m over the course of the study period. Contrary to our expectations, 9 out of 11 high-elevation species had lower elevational boundaries that shifted downslope an average of 19 m. The opposing elevational shifts of two distinct and adjacent bird communities is, to our knowledge, unprecedented and highlights the need for caution when applying conventional expectations to species' responses to climate change.

Keywords Distribution · Climate change · Range boundary · Elevational shift · Mountains · Birds

Zusammenfassung

Trotz aktueller Erwärmung verlagern Gebirgsvögel in den nördlichen Appalachen ihr Vorkommen hangabwärts

Bergregionen beherbergen besondere Tier- und Pflanzengemeinschaften, die aufgrund ihres erheblichen Beitrags zur regionalen Biodiversität weithin als Gesellschaften mit hohem Schutzbedarf betrachtet werden. Diese Artengemeinschaften gelten auch als besonders anfällig für anthropogen verursachte Stressfaktoren wie den Klimawandel, von dem allgemein angenommen wird, dass er Verschiebungen in höhere Lagen und potenzielle Beschränkungen des Verbreitungsgebietes für Gebirgspflanzen und -tiere verursacht. In den nördlichen Appalachen Nordamerikas wird es nicht nur in den mittleren Höhenlagen wärmer, sondern auch der Ökoton zwischen nördlichen Hartholzwäldern und Bergnadelwäldern verschiebt sich. Daher könnte sich auch die Verbreitung von Arten, welche durch Klima oder Habitat entlang des

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Gebirgshöhengradienten Beschränkungen unterliegen, verändern. Zwischen 1993 und 2003 untersuchten wir Vögel entlang vergleichbarer Höhengradienten in den White Mountains in New Hampshire, USA, und verwendeten gemischte Modelle zur Schätzung der Höhenänderungsrate, um die Hypothese zu überprüfen, dass Vögel, die auf nördliche Hartholzwälder und Bergwälder angewiesen sind, sich gemäß den Vorhersagen zum Klimawandel hangaufwärts verlagern. Entsprechend den Vorhersagen verschob sich die obere Höhengrenze bei neun von 16 Tieflandarten im Laufe des Untersuchungszeitraumes im Schnitt um 99 m hangaufwärts. Anders als erwartet wiesen neun von elf Hochgebirgsarten niedrigere Höhengrenzen auf, die sich im Schnitt um 19 m hangabwärts verschoben hatten. Die entgegen gerichtete Höhenverschiebung zweier distinkter und benachbarter Vogelgesellschaften ist unseres Wissens nach beispiellos und betont, wie wichtig es ist, bei der Annahme gängiger Erwartungen bezüglich der Reaktion einer Art auf den Klimawandel Vorsicht walten zu lassen.

Introduction

Montane ecosystems contribute significantly regional biodiversity due to the variety of climate conditions along the elevational gradient as well as the contrast of those conditions to the surrounding landscape (Cadena et al. 2012). However, montane biodiversity is particularly vulnerable to many anthropogenic stressors including land use conversion and climate change (Rodenhouse et al. 2008; McCain and Colwell 2011). This vulnerability is exacerbated by the fact that spatially compressed biotic and abiotic zones of mountains often restrict montane species' ranges, leaving them more susceptible to extirpation (Şekercioglu et al. 2007). Understanding how recent anthropogenic alterations of the environment are influencing the distribution of vulnerable montane species is an integral step towards maintaining global biodiversity.

Climate change has been linked to spatial shifts in the distributions of many species and ecosystems (McCain and Colwell 2011; Freeman and Freeman 2014). For example, Fisichelli et al. (2014) related the regeneration of temperate trees in boreal forests to temperature changes in central North America. Furthermore, of 40 western North American bird species considered, all had upper-elevation boundaries that shifted upslope over a recent 35-year period (Auer and King 2014). Beckage et al. (2008) used plot-based sampling and reported that the ecotone between northern hardwood forests and montane boreal forests shifted approximately 100 m upslope over the last 40 years on three mountains in Vermont. However, Foster and

D'Amato (2015) used remote sensing to examine the White Mountains, NH, and the Green Mountains, VT, at a regional scale and found that the ecotone has primarily shifted slightly downslope between 1991 and 2010 (Foster and D'Amato 2015).

Climate change can cause shifts in the geographic distribution of species via several mechanistic pathways. Physiological adaptations can constrain a species within a range of climate conditions, outside of which individuals' reproductive success and/or survival is compromised, ultimately influencing the spatial distribution of the species (Root 1988). Geographic shifts in climate could then cause species' distributions to shift spatially to track favorable climatic conditions (Tingley et al. 2009; Zuckerberg et al. 2009). Alternatively, recent evidence suggests that some montane species are not limited directly by climate (Londoño et al. 2016). Shifts in climate conditions could affect species' distributions indirectly by altering habitat composition and structure (e.g., Beckage et al. 2008; Vogelmann et al. 2012; Foster and D'Amato 2015), forcing species to track changes in the spatial distribution of their preferred habitat conditions (Rodenhouse et al. 2008). Climate change can also alter the distribution of food resources (Battisti et al. 2006; Visser et al. 2006), competitors (Freeman and Montgomery 2016), predators (DeGregoria et al. 2015) and pathogens (Garamszegi 2011), all of which may cause a corresponding geographic shift to related species.

As the climate warms, it is predicted that many climatic conditions typical of southerly latitudes and low elevations will shift away from the equator and increase in elevation (Lenoir and Svenning 2015). It is becoming apparent that the climate of montane environments is changing consistent with these predictions, including in northeastern North America. On Mount Mansfield (1204 m) in the Green Mountains, average annual temperature increased by 0.86 °C and precipitation increased by 38% between 1964 and 2004 (Beckage et al. 2008). A mid-elevation station (612 m) on Mount Washington in the White Mountains has exhibited significant warming trends since the 1930s, where average annual temperature increased by 0.07 °C/decade. At the summit (1914 m), although spring temperature showed some warming (0.12 °C/decade), the trend was not significant (Seidel et al. 2009).

Despite established theory and empirical evidence supporting the expectation that species will shift upwards in elevation in response to climate change, there are increasingly numerous reports of species exhibiting contrary patterns of range shifts (Tingley et al. 2012). These variable responses likely reflect the diverse mechanisms influencing species' positions on elevational gradients. Given heightened conservation concern regarding montane biodiversity, and the growing evidence that the spatial distribution of this ecosystem is changing (Beckage et al.

2008; Foster and D’Amato 2015), we examined elevational distributions of birds in the White Mountains of New Hampshire to test whether they exhibited shifts consistent with upslope predictions of species’ distributional shifts due to climate change.

Materials and methods

Study sites

This study was conducted in the White Mountain National Forest in northern New Hampshire (43°53′ to 44°32′N, 71°51′ to 71°6′W) between the elevations of 740 and 1470 m. The White Mountain National Forest consists of an extensively forested area (>90%) encompassing 330,000 ha, 47,000 ha of which are designated as wilderness. Other areas of the forest are managed for timber harvest, recreation, and wildlife habitat (King et al. 2008). High elevation habitats (>~1000 m) are currently managed for recreation only.

The White Mountains provide suitable conditions for extensive montane boreal forests, with 30 peaks rising over 1300 m. Along the elevational gradient, forest community composition and structure changes rapidly. Below 750 m, northern hardwood forests are dominant. Between 750 and 1100 m, a mixture of deciduous and coniferous trees is present. With increasing elevation, coniferous species of the boreal forest become rapidly dominant. Above 1100 m, the forest matrix consists primarily of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) which supports avifauna distinct from lower elevation forests (Sabo 1980; King et al. 2008). Within this elevational range, forests are structured by frequent and widespread wind disturbances (Sprugel 1976). From 1275 m to the treeline, the forest becomes dense with an associated decrease in canopy height (Cogbill and White 1991). The climate in the White Mountains during the spring and summer is cool with high and variable winds. Orographic cooling causes increased precipitation with increasing elevation (Sabo 1980).

Field methods

Birds were surveyed by trained observers at fixed survey locations between 740 and 1470 m annually from 1993 to 2000, then in 2003, 2005, 2007, and 2009. Surveys consisted of 5-min point counts, in which all birds seen or heard were recorded as being either less than or greater than 50 m from the observer. All surveys were conducted once per year during the height of the breeding season (1–25 June), under minimal wind and rain conditions between 0500 and 1100 hours EST. A total of 768 survey locations were surveyed on 42 separate transects located

along hiking trails. Transects were established to provide broad coverage of nearly all the trails in the White Mountains within high elevation habitats (Fig. 1). Individual survey locations were sampled 250 m apart along transects. Due to severe weather conditions, not all points were surveyed in all years. Elevation data for survey locations were recorded with a global positioning system (GPS). To acquire aspect and slope for survey locations, we used a 10-m digital elevation model in ArcGIS 10 geographical information system (GIS).

Statistical analyses

We used a separate linear regression model for each of seven 100-m elevation bands from 740 to 1470 m to determine whether the mean survey elevation changed over the 17-year period within each band. This analysis tested for potential fine-scale elevational sampling biases that could either mask or mimic potential species’ boundary shifts. Only bird detections within 50 m of survey locations for species with >30 total occurrences were included in the analysis. Count data were transformed to presence or absence, and the binary data were then used to obtain an elevation for each occurrence of each species, which is henceforth termed its “elevational occurrence”.

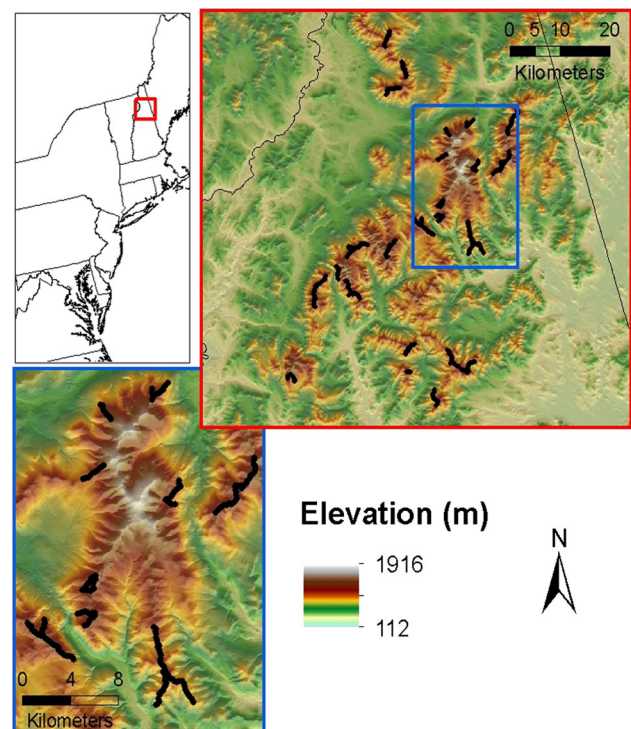


Fig. 1 Digital elevation model of the study area within the White Mountain National Forest, NH, USA. *Black lines* in the first inset identify transect locations. *Black dots* in the second inset are bird survey locations

Species detected during the study included those associated with lower elevations, for which survey points likely represented only the upper extent of their elevational distribution, as well as those considered high-elevation forest obligates, which had elevational ranges that were encompassed within the elevational range of the surveys. To determine the extent to which a species' elevational distribution was captured within the elevation range of the surveys, we first calculated the proportion of points at which each species was present for every 25-m elevation bin between 740 and 1470 m. A generalized linear model with a quadratic polynomial term for elevation was then fit using the stats library in R for each species. The predicted values of a species' proportional presence were then plotted against the elevational midpoint of each elevation bin within the range of elevations included in the survey. If the mode of the elevational distribution occurred below the survey elevation range, then the species was considered to be a low-elevation species, with a mode <750 m (e.g., Fig. 2a). Conversely, species whose elevational distribution mode fell within the elevation range of the surveys were considered high-elevation species (e.g., Fig. 2b).

We used linear mixed effects models to test for changes in species elevational occurrences between 1993 and 2009. We used a random intercept model with species' elevational occurrence as the response variable, year as the predictor, and transect as the random effect. Mixed effects models were used to account for the non-independent errors of surveys spatially aggregated by transect (Zuur et al. 2009). Separate models were run for each species. Mixed models were implemented using the nlme library in R (Pinheiro and Bates 2000). Spearman's rank correlation was used to determine that survey location slope and aspect, two potentially important variables in determining species elevational distributions, were each highly correlated within transects ($P = 0.04$ and $P = 0.03$, respectively). Therefore, the transect variable also accounted for the potentially confounding effects of slope and aspect, enhancing the model's ability to test specifically for a change in elevation over time.

Since only the upper elevation distributions of low-elevation species were captured within the elevation range of the survey (Fig. 2a), only the upper elevation boundary could be tested for elevation shifts over time for these species. We tested for elevation shifts in the sampled center of occurrence by applying the mixed effects model to the complete set of elevational occurrences for every low-elevation species. To test for a shift in the extreme upper elevational boundary of low-elevation species, we first selected the upper 90th percentile of elevational occurrences for each year for each species, then applied the mixed effects model only to elevational occurrences

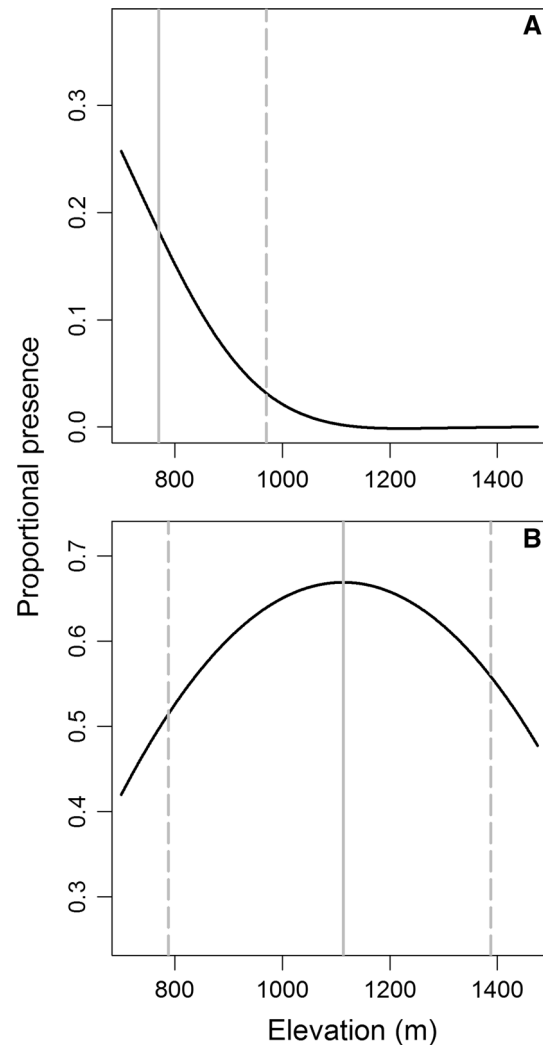


Fig. 2 Examples of elevation distributions for **a** a low-elevation species (Black-throated Blue Warbler, *Setophaga caerulescens*) and **b** a high-elevation species (Blackpoll Warbler, *Setophaga striata*). *Black lines* are fitted predictions from regression models from 768 locations within the White Mountain National Forest from 1993 to 2009. *Solid gray lines* represent the center of occurrence of the elevation distribution. *Dashed gray lines* represent either the lower or upper elevational boundary as measured by the 10th and 90th percentiles, respectively, of the distribution

greater than the 90th percentile. Because the distribution mode of elevational occurrences for low-elevation species was not sampled, it is likely that the sampled center of occurrence and the sampled 90th percentile represent a different portion of the upper boundary for each species. However, both measures are representations of the upper elevational boundary for low-elevation species. Mixed models were also applied to the 60th, 70th, and 80th percentiles of each species elevational distribution to retain the ability to examine general patterns, because it is difficult to identify specific ecologically meaningful range boundaries (Maggini et al. 2011).

For high-elevation species, the majority of each species elevation distribution was sampled; therefore, we tested for shifts over time in the actual lower elevational boundary, center of occurrence, and upper elevational boundary (e.g., Fig. 2b; Maggini et al. 2011). Shifts in the lower elevational boundary were tested by selecting elevational occurrences within the 10th percentile for each year, for each species, and then implementing the mixed model. Mixed models were applied to all elevational occurrences for each species to test for shifts in the center of occurrence (mean of a species’ elevation distribution). Changes in the upper elevational boundary were examined by applying mixed models to elevational occurrences within the 90th percentile in each year for each species. Delineating a specific elevational “boundary” can be somewhat arbitrary (Maggini et al. 2011), thus we applied the mixed models to every 10th percentile for comparison. The 90th and 10th percentiles were highlighted because they reflected elevational range extent and were not subject to the high variability that would be associated with the highest or lowest occurrence of each species. Sample sizes for each model considered are reported in Online Resource 1.

We applied a nonparametric bootstrapping procedure to species’ elevational occurrences using the boot library in R to estimate the total change in elevation over the 17-year study period for the sampled center of occurrence and the upper elevational boundary for low-elevation species, and for the lower elevational boundary, center of occurrence, and the upper elevational boundary for high-elevation species. The data were sampled 10,000 times using the ordinary resampling method. For each sample, the mixed model was applied to the data and the fixed effects estimates for the intercept and slope of the mixed model were inserted into the linear equation for 1993 and again for 2009. This procedure provides an elevation estimate, in meters, for the specific measure of the elevation distribution being considered. We then calculated the change in elevation for each species by subtracting the elevation estimate for 1993 from the elevation estimate for 2009. The statistical significance of observed shifts was assessed using 95% confidence intervals (CI) extracted from the 10,000 elevation change estimates. The bootstrapping procedure was applied to all high-elevation species, but only to low-elevation species that exhibited some evidence of a range shift (i.e., the fixed effect estimate of year differed from zero) during the original mixed modeling procedures for any of the distribution percentiles.

For all measures of a species’ elevational distribution (lower elevational boundary, center of occurrence, and upper elevational boundary), we considered there to be evidence of a shift between 1993 and 2009 if the coefficient for the fixed effect of year on a species’ elevational occurrence (from the mixed models) was different from

zero. To determine if the fixed year coefficient was different from zero, we first evaluated whether the 95% CI of the year estimate did not include zero and, secondly, determined if the *P* value for the year estimate was <0.05. Additional support for elevation shifts was provided by the assessment of whether the 95% CI for the total change in elevation (m) between 1993 and 2009 included zero.

We used the population change analysis of the North American Breeding Bird Survey (BBS) for New Hampshire conducted by Sauer et al. (2014) to address the possibility that range expansions (e.g., the upper elevational boundary of low-elevation species shifting upslope or the lower elevational boundary of high-elevation species shifting downslope) were due to regional population increases (Fuller et al. 1995) rather than to an environmental response. We also assessed whether range retractions (e.g., lower elevation boundary of high-elevation species shifting upslope) were due to regional population declines. For species exhibiting significant shifts in elevation with either the absence of significant BBS trends or with significant trends opposite of what would be expected given the elevation shift (e.g., expanding boundary with population decline), we concluded that the observed changes in the elevational boundary were due to an environmental response and not to population fluctuations (Parmesan et al. 2005). All analyses were conducted using R.3.0.1 (R Development Core Team 2013).

Results

The elevations at which surveys occurred did not change between 1993 and 2009 in any of the 100-m elevation bands between 700 and 1500 m (Table 1). Therefore, all surveys were used in subsequent analyses. There were 75 species detected, 28 of which had sufficient sample sizes and were used for analysis (Online Resource 1). Of these

Table 1 Least squares regressions testing changes in bird survey location elevations in White Mountain National Forest, NH, USA, over time within each 100-m elevation band between 700 and 1500 m from 1993 to 2009

Elevation band (m)	<i>t</i>	<i>df</i>	<i>P</i>
700–800	0.166	35	0.869
801–900	0.206	290	0.837
901–1000	0.313	963	0.755
1001–1100	−0.708	1344	0.480
1101–1200	−0.050	1623	0.960
1201–1300	−0.614	1314	0.540
1301–1400	0.331	597	0.741
1401–1500	−0.405	131	0.686

28 species, 16 were designated as low-elevation species (elevation mode <750 m) and 12 as high-elevation species (elevation mode \geq 750 m; Table 2).

Low-elevation species

Ten of the 16 low-elevation species analyzed (62.5%) showed evidence of a shift in their upper elevational boundary between 1993 and 2009 (Fig. 3; Online Resource 1). Nine of the ten shifting low-elevation species expanded upslope over the course of the study. Black-capped Chickadee (see Table 2 for scientific names) was the only species that exhibited a downslope shift across the range of the study, which was evident in both its sampled center of occurrence (−44.2 m downslope) and sampled upper elevational boundary (−154.1 m downslope; Fig. 3; Table 2).

Of the nine species exhibiting an upslope shift, the sampled center of occurrence shifted for seven species and the upper elevational boundary shifted for three species (Fig. 3). Of the seven species with sampled center of occurrences that shifted upslope (Fig. 3), five also had 95% CIs of elevation change estimates, based on the bootstrapping procedure, that did not include zero (Table 2). For those five species, Hermit Thrush, Black-throated Blue Warbler, Black-and-white Warbler, Blackburnian Warbler, and American Redstart, the average shift upslope was 125.2 m, with a range from 62.6 to 184.5 m (Table 2). The bootstrapping procedure also indicated that all three species, Black-throated Blue warbler, Black-throated Green Warbler, and American Redstart, with sampled upper elevational boundaries that shifted upslope (Fig. 3) had 95% CIs of elevation change estimates that did not include zero (Table 2). The average upward shift of the sampled upper elevational boundaries for these species was 260.1 m (Table 2).

High-elevation species

Nine of the eleven high-elevation species analyzed (82%) showed evidence of a shift in either their center of occurrence, upper boundary or lower boundary between 1993 and 2009. However, only one species, Magnolia Warbler, exhibited evidence of an upslope shift and was the only species which had an upper elevational boundary that shifted upslope (Table 2). The bootstrapping technique provided further evidence that Magnolia Warbler's upper elevational boundary shifted upslope, increasing by 41.1 m over the 17-year period (Table 2).

Eight high-elevation species (89%) showed evidence of shifting downslope (Fig. 4). Yellow-bellied Flycatcher, White-throated Sparrow and Winter Wren had significant downslope shifts of their upper elevational boundary (Fig. 4). Only winter wren had a center of occurrence that

shifted downslope (Fig. 4), shifting by −14.2 m from 1993 to 2009 (Table 2). Six of the eleven (55%) high-elevation species exhibited evidence of a downslope shift in their lower elevational boundary (Fig. 4). Although a significant shift was not detected at the 10th percentile measure of the lower elevational boundary for Yellow-bellied Flycatcher, the coefficient estimates were significant for the other measures of the lower elevational boundary (20–40th percentiles; Online Resource 1). Further evidence of a downslope shift of the lower elevational boundary was provided by the bootstrapping technique for five of the six species (Table 2). Swainson's Thrush, Winter wren, Nashville Warbler, Yellow-rumped Warbler, and Dark-eyed Junco had lower elevational boundaries that shifted downslope an average of −24.6 m (Table 2). Only Blackpoll Warbler had 95% CI that included zero (95% CI −21.84 to 0.02 m). In general, the downslope shift of the lower elevational boundary of high-elevation species was consistent regardless of the percentile used to measure range boundaries (Online Resource 1).

Population trends

Of the 19 species that exhibited elevational range shifts in this study, 6 exhibited significant population changes in New Hampshire based on BBS data (Sauer et al. 2014). Therefore, population changes were not responsible for the shifts in distributions of those 13 species which did not exhibit significant population trends according to BBS. The three species with decreasing population trends exhibited evidence of elevational range expansions (Black-and-white Warbler, American Redstart and Nashville Warbler; Table 2). Although Red-eyed Vireo had some evidence of elevational range contraction, its population is increasing (Sauer et al. 2014). Population trends could be a potential explanation of range shifts for only two species. The first was Swainson's Thrush, which had an elevational range expansion (downslope) and has an increasing population (Sauer et al. 2014). The second species was White-throated Sparrow, which has a decreasing population (Sauer et al. 2014) and exhibited evidence of elevational range shifts consistent with contraction.

Discussion

Despite prevailing theory and evidence that species' distributions will move towards the poles and increase in elevation over time as a consequence of climate change (Parmesan and Yohe 2003; Parmesan et al. 2005; Şekerçioğlu et al. 2007; Sorte and Thompson 2007; Beckage

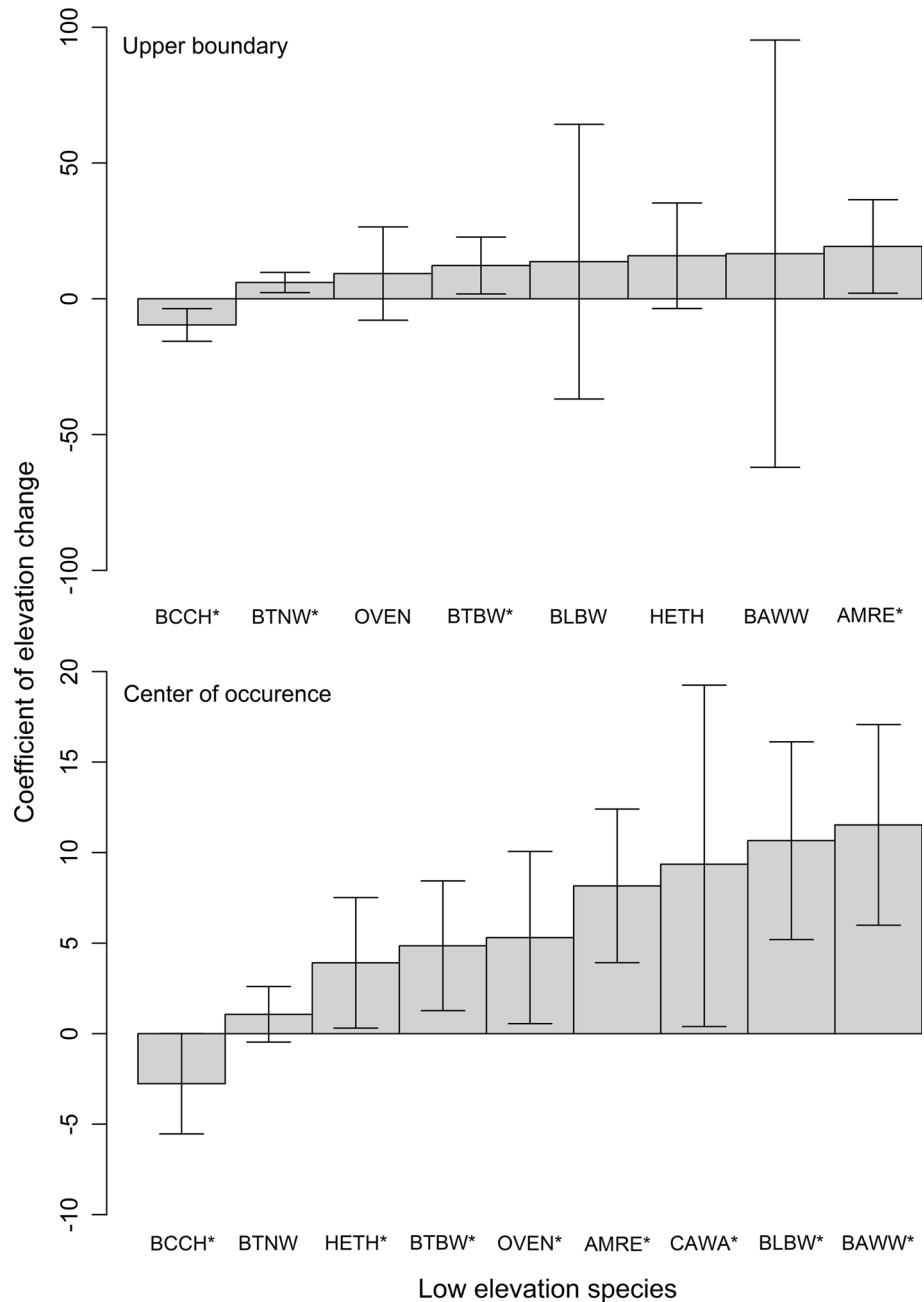
Table 2 Change in elevation (m) between 1993 and 2009 for the lower elevation boundary (10th percentile of a species elevation distribution), center of occurrence (mean of a species elevation distribution), and upper elevation boundary (90th percentile of a species elevation distribution) of birds along an elevation gradient

Elevation	Species	Percentile of elevation distribution					
		10th		Mean		90th	
		Δ Elevation	95% CI	Δ Elevation	95% CI	Δ Elevation	95% CI
Low							
<750 m	Black-capped Chickadee (<i>Poecile atricapilla</i>)	–	–	–44.24	–87.77 to –3.29	–154.13	–318.96 to –6.50
<750 m	Hermit Thrush (<i>Catharus guttatus</i>)	–	–	62.60	8.68 to 131.06	253.42	117.02 to 619.43
<750 m	Red-eyed Vireo (<i>Vireo olivaceus</i>)	–	–	11.28	–70.61 to 131.71	^a	^a
<750 m	Black-throated Green Warbler (<i>Setophaga virens</i>)	–	–	17.09	–10.44 to 43.35	95.92	–4.05 to 148.05
<750 m	Black-and-white Warbler (<i>Mniotilta varia</i>)	–	–	184.48	25.08 to 317.98	265.72	–298.76 to 394.77
<750 m	Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	–	–	77.65	9.99 to 145.31	196.03	–35.57 to 300.32
<750 m	Canada Warbler (<i>Wilsonia canadensis</i>)	–	–	149.77	–104.90 to 309.29	^a	^a
<750 m	Blackburnian Warbler (<i>Setophaga fusca</i>)	–	–	170.58	18.88 to 272.97	218.75	87.28 to 1025.36
<750 m	American Redstart (<i>Setophaga ruticilla</i>)	–	–	130.59	57.87 to 202.65	308.20	48.00 to 449.61
<750 m	Ovenbird (<i>Seiurus aurocapillus</i>)	–	–	84.92	–11.54 to 142.25	148.68	–76.70 to 462.56
High							
835 m	Magnolia Warbler (<i>Setophaga magnolia</i>)	–5.58	–28.16 to 16.38	7.62	–9.15 to 24.89	41.06	10.45 to 72.40
979 m	Swainson’s Thrush (<i>Catharus ustulatus</i>)	–33.09	–52.07 to –13.47	–6.48	–23.05 to 10.52	13.89	–9.17 to 37.10
987 m	Winter Wren (<i>Troglodytes troglodytes</i>)	–21.33	–35.81 to –7.15	–14.17	–28.31 to –0.32	–15.99	–30.83 to 0.12
1046 m	Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	–11.20	–29.41 to 8.14	–5.69	–20.19 to 8.90	–22.05	–44.42 to 0.66
1079 m	Nashville Warbler (<i>Vermivora ruficapilla</i>)	–24.53	–43.36 to –7.43	–7.43	–35.24 to 19.17	50.94	–44.71 to 127.14
1113 m	Blackpoll Warbler (<i>Setophaga striata</i>)	–11.30	–21.84 to 0.02	–1.87	–11.45 to 7.82	9.11	–0.003 to 18.55
1232 m	Yellow-rumped Warbler (<i>Setophaga coronata</i>)	–13.89	–26.14 to –0.96	–1.01	–12.85 to 10.85	1.75	–10.89 to 14.05
1240 m	Boreal Chickadee (<i>Poecile hudsonicus</i>)	2.21	–42.11 to 51.95	4.46	–17.46 to 26.14	–10.09	–36.71 to 28.85
1367 m	White-throated Sparrow (<i>Zonotrichia albicollis</i>)	2.60	–6.86 to 13.65	3.10	–8.47 to 14.84	–10.94	–22.21 to –0.12
1416 m	Bicknell’s Thrush (<i>Catharus bicknelli</i>)	–17.40	–44.35 to 17.01	2.00	–17.12 to 21.10	13.67	–12.40 to 32.76
1500 m	Dark-eyed Junco (<i>Junco hyemalis</i>)	–30.10	–48.70 to –11.33	–12.07	–27.11 to 3.23	1.36	–12.41 to 13.89

Intercept and slope estimates were taken from linear-mixed models and applied to the linear equation to derive elevation change. A nonparametric bootstrap procedure (10,000 samples) was implemented to derive 95% CI. Estimates in bold indicates that 95% CI do not include zero. All low-elevation species have elevation distribution modes <750 m and are arranged taxonomically. High-elevation species are ordered by their elevation distribution modes (e.g., Fig. 2b) which are reported as *Elevation*.

^a Sample size was inadequate for analysis

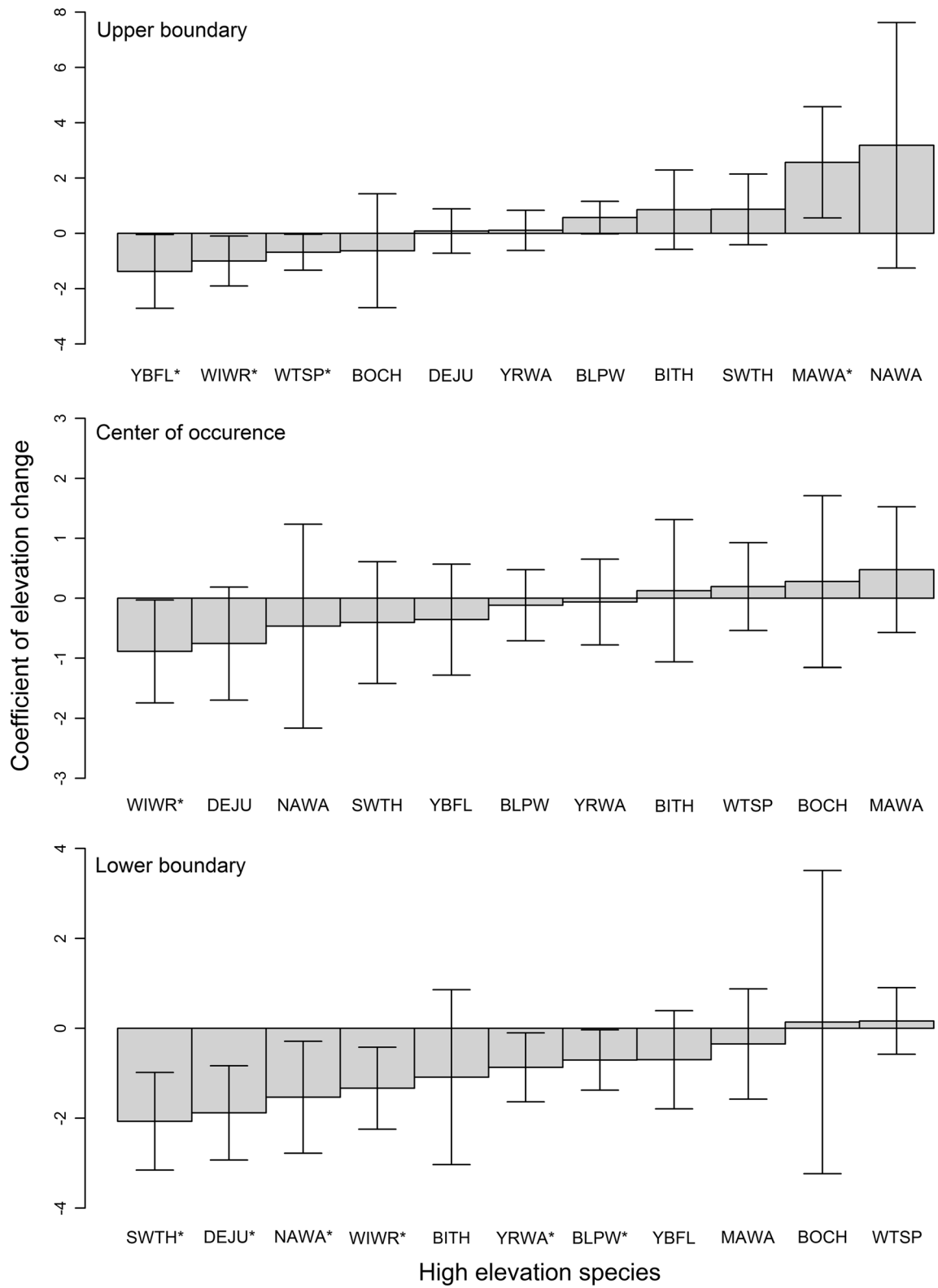
Fig. 3 Coefficient estimates and 95% CI from linear-mixed models for the change in elevation between 1993 and 2009 for low-elevation species. *Positive coefficients* indicate an elevation increase while *negative coefficients* indicate an elevation decrease. *Asterisks* indicate that the 95% CI do not include zero and that the fixed coefficient estimate for change in elevation over time is different than zero ($P < 0.05$). *AMRE* American Redstart, *BAWW* Black-and-white Warbler, *BCCH* Black-capped Chickadee, *BLBW* Blackburnian Warbler, *BTBW* Black-throated Blue Warbler, *BTNW* Black-throated Green Warbler, *CAWA* Canada Warbler, *HETH* Hermit Thrush, *OVEN* Ovenbird



et al. 2008; Rodenhouse et al. 2008; Zuckerberg et al. 2009; Ralston and Kirchman 2013), we provided evidence that, even in the face of regional warming trends at mid-elevations, montane birds shifted downslope while low-elevation birds shifted upslope. Previous studies have documented species range shifts contrary to climate change predictions (Tingley et al. 2009, 2012; Zuckerberg et al. 2009); however, our findings that the majority of a sampled bird community, in this case montane forest birds, responded contrary to this prediction, are unique. Moreover, our results that two adjacent bird communities are undergoing elevational range shifts in different directions

Fig. 4 Coefficient estimates and 95% CI from linear-mixed models for the change in elevation between 1993 and 2009 for high-elevation species. *Positive coefficients* indicate an elevation increase while *negative coefficients* indicate an elevation decrease. *Asterisks* indicate that the 95% CI do not include zero and that the fixed coefficient estimate for change in elevation over time is different than zero ($P < 0.05$). *BITH* Bicknell’s Thrush, *BLPW* Blackpoll Warbler, *BOCH* Boreal Chickadee, *DEJU* Dark-eyed Junco, *MAWA* Magnolia Warbler, *NAWA* Nashville Warbler, *SWTH* Swainson’s Thrush, *WTSP* White-throated Sparrow, *WIWR* Winter Wren, *YBFL* Yellow-bellied Flycatcher, *YRWA* Yellow-rumped Warbler

suggest that the mechanisms driving these opposing elevational shifts are potentially different for each bird community.



We found that shifts of low-elevation species were consistent with predictions of increasing temperature. Temperature is a limiting factor defining the geographic range extent of many species (Root 1988), particularly along the compressed climatic zones of mountainous regions (Terborgh 1971; La Sorte et al. 2014) and including many of the low-elevation species considered in this study (Venier et al. 1999). Shifts in species' distributions could, thus, reasonably be associated with shifts in temperature. Although it would have been ideal to analyze elevational distributions directly in relation to changes in temperature and precipitation, the spatial and temporal scales that we considered for bird distribution shifts were sufficiently mismatched with reasonable expectations of changes in climate patterns that this comparison was not plausible. Nevertheless, the fact that temperature has changed significantly across the study site (Seidel et al. 2009) suggests increasing temperature is a factor worth considering in association with some of the observed shifts. Data from Pinkham Notch, a site within our study area and at the approximate elevation of the hardwood forest–montane spruce–fir ecotone (612 m) indicates significant warming trends over the past 70 years (Seidel et al. 2009). Therefore, if low-elevation birds are limited to lower elevations by cooler temperatures at higher elevations, then this rise in temperature at mid-elevations may release them to shift their upper elevational boundaries upslope.

Climate-mediated changes in habitat are another potential mechanism by which climate change could affect the distribution of species. For example, Able and Noon (1976) determined that most bird species inhabiting mountains in northeastern North America have distributional ranges that coincide with changes in ecotone. Elevational shifts in habitat consistent with those predicted from climate change were reported by Beckage et al. (2008), who found that the ecotone between the northern hardwoods and the montane forest has shifted upslope by approximately 100 m over the past 40 years on three mountains in VT. These upslope shifts in habitats characteristic of lower elevations and their associated resources could further explain the upslope shift of the lower-elevation bird species typical of northern hardwood forests observed in this study. However, this potential explanation should be applied cautiously, as two other studies provide evidence that the montane conifers are shifting downslope, further into the ecotone (Vogelmann et al. 2012; Foster and D'Amato 2015). Although an upward-shifting ecotone supports the hypothesis that shifts in the elevational distribution of low-elevation birds are caused by shifts in habitat, in the absence of data on how climate limits bird distributions, it is difficult to determine with certainty whether or not such shifts are driven directly by increasing temperatures or an upslope shift of suitable habitat.

Compositional changes of the forest structure in the ecotone may also be allowing high-elevation birds to expand their range downslope. Red spruce has experienced a significant decline in northeastern North America and this decline is possibly caused by climate change (McLaughlin et al. 1987; Johnson et al. 1988), historical land use (Foster and D'Amato 2015) and higher levels of acidic deposition at higher elevations (Joslin et al. 1992; Lawrence et al. 1997; Shortle et al. 1997). Furthermore, climate change has also been implicated in decreasing paper birch (*Betula papyrifera*) communities within the ecotone (Beckage et al. 2008; Vogelmann et al. 2012). The void left by decreasing red spruce and paper birch within the ecotone may be responsible for the downslope shift of montane conifers documented by several studies (Beckage et al. 2008; Vogelmann et al. 2012; Foster and D'Amato 2015). All the high-elevation species we found to be shifting downslope are closely and specifically associated with balsam fir (Sabo 1980; DeLuca and King 2014). Therefore, the lower elevational boundary of some high-elevation birds may be shifting downslope to track relatively recent increases in suitable habitat.

Changes in climate could also explain the downslope shift of the lower elevational boundary of high-elevation birds. Although temperature may be an important climatic factor limiting the distribution of some species (Chen et al. 2011), it does not seem to be a plausible driver of the downslope shift of high-elevation birds. Data from higher elevations in the White Mountains at the Mount Washington Observatory (1914 m) did not indicate any significant change in temperature over the past 70 years, but significant warming occurred at lower and mid-elevations (Seidel et al. 2009), where our observed shifts occurred. Other climatic variables such as changes in precipitation, which can result in a tenfold increase in the extirpation risk of montane species, may be particularly important for understanding elevational shifts in montane ecosystems (McCain and Colwell 2011). Precipitation has increased in northeastern North America over the past few decades (Huntington et al. 2009), and that increase is likely to be more pronounced at higher elevations (Howat et al. 2007). If precipitation is an important determinant of the distribution of high-elevation birds in the White Mountains, as it is for many montane species (McCain and Colwell 2011), then some species may have to shift down in elevation to track their precipitation climatic niche.

The elevational shifts observed in this study could be the response to one or more environmental stressors (i.e., direct climate change effects, changes in the composition and structure of habitat caused by climate change, historical land use, or atmospheric deposition). An alternative hypothesis, however, suggests that range shifts could also be caused by population-level processes, regardless of stressors. Under

this hypothesis, population increases cause individuals to move into previously unoccupied locations, albeit of lower quality, and population declines can cause the abandonment of lower-quality habitat often found at the edges of a species' distribution (Thomas and Lennon 1999). Our results do not support this alternative hypothesis. Of the 16 species in this study that showed evidence of range expansion (i.e., boundary shifting away from its center of occurrence), 15 (94%) had populations that were either decreasing or stable, contrary to expectations if range shifts were associated with population trends. Only 2 of the total 19 species that exhibited elevational shifts were consistent with the hypothesis that shifts could be due to regional population changes. Swainson's Thrush had increasing population trends and expanded their range downslope, and White-throated Sparrow populations decreased while their upper elevational boundary contracted.

Developments in modeling species occurrence have highlighted the value of accounting for imperfect detection probabilities (Royle and Dorazio 2008). This may be particularly important when using historical data to test for changes in a species geographic range because, for example, differences in sampling methodologies may result in false absences (Tingley et al. 2009). Correction for imperfect detection probabilities was not possible for our analyses because these models require either spatial or temporal replicate surveys within a season, and the surveys used for this study were only conducted once per breeding season. Spatial replicates would have required summarizing data at the transect level, and for this study it was essential to associate occurrence at the site level to acquire elevational occurrence. However, surveys were conducted by highly trained observers who employed the same, standardized, methodology for the entire study period (King et al. 2008). In addition, the detection probability of montane birds in the White Mountains, NH, do not appear to be influenced by elevation or habitat, and for several species, detection probabilities approached one (DeLuca and King 2014). Some evidence suggests that, if detection probabilities approach one, accounting for these imperfections will not improve species' distribution models (Comte and Grenouillet 2013). Thus, there is no reason to believe that heterogeneous or imperfect detection probabilities were responsible for the patterns found in this study.

Although prevailing theory states that montane species will respond to the changing climate by shifting their distributions up in elevation, our results have highlighted the need to apply this understanding with caution in northeastern North America. In an extensive review, Hargreaves et al. (2014) found that many species' lower elevation (warm) boundaries are driven by biotic interactions while high-elevation (cold) boundaries are more likely to be caused by abiotic factors. In the White Mountains, the ecotone, which

acts as the cold boundary for low-elevation species and the warm boundary for high-elevation species, is warming and suitable high-elevation habitat is moving downslope. Therefore, the cold-limited range boundary of low-elevation species may be responding to the warming temperatures (Seidel et al. 2009) while the warm-limited range boundary of high-elevation species may be responding to the downward march of spruce and fir (Foster and D'Amato 2015), consistent with the results of Hargreaves et al. (2014). With the apparent increase of species using the transition zone, understanding the role of competition in shaping novel montane bird communities becomes increasingly important. Further insight into the demographic mechanisms driving elevational shifts in the northern Appalachian Mountains is an integral component in developing conservation strategies to maintain regional biodiversity.

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