Climatic constraints on wintering bird distributions are modified by urbanization and weather

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Summary

1. Ecologists have long been interested in the role of climate in shaping species' ranges, and in recent years, this relationship has taken on greater significance because of the need for accurate predictions of the effects of climate change on wildlife populations. Bioclimatic relationships, however, are potentially complicated by various environmental factors operating at multiple spatial and temporal scales. Here, we test the hypothesis that climatic constraints on bird distributions are modified by species-specific responses to weather, urbanization and use of supplemental food.
2. Our analyses focused on 18 bird species with data from over 3000 sites across the north-eastern United States and adjacent Canadian provinces. We use hierarchal occupancy modelling to quantify the effects of short-term weather variation and surrounding urbanization on food stress and probabilities of detection, and how these fine-scale changes modify the role that climate has on the distributions of wintering bird populations at regional scales.
3. Examining site occupancy and supplemental food use across the study region, we found that average minimum temperature was an important factor limiting bird distributions, supporting the hypothesis that the occupancy of wintering birds is limited by climatic constraints. We found that 15 of 18 species (83%) were more energetically stressed (had a higher likelihood of visiting a feeder station) as minimum temperature declined from the seasonal average. Because we found these patterns in populations that regularly visit supplemental food sites and were likely not food-limited, we suggest that resource availability is less important than climate in constraining wintering bird distributions. Across a winter season, local within-winter extinction probabilities were lower and colonization probabilities higher at warmer sites supporting the role of climate-mediated range shifts. Importantly, however, these relationships were modified by the degree of urbanization and species' abilities to persist in human-modified landscapes.
4. Our results suggest that urbanization and behavioural adaptation can modify the role of climate on bird ranges and should be included in future analyses of range shifts because of climate change.

Key-words: Feeder Watch, climate change, habitat loss, wintering birds, supplemental feeding, occupancy modelling, ranges, citizen science

Introduction

Ecologists have long been interested in the role of climate in shaping species' ranges (Lack 1966; Fretwell 1972), and evidence suggests that both summer (Jiguet *et al.* 2006) and winter (Root 1988a; Meehan, Jetz & Brown 2004) distributions of birds are directly affected by their thermal environments. Our understanding of the importance of climate in determining species distributions, however, is limited by a lack of information on how these relationships operate at multiple scales and change as a function of human land use. As the

global human population grows, land-use change continues to alter native habitats for many bird species (Fahrig 2003; Jetz, Wilcove & Dobson 2007), necessitating a more comprehensive approach that incorporates landscape, weather and food supply to understand the complex interactions between climate and urbanization and how these interactions ultimately shape species' distributions.

The biological mechanism underlying range limits is an active area of debate in ecology (Gaston 2009; Sexton *et al.* 2009). It has been suggested by Root (1988b) that the northern limit of many wintering birds in North America is primarily set by species' metabolic rates. This conclusion has been questioned by Repasky (1991) and Canterbury (2002),

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who pointed out that birds can adjust their metabolic rates or behaviours to adapt to thermal environments, through choice of roosting sites, topor, adjusting activity patterns and supplemental food use (Chaplin 1974; Mugaas & King 1981; Kwit *et al.* 2004). In recent years, this debate has received renewed attention as winter temperatures have risen steadily in the Northern Hemisphere (IPCC 2007), and although milder winter temperatures have been implicated as a primary driver of recent northward shifts for many wintering birds (La Sorte & Thompson 2007; La Sorte *et al.* 2009), the importance of underlying climatic constraints limiting bird distributions has not been firmly established.

Studies at both local and geographical scales suggest that species can adapt to changing climatic conditions through behavioural flexibility or an increased reliance on supplemental and natural food sources. For example, Canterbury (2002) suggested that birds can adjust their basal metabolic rates and thus their ranges in the face of increased cold, a hypothesis requiring that sufficient food be found to meet increased demands. Supporting this hypothesis, fine-scaled studies have found that winter mortality can be reduced in areas where supplemental food is present, but that this effect will be more profound when natural food is scarce (Perdeck, Visser & Van Balen 2000; Siriwardena *et al.* 2007; Siriwardena, Calbrade & Vickery 2008). If natural food supplies are low in landscapes dominated by human disturbances, the effects of extreme weather events on winter mortality have been found to be more severe (Doherty & Grubb 2002). At continental scales, Meehan, Jetz & Brown (2004) found that, in addition to temperature, net primary productivity was an important predictor of wintering bird abundance across North America. These results have led some researchers to suggest that the northward shift of some wintering birds may not be the result of climate change *per se*, but increased supplemental feeding by humans and the increased availability of artificial food resources at more northerly latitudes (Robb *et al.* 2008). This would imply that areas with greater supplies of supplemental food (through recreational bird feeding in urban areas) may allow some species to persist in colder areas than would be possible, leading to a decoupling between species ranges and climate.

The extent to which there are thermoregulatory constraints on species' distributions is particularly relevant because bioclimatic envelope models that explicitly assume a key role of climate in determining species' ranges are the standard tool for predicting the impacts of climate change on species' distributions (Pearson & Dawson 2003; Lawler *et al.* 2009; Tingley *et al.* 2009). Beale, Lennon & Gimona (2008) tested the assumption that species distributions are limited primarily by climate by generating synthetic distributions that retained the same spatial structure as data from the European Breeding Bird Atlas, but were randomly aligned with respect to climate. They found that most climate-based models were no better than random associations and questioned whether most species were limited by climate. Several researchers have questioned these findings and conclusions (Araújo, Thuiller & Yoccoz 2009; Aspinall, Miller & Franklin 2009; Peterson

et al. 2009) and considerable debate remains about the role of climate as the dominant factor limiting species distributions.

Occupancy modelling (MacKenzie *et al.* 2006) is a form of hierarchical modelling able to account for imperfect detectability among species and quantify unbiased patterns of site occupancy, a method that is so far rare in most climate change studies (Altwegg, Wheeler & Erni 2008). Additional information can also be extracted with appropriate data. For bird surveys focused on documenting visitation to supplemental food sites, the detection probability parameter estimated in occupancy modelling is not merely a nuisance parameter, but can serve as a biological index of energetic stress in relation to changing local environmental conditions: increased probabilities of detection indicate more frequent use of supplementary food sources, which implies a greater need for supplemental food at local scales. Furthermore, in a 'multi-season' occupancy model, the probabilities of local colonization and, more importantly, local extinction can be estimated as a function of environmental features such as winter temperature and the degree of urbanization (MacKenzie *et al.* 2003).

In this paper, we combine fine-scale meteorological data, land use information, and data from a winter-long survey of birds at thousands of supplemental food sites to test four hypotheses regarding the influence of winter weather, climate and urbanization on feeder visitation and dynamic site occupancy. First, if birds alter their feeding behaviours to compensate for energy deficits during unusually severe winter weather, then birds should be more likely to visit supplemental food sites during abnormally harsh weather conditions. Second, if urbanization leads to fewer natural food sources, wintering birds should demonstrate a greater propensity to visit supplemental food sites in heavily developed landscapes. Third, if the distributions of wintering birds are a function of climatic constraints, then site occupancy should be positively correlated with increasing winter temperatures, despite the availability of supplemental food sources. Fourth, if the distributions of wintering birds are restricted primarily by thermoregulatory constraints, then the probability of local site extinction should be higher and the probability of colonization should be lower in colder environments as winter progresses.

We tested these hypotheses for 18 bird species in the northeastern United States and adjacent Canadian provinces. In all of our analyses, we tested for the hierarchical effects of weather, climate and urbanization to evaluate how the relationship between species occupancy and temperature varies across a diversity of human-modified landscapes at multiple spatio-temporal scales.

Materials and methods

BIRD DATA (PROJECT FEEDER WATCH)

Project Feeder Watch (PFW) is a winter-long repeated survey of birds that regularly visit supplemental feeding stations throughout

the United States and Canada and is operated by the Cornell Lab of Ornithology and Bird Studies Canada (Wells *et al.* 1998). From early November to late April, programme participants record the maximum numbers of each species seen at a supplemental feeding station during periodic 2-day counts. For our analyses, we collapsed these counts down to whether a species was detected or not detected. Two-day count periods are repeated throughout the PFW season and are separated by a minimum of five calendar days. More than 10 000 PFW sites are located across the United States and Canada annually with as many as 22 counts submitted from each site per winter.

To match the spatial and temporal extent of the meteorological data available at the time of this study (see Climate Data section), we limited the PFW sites to those in north-eastern United States and bordering sites in the adjacent Canadian provinces and include data from the 2007–2008 PFW season (10 November 2007–4 April 2008) (Fig. 1). Participants reported the geographical location (latitude and longitude) of their feeding station(s) using online mapping tools, geographical positioning systems or address information. When only address information was provided, we used geocoding to obtain precise spatial coordinates. For each count, participants recorded their level of effort including the number of hours (≤1, 1–4, 4–8 or >8 h) and number of half-day periods (1, 2, 3 or 4 half-days), and they spent observing their feeder station during the 2-day count. Participants also collected data on snow depth for each observation period (0, 0–5, 5–15 and >15 cm). We analysed data from a subset of 18 resident bird species that frequent bird feeders were relatively common (>10% of sites included in this study reporting a sighting at least once during the winter season), but represented a wide range of distributions throughout the north-eastern United States (Appendix S1, Supporting Information).

CLIMATE DATA

Daily temperature and precipitation models data came from models that were developed by the Northeast Regional Climate Center (De-Gaetano & Belcher 2007; DeGaetano & Wilks 2009). These models are spatial interpolations of daily minimum and maximum temperature (°C) at a 5 × 5 km resolution and daily precipitation (mm) at a 3 × 3 km resolution. Using the spatial coordinates for each PFW site, we extracted daily minimum temperature (°C), maximum temperature (°C) and precipitation (mm) at a given location for every day from 1 October 2007 to 1 May 2008. These data were then associated with PFW observation events.

LAND COVER DATA

We acquired land cover data from the Land Processes Distributed Activate Archive Center. We used the MODIS Land Cover Type product that contains multiple classifications to describe land cover properties derived from observations spanning 1 year of input of Terra and Aqua data. The primary land cover scheme identified 17 land cover classes defined by the International Geosphere Biosphere Programme. Land cover classification was derived through a supervised decision-tree classification method and has a resolution of 500 m. We chose the MODIS Land Cover product because it had data for Canada and additionally for the same year in which the PFW data were collected (2007–2008). For our purpose of identifying sites embedded in the most anthropogenically disturbed landscapes, we calculated the proportion of land cover classified as Urban/Built-up in a 3-km landscape surrounding each PFW site (Urban).

OCCUPANCY MODELLING AND CLIMATE COVARIATES

Occupancy modelling is a conceptual and analytical extension of mark–recapture analyses where a 2-level hierarchical analysis is used to fit integrated likelihood models of site occupancy (ψ) and detectability (ρ) (MacKenzie *et al.* 2002, 2006). The occupancy analysis fits zero-inflated binomial models that allowed for the specification of covariates for both the state occupancy (ψ) and detection (ρ) processes. In brief, the binary occupancy state process (z_i) of site i was modelled as:

$$z_i \sim Bernoulli(\psi_i)$$

The occupancy state was imperfectly observed because even if a bird occupied a site throughout a sampling period, it may not be observed at a feeder station. Consequently, the conditional
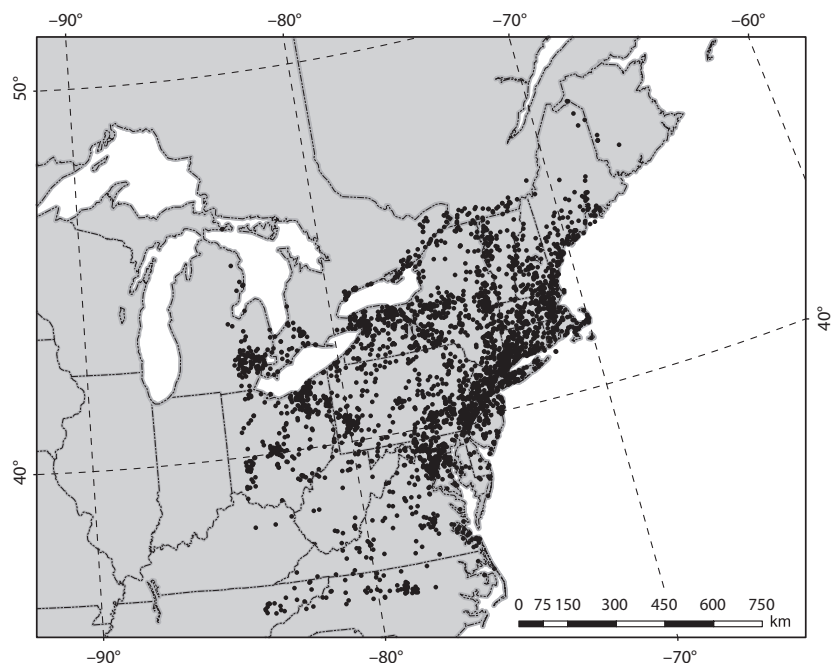

Fig. 1. Distribution of 3195 Project Feeder-Watch sites that were used for this study. We included only those sites that fell within the extent of the meteorological interpolations and contributed a minimum of 3 counts during the core winter season (1 December 2007–8 February 2008).

observation process was modelled for a site (i) and count period (j) for a specific observation (y_{ij}) as:

$$y_{ij}|z_i \sim \textit{Bernoulli}(z_i \rho_{ij})$$

Using this framework, we assumed that the observations were independent Bernoulli trials with parameter ρ_{ij} (detection probability) that varied with observation-specific weather and sampling conditions. Our first analytical objective was to quantify patterns of occupancy and detectability using a 'single season' model approach (MacKenzie *et al.* 2002). We used data from the 10 weeks in the winter season from 1 December 2007 to 8 February 2008 to represent the 'core winter' season for over-wintering birds in the north-eastern United States, meant to capture the time during the winter season when species were least likely to be migrating. We identified this core winter season by reviewing annual cycles using species accounts from the Birds of North America (Poole 2005). We included only those data from PFW participants within the study area who submitted a minimum of three counts during this 10-week period. For models quantifying occupancy during the core winter period, we analysed occurrence data from 3195 PFW sites that contributed data from an average of 6 of the 10 count periods (Fig. 1). Participants contributed 19 360 checklists during this 10-week observation period.

To estimate patterns of occupancy and detectability, we used both observation- and site-specific covariates. Observation-specific covariates were calculated over the 2-day count period and were deviation in minimum temperature from the average minimum temperature of the winter season (MinTemp), 2-day average precipitation (Precip), snow depth (SnowDepth), survey hours (Hours), and number of survey half-day periods (Days). All categorical covariates (i.e. effort and snow depth) were modelled as dummy variables, and MinTemp and Precip were standardized across the entire data set by centring to a mean value of zero. Site-specific covariates did not vary across the core winter season, but climatic variables are often highly correlated and multicollinearity among predictor variables is a common issue. We used a suite of site-specific covariates that were calculated over the core winter season and relatively uncorrelated($r < 0.60$) including the climate covariates average winter minimum temperature (AvgMin), average winter precipitation (AvgPrec), and proportion of counts reporting snow cover (PSnow). We only analysed counts for which we had both observation data and their associated observation-specific covariates.

We constructed an *a priori* set of candidate approximating models with various combinations of weather, climate and landscape variables for modelling the detection and site occupancy processes in two separate steps. First, we modelled the detection process using 40 models including all combinations of observation- and site-specific covariates. Second, we modelled the occupancy state process using 15 models including only the site-level covariates and the predictors of detection probability from the model in the first step. To assess the relative support of the models in each step of the analysis, we calculated the log likelihood value, number of model parameters (K), AIC values, ΔAIC, and model probabilities (Akaike weights) (Burnham & Anderson 2002). When there was more than one competing model (Δ AIC < 2), we used model-averaging to calculate detection probabilities (ρ), predicted occupancy (ψ), and beta estimates (β).

Our second analytical objective was to model changes in occupancy throughout the winter season as conditional states of site-level extinction (ε) and colonization (γ) processes, analogous to the local population processes of mortality and recruitment using a 'multi-season' model (MacKenzie *et al.* 2003, 2006). Data from the PFW season were stratified into three 7-week sampling periods to capture changes in occupancy between the early (10 November 2007–28 December 2007), mid (29 December 2007–8 February 2008), and late (9 February 2008–4 April 2008) winter season. Similar to our criterion for selecting sites whose data were used in the 'single season' models, we included only data from those PFW participants who submitted a minimum of three counts during each of the 7-week period to ensure consistent minimal sampling across the sampling periods. In this case, we defined $z_{(i,t)}$ to be the binary occupancy status of site i during each of the three separate winter periods (t). Multiseason modelling was restricted to 1658 sites that contributed a minimum of three counts from the early, mid and late-winter season periods. The maximum number of counts contributed for the multiseason models was 21, while the average was 15 counts.

We performed all occupancy modelling with R (Version 2.10.1; R Development Core Team 2009) and the extension package unmarked (Fiske & Chandler 2010). Except for otherwise stated, values presented are means $\pm$ SE.

MODEL EVALUATION

To evaluate the adequacy of models for predicting the observed pattern of occurrence of each species, we calculated the Area Under the Curve (AUC) as a measure of discriminatory power (Fielding & Bell 1997; Hosmer & Lemeshow 2000). The AUC statistic represents the probability that a model will rank a randomly chosen positive occurrence higher than a randomly chosen negative occurrence. Although there are several performance criteria available for binary model evaluation, AUC is considered a valuable metric for quantifying the extent to which models correctly predict observed occurrence better than chance alone (Mouton, Baets & Goethals 2010). AUC values < 0.70 suggests poor discriminatory power of the model, values between 0.70 and 0.80 suggest acceptable discrimination, and values > 0.80 suggest excellent discrimination (Hosmer & Lemeshow 2000).

Results

For the 3195 PFW sites, average minimum temperature sites ranged from $-18.94°C$ to $7.07°C$ ($\overline{x} = -4.66°C$),average precipitation ranged from 1.13 to 6.13 mm ($\overline{x} = 3.52$ mm), the proportion of counts reporting snow ranged from 0 to 1 ($\overline{x} = 0.63$), and urban composition ranged from 0 to 1 ($\overline{x} = 0.24$).

FEEDER VISITATION AND DETECTABILITY

Species varied widely in their detectability, and no species was always detected when present at a site during the 10-week core winter period. Given that a site was occupied and a minimum sampling effort of 1 h and 1 half-day of observation, baseline detection probability estimates varied from 0.11 for Yellow-bellied Sapsuckers *Sphyrapicusvarius* (Linnaeus) to 0.74 for Tufted Titmice *Baeolophus bicolor* (Linnaeus) (across all species; $\overline{x} = 0.51$) for a typical PFW site (Table 1). As expected, the likelihood of observing a species increased sharply with greater sampling effort, but a saturation effect was apparent. Across all species, the model-averaged probability of detection increased from 0.50 ± 0.04 for 0–1 observation hours to 0.59 ± 0.05 (1–4 h), but then levelled off at 0.63 ± 0.06 (4–8 h) and 0.64 ± 0.07 (> 8 h). Similarly, we

Table 1. Results of modelling feeder visitation as a function of observation covariates (MinTemp, Precip, and SnowDep) and site-level covariates (AvgMin, AvgPrec, PSnow, and Urban). Sampling effort covariates (Hours and Days) are included in every model. We report model probabilities (Akaike weights) for all 18 bird species. Only models with a Δ AIC < 2 are given. Detection probability (ρ), given minimum sampling effort, is given for each bird species. We report only those models with probabilities > 0·01, the full list of all models can be found in Appendix S2

Covariates																	Models				
MinTemp	+		+		+		+	+	+	+		+		+	+		+	+	+	+	
Precip	+	+	+	+			+	+	+	+	+			+	+	+		+	+	+	
SnowDep	+	+					+	+		+			+		+			+		+	
AvgMin	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+			
AvgPrec	+	+	+	+	+	+	+	+	+	+								+	+		
Psnow	+	+	+	+	+	+	+	+	+					+	+	+	+				
Urban	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+		

Species								Model Probabilities													ρ
MODO	0·17																0·40	0·15			0·67
RBWO	0·15														0·39	0·29					0·45
YBSA				0·06				0·09	0·08		0·14		0·08	0·07		0·16			0·11		0·11
DOWO			0·11	0·13	0·25						0·11	0·19									0·72
HAWO		0·15						0·15	0·41												0·48
BLJA	0·52	0·29																			0·56
TUTI	0·11	0·13		0·24				0·10	0·10		0·13										0·74
WBNU		0·14						0·19	0·33										0·13		0·68
CARW	0·16	0·39					0·15						0·16								0·31
AMRO			0·09							0·22				0·2							0·13
ATSP	0·25							0·43													0·26
SOSP	0·14	0·31				0·17	0·36														0·25
WTSP	0·14					0·35						0·3									0·48
DEJU	0·27							0·49													0·71
NOCA	0·59											0·36									0·65
HOFI	0·17	0·30				0·14	0·25														0·59
AMGO		0·16								0·25			0·13	0·32							0·67
HOSP			0·49							0·30											0·63

MODO, Mourning Dove, RBWO, Red-bellied Woodpecker; YBSA, Yellow-bellied Sapsucker; DOWO, Downy Woodpecker; HAWO, Hairy Woodpecker; BLJA, Blue Jay; TUTI, Tufted Titmouse; WBNU, White-breasted Nuthatch; CARW, Carolina Wren; AMRO, American Robin; ATSP, American Tree Sparrow; SOSP, Song Sparrow ; WTSP, White-throated Sparrow; DEJU, Dark-eyed Junco; NOCA, Northern Cardinal; HOFI, House Finch; AMGO, American Goldfinch; HOSP, House Sparrow.

found that detection probability increased with number of half-day observation periods from 0·50 ± 0·04 for 1 half-day to 0·55 ± 0·07 (2 half-days), but also plateaued at 0·59 ± 0·07 (3 half-days) and 0·61 ± 0·07 (4 half-days).

The global model, including all observation and site-level covariates, was competitive (Δ AIC < 2) for 11 of 18 species (61%), suggesting that both weather and site-level characteristics influenced feeder visitation (Table 1). Deviation in minimum temperature over the 2-day count period (MinTemp) was supported through model selection as a predictor of feeder visitation for 15 of 18 species (83%) (Fig. 2). This effect was stronger for some species than others. For example, the odds of detecting a White-throated Sparrow *Zonotrichiaalbicollis* (Gmelin) or Carolina Wren *Thryothorusludovicianus* (Latham) at a feeder were 1·3 and 1·1 times greater for every 1°C decrease in minimum temperature from the seasonal average, respectively (Table 2). Other species, such as Downy Woodpecker *Picoidespubescens* (Linnaeus), American Robin *Turdusmigratorius* (Linnaeus) and House Finch *Carpodacusmexicanus* (Müller), had well-supported models not including the effect of MinTemp and demonstrated little change in

detection probability with changes in minimum temperature (Table 1; Fig. 2).

We found that species such as American Tree Sparrow *Spizellaarborea* (Wilson), White-throated Sparrow, Dark-eyed Junco *Juncohyemalis* (Linnaeus), Northern Cardinal *Cardinaliscardinalis* (Linnaeus) and House Finch were more likely to visit feeder stations during wet conditions (Fig. 2). However, snow depth during the count period had relatively limited impact on feeder visitation even though the effect of snow depth was supported by model selection and its inclusion in the global model (Table 1). Few species showed a distinct change in detection probability with varying levels of snow cover and no species showed support (ΔAIC < 2) for the inclusion of snow depth as a sole predictor of detectability (Appendix S2, Supporting Information).

Site characteristics also had a strong influence on feeder visitation. The average minimum temperature of a site was an important factor influencing feeder visitation for most species and only two [Mourning Dove *Zenaidamacroura* (Linnaeus) and White-breasted Nuthatch *Sittacarolinensis* (Latham)] had well-supported models that did not include
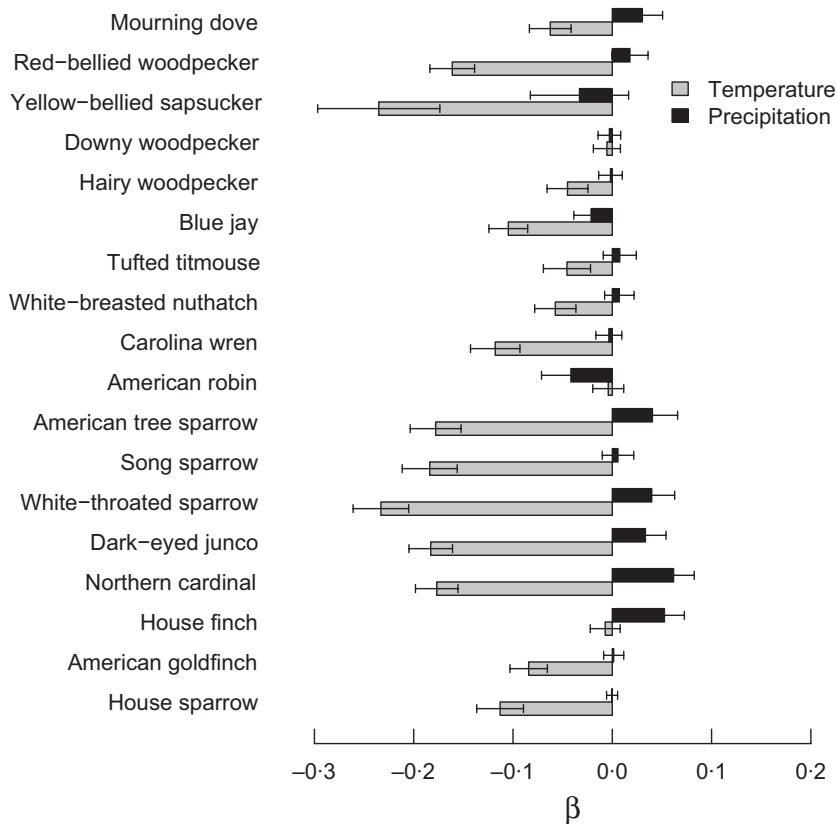
Fig. 2. Detection probability describing the relationship between feeder visitation rate (β) and weather over the 2-day count period. Most birds were more likely to visit feeders, and thus more likely to be detected, during abnormally cold count periods. Higher average precipitation across the 2-day count period generally resulted in a higher probability of bird visitation, but this effect was not as strong as deviation in minimum temperature from the seasonal average.

Table 2. Odds ratios of the association between site-level covariates and the probability of detection (ρ) and occupancy (ψ) for each species. An odds ratio > 1 indicated that the probability is more likely as the covariate increased while odds ratios < 1 indicated that the probability is less likely. We report only odds ratios that do not include 1 in the 95% confidence intervals

Species	AvgMin		AvgPrec		PSnow		Urban	
	ρ	ψ	ρ	ψ	ρ	ψ	ρ	ψ
Mourning Dove		1·18			0·42		1·64	
Red-bellied Woodpecker	1·03	1·53		1·25	0·76		0·45	0·39
Yellow-bellied Sapsucker		1·12		0·72		0·35	0·44	0·34
Downy Woodpecker	1·04		1·21				0·62	0·63
Hairy Woodpecker	0·87	0·82				1·60	0·51	0·48
Blue Jay			1·34	1·30	0·55		0·45	0·58
Tufted Titmouse	1·09	1·23	1·21	1·63		0·46	0·34	0·23
White-breasted Nuthatch			1·19	1·31			0·55	0·47
Carolina Wren	1·17	1·34			0·57	0·35		
American Robin	1·13	1·12				0·45		
American Tree Sparrow			1·11	1·32		6·80	0·32	0·26
Song Sparrow	1·11	1·18	1·12	1·22	0·41	0·38		1·55
White-throated Sparrow	1·15	1·29		1·16	0·52	0·24		
Dark-eyed Junco	1·13	1·39	1·13	1·30		2·89	0·62	0·60
Northern Cardinal	1·15	1·51			0·72		1·29	2·58
House Finch	1·05	1·42	0·93		0·51			1·91
American Goldfinch	1·13	1·20		1·22			0·48	0·38
House Sparrow	1·09	1·19	1·16	1·22		1·55	3·82	21·49

average minimum temperature (Table 1). Counter to our predictions, we found that most species were more likely to visit feeders located in sites that were warmer, wetter, and less urban throughout the core winter season (Table 2). We did find, however, that a few species including Mourning Dove, Northern Cardinal and House Sparrow *Passer domesticus* (Linnaeus) were more likely to visit feeders in more urban settings (Table 2).

Table 3. Results of modelling core winter occupancy as a function of average minimum temperature (AvgMin), average precipitation (AvgPrec), proportion of counts reporting snow (PSnow), and the per cent of the landscape (3-km) classified as urban development (Urban). We present model probabilities (Akaike weights) for all 18 bird species. Only models with a Δ AIC < 2 are shown. The AUC statistic is reported for each bird species, and AUC values > 0·70 are in bold. We report only those models with probabilities > 0·01, the full list of all models can be found in Appendix S3

Covariates	Models											AUC
AvgMin	+	+	+	+	+	+	+	+				
AvgPrec	+	+	+		+				+	+		
PSnow	+	+		+		+			+		+	
Urban	+		+	+			+		+	+	+	
Species	**Model Probabilities**											**AUC**
MODO					0·24	0·11	0·11	0·28				0·68
RBWO	0·30		0·68									**0·76**
YBSA	0·78											**0·72**
DOWO				0·10					0·19	0·11	0·27	0·58
HAWO	0·30			0·67								**0·72**
BLJA	0·18		0·46						0·19			0·6
TUTI	1·00											**0·71**
WBNU	0·26		0·44						0·25			0·64
CARW	0·16	0·35		0·15		0·33						**0·78**
AMRO	0·2			0·39		0·27						0·65
ATSP	0·47								0·52			**0·72**
SOSP	0·95											0·65
WTSP	0·23	0·60										**0·75**
DEJU	0·61	0·23										0·65
NOCA					0·19	0·26		0·43				**0·85**
HOFI						0·26		0·47				**0·8**
AMGO	0·43		0·48									0·61
HOSP	0·90											**0·75**

MODO, Mourning Dove; RBWO, Red-bellied Woodpecker; YBSA, Yellow-bellied Sapsucker; DOWO, Downy Woodpecker; HAWO, Hairy Woodpecker; BLJA, Blue Jay; TUTI, Tufted Titmouse; WBNU, White-breasted Nuthatch; CARW, Carolina Wren; AMRO, American Robin; ATSP, American Tree Sparrow; SOSP, Song Sparrow; WTSP, White-throated Sparrow; DEJU, Dark-eyed Junco; NOCA, Northern Cardinal; HOFI, House Finch; AMGO, American Goldfinch; HOSP, House Sparrow.

WINTER SEASON OCCUPANCY

When modelling occupancy during the core winter season, the global model incorporating the influence of average minimum temperature (AvgMin) and precipitation (Avg-Prec), snow (PSnow), and urban composition (Urban) on occupancy was competitive (Δ AIC < 2) for 14 of the 18 bird species (78%) (Table 3). As with detectability, this finding suggests that all of these environmental factors played a role in limiting bird distributions during the core winter season. However, the ability of the global model to effectively discriminate the observed distribution of birds during this season varied across species. AUC values ranged from 0·58 (Downy Woodpecker) to 0·85 (Northern Cardinal) ($\bar{x} = 0.70$) and 10 species had an AUC value over 0·70 (suggesting effective model discrimination) (Table 3). For most bird species, minimum temperature was a strong determinant of occupancy, and generally warmer and wetter sites were more likely to be occupied during the core winter season (Table 2). Only four species [Downy Woodpecker, Blue Jay *Cyanocittacristata* (Linnaeus), White-breasted Nuthatch, and American Tree Sparrow] had support for models that did not include average mini-mum temperature (Table 3), and only Hairy Woodpecker *Picoidesvillosus* (Linnaeus) were more likely to occupy colder sites (Table 2). For the six species that were more likely to occur in warmer sites throughout the core winter season and had an AUC value > 0·70, the probability of occupancy declined when average minimum temperatures were close to −5°C (Fig. 3).

All the species included in this study regularly visit supplemental feeding sites, but they varied in their response to urbanization (Table 2). Most of the woodpeckers (Family Picidae) were less likely to occupy urban landscapes as were other species such as Blue Jay, Tufted Titmouse, White-breasted Nuthatch, Dark-eyed Junco and American Gold-finch *Spinustristis* (Linnaeus) (Table 2). We did find, however, that some species were more likely to occupy these modified landscapes including Song Sparrow *Melospizamelo-dia* (Wilson), Northern Cardinal, House Finch and House Sparrow. In addition, we found that the urbanization effect influenced the species-specific relationship with average mini-mum temperature. For example, in predicting the relation-ship between average minimum temperature and the probability of occupancy for an urban-adapted species (e.g. House Finch), urbanization tends to allow urban species to
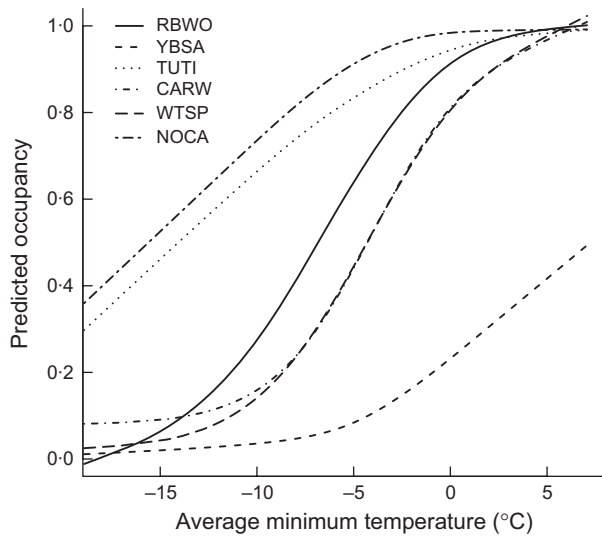
Fig. 3. The relationship between average minimum temperature (°C) and the model-averaged probability of regional occupancy for six bird species Red-bellied Woodpecker (RBWO), Yellow-bellied Sapsucker (YBSA), Tufted Titmouse (TUTI), Carolina Wren (CARW), White-throated Sparrow (WTSP) and Northern Cardinal (NOCA). All species were more likely to occupy areas that were, on average, warmer throughout the core winter season.
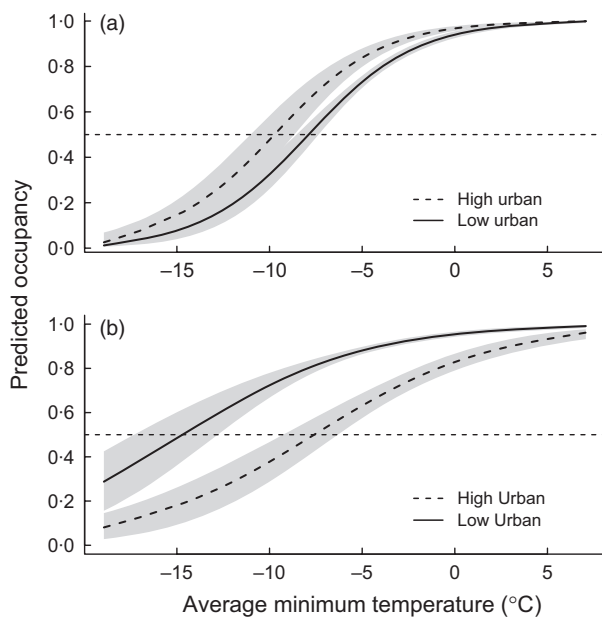

Fig. 4. The relationship between average minimum temperature (°C) and the conditional probability of occupancy. We modelled predicted occupancy for an urban-adapted species (a., House Finch) and a non-urban-adapted species (b., Tufted Titmouse) under two land-use scenarios where urbanization is 0 (Low Urban) and maximized to 1 (High Urban). Shaded areas represent 95% confidence intervals and horizontal dashed lines designate 0·50 probability.

tolerate colder environments than less disturbed landscapes (Fig. 4). Conversely, birds less likely to occur in urban landscapes (e.g. Tufted Titmouse) were also less likely to occupy urban sites with colder winter temperatures (Fig. 4).
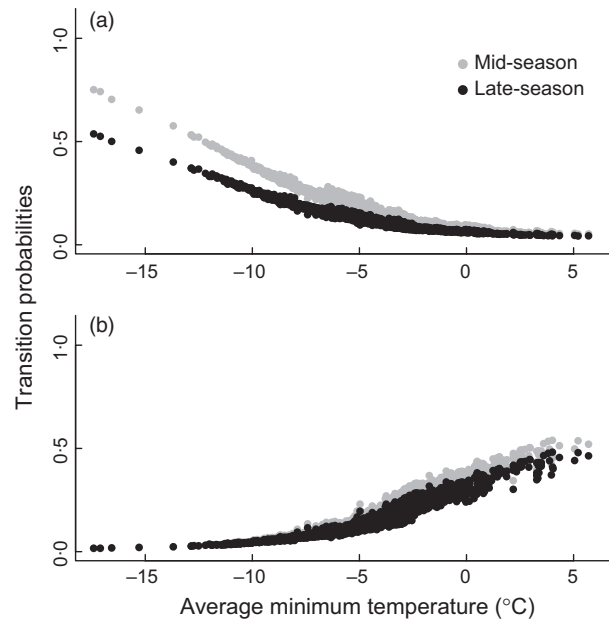
Fig. 5. Site-level probabilities of extinction (a) and colonization (b) were averaged across 6 climate-restricted species (Red-bellied Woodpecker, Yellow-bellied Sapsucker, Tufted Titmouse, Carolina Wren, White-throated Sparrow, and Northern Cardinal) and plotted against average minimum temperature. At warmer sites, birds had lower probabilities of extinction and higher probabilities of colonization. Although probabilities of extinction were slightly higher in from early to mid-season periods, there were no systematic differences in rates of seasonal colonization.

We used the environmental factors that were found to influence core winter distribution in modelling regional patterns of changes in site occupancy over the winter season. In analysing winter-long changes in occupancy (i.e. colonization and extinction) using a global model for the six climate-restricted species (Red-bellied Woodpecker *Melanerpescarolinus* (Linnaeus), Yellow-bellied Sapsucker, Tufted Titmouse, Carolina Wren, White-throated Sparrow and Northern Cardinal), we found that the probability of extinction was generally higher at colder sites, while the opposite was true for patterns of colonization (Fig. 5). These transition probabilities, however, were relatively low with an average extinction and colonization probability of 0·18. Although there was a slight increase in extinction probabilities for species occupying sites during the mid-winter season compared to extinctions during the late-winter season, there did not appear to be any systematic patterns of higher colonization probabilities during the mid- or late-winter seasons (Fig. 5).

Discussion

We found average minimum temperature, calculated across a single winter season, to be an important factor limiting the distributions of birds throughout the north-eastern United States and adjacent Canadian provinces. This finding supports the hypothesis that the distributions of wintering birds are limited by climatic constraints (Root 1988a,b). Given that the populations we studied regularly visited supplemental

food sites and were likely not food-limited, this further indicates that resource availability is not as important in constraining wintering bird distributions as climate. We also found that these distributional relationships were modified by local changes in behaviour, degree of human land use and species' abilities to persist in human-modified landscapes.

Weather conditions influenced feeder attendance and the regional variation in use of supplemental food sites, both of which have important implications for the study of climatic constraints in bird populations. By documenting variation in birds' attendance at feeders (i.e. detection probability) as an indirect measure of a bird's ability to adjust to their thermal environment, we found that most species increased their use of supplemental food during inclement weather (Fig. 2). Although large-scale studies of supplemental food use are rare, other studies have found similar patterns of increased dependency on supplement food during colder winter periods (Siriwardena *et al.* 2007; Siriwardena, Calbrade & Vickery 2008). For example, Chamberlain *et al.* (2005) analysed data from 458 garden feeders as part of Britain's Garden Bird Feeding Survey and found that the probability of bird occurrence was higher when the mean daily temperature over the preceding week was lower. These results provide further support for temperature having an important influence in driving behavioural decisions that may, in turn, affect overwinter mortality and overall estimates of occupancy. From a sampling perspective, if ornithological surveys include data from visitations to supplemental food sites, as is frequently the case, the likelihood of detecting a species will be conditional on the prevailing weather conditions and potentially introduce a significant bias in broad-scale surveys.

Local weather was not the only factor influencing feeder visitation, as landscape characteristics of the site were also important predictors affecting the likelihood of supplemental food use. We hypothesized that birds would be more dependent on feeders in harsher conditions (e.g. colder, more urban sites), but we found that most species were more likely to visit supplemental food stations at warmer sites that were characterized by less snow cover and lower urbanization. This finding is likely a result of the strong variation in site-level characteristics such that these colder and more urban landscapes are the least favourable sites, and as a consequence, birds are likely less abundant, less active and less likely to be detected at feeders. Many of the species more likely to occupy urban landscapes were also more likely to visit feeders in urban landscapes, suggesting a greater ability and potential adaptation to use bird feeders as a supplementary food source.

Not only were birds more likely to occupy and persist in warmer regions, they were also more likely to be detected at feeders in these landscapes. Consequently, accounting for this potential bias in detectability is crucial for accurately estimating patterns of occupancy for wintering birds across a dynamic and changing winter season (Altwegg, Wheeler & Erni 2008). That is, if climate change studies rely on broad-scale surveys, there is a potential that range-expanding species are not necessarily occupying new warmer regions, but

are simply more likely to be detected in those regions, with the result that range expansions are over-estimated. More realistic projections of the impact of climate on species' distributions will require a better understanding of the multi-scaled effects of environmental drivers on biological processes.

Species are being affected by both widespread changes in land use and climate, yet the interactions of urbanization and bioclimatic relationships are typically ignored. By definition, bioclimatic models in their purest form consider only climatic factors, but the effects of land-use change and urbanization on wildlife populations are of critical importance (Jetz *et al.* 2007). In regions where human-dominated landscapes are common, predictions from bioclimatic models will likely be erroneous (Pearson & Dawson 2003). Unfortunately, many distributional surveys are not amenable to landscape-scale analyses because of their sampling protocol. For example, the basic sampling unit of the North American Christmas Bird Count is a 24-km-diameter circle, and surveys can be conducted within any part of the circle. Because PFW observations are point-based, we were able to characterize the degree of urbanization in 3-km landscapes surrounding sampling points, allowing us to capture relatively fine-scaled variation in both average minimum temperature and urbanization. In species that were less likely to occupy urbanized landscapes, we found that urbanization generally exacerbated the effect of minimum temperature by lowering the ability of birds to tolerate cold conditions. Human-modified landscapes may, however, also provide artificial refugia for many urban-adapted species. We found evidence that urban-adapted species may benefit from the presence of human-modified landscapes, with such species predicted to tolerate colder conditions in more urban landscapes. Our results show that accurate predictions of future distributional shifts will require detailed knowledge of how individual species are affected by both habitat alteration and climate to accurately predict climate-induced range shifts across human-dominated landscapes (Mustin, Sutherland & Gill 2007).

For wintering birds, milder winter temperatures may lead to behavioural changes, and as such, survival probabilities at a given location for climate-restricted species will likely increase under warming conditions (Broggi *et al.* 2004). Extreme weather conditions (e.g. cold snaps) have been implicated in lower survival and regional population declines (Link & Sauer 2007; Robinson, Baillie & Crick 2007). In focusing on the six most climate-restricted species, we found that large changes in regional occupancy were not common for these species as indicated by generally low transition probabilities, but higher within-winter stability (i.e. lower probabilities of extinction and higher probabilities of colonization) in warmer environments are consistent with the predictions of climate-mediated range change. In our study, extinction and colonization probabilities were all conditional on the species being detected at least once during a minimum of three observation counts across the preceding 7-week time period. As a result, extinction events generally represented a period of prolonged absence (either mortality or emigration) from a previously occupied site and most of these events

occurred in the first transitional period (early to mid-winter) (Fig. 5). Colonization events represented a species appearing at a feeder site when it was not detected during a previous time period and likely indicated either an immigration event or a seasonal shift to increased use of supplemental food sites. Unlike extinction events, the probability of colonization was higher at warmer sites (Fig. 5).

Understanding the synergistic effects of weather and landscape context on localized behaviour and patterns of occupancy is critical to the basic understanding of the biological processes underlying range shifts and has important ecological implications as many researchers make assumptions about these relationships to predict the future effects of climate change. To better understand the effects of climate change on species distributions, there should be a greater appreciation for how local-scale behaviour and geographical processes might be affected by the same environmental factors. We found that most bird species respond to changes in winter conditions by altering their rate of supplemental food use over the short term, and these fine-scaled shifts in behaviour influenced detectability across thousands of survey sites. By accounting for this potential bias, we found that many species demonstrated strong patterns of occupying warmer sites in the middle of winter, suggesting that climate plays a critical role in shaping distributions, even while food availability remained relatively constant. Future research into the response of species to climate should place greater emphasis on modelling ranges in a dynamic fashion, accounting for behavioural plasticity and identifying additional environmental factors that could influence how species are limited by climate.

Acknowledgements

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Supporting Information

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

Appendix S1. Complete list of study species in taxonomic order.

Appendix S2. Complete results of modeling feeder visitation as a function of observation covariates (MinTemp, Precip, and SnowDepth) and site-level covariates (AvgMin, AvgPrec, PSnow, and Urban).

Appendix S3. Complete results of modeling core winter occupancy as a function of average minimum temperature (AvgMin), average precipitation (AvgPrec), proportion of counts reporting snow (PSnow), and the percent of the landscape (3-km) classified as urban development (Urban).

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