EFFECTS OF EXTREME WEATHER EVENTS ON BIRD PRODUCTIVITY IN THE NORTHEASTERN UNITED STATES

By

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Abstract

Extreme weather events are projected to be more frequent and intense in the future. The effects of local extreme weather events on bird productivity at regional scale are not yet well understood. The aims of this study were to determine whether local extreme weather events (drought, extreme cold/warm breeding season and extreme cold winter) have a detectable effect on regional bird productivity and how landscape-level habitat patterns may buffer those effects in the Northeastern United Stated. I calculated bird productivity as the proportion of juveniles to total birds captured, by species, for 8 commonly captured passerines using banding data provided by the Monitoring Avian Productivity and Survivorship (MAPS) program. Productivity of Common Yellowthroat, Grey Catbird and Song Sparrow were negatively associated with the occurrence of extremely high temperatures during the breeding season, while the productivity of the resident Black-capped Chickadee was lower during years that were extremely cold and wet in the early breeding season. In contrast, productivity of Black-capped Chickadee was higher following extremely cold winter temperatures.

I found some evidence that extreme weather events can have greater negative impact on bird productivity in suboptimal habitats than in optimal habitat, as productivity in the Black-capped Chickadee, a species dependent on forest, was lower during years when spring was extremely cold and wet at sites with little core forest area than at sites

with a large proportion of core forest in the surrounding landscape. Additionally, productivity of Gray Catbird, a species of thickets, open woodlands, and forest edges, was significantly lower in more forested habitats during extremely cold breeding seasons than in breeding seasons with more typical weather. Both of these species' productivity did not exhibit a pattern related to the surrounding landscape when weather in the breeding season was normal, but did when weather was extreme. Knowing how extreme weather events and landscape-level habitat patterns interact to shape bird productivity is fundamental to assessing the region-level effects that extreme weather events may have on birds. This is necessary information for planning effective future habitat management that can mitigate the effects of climate change on birds and other wildlife species.

Introduction

Climate change is manifest in part by anomalies in temperature and precipitation patterns (IPCC, 2013). Large scale climatic fluctuations, such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) can influence local weather, including extreme weather events (Schubert et al. 2008, Brigode et al. 2013). Occurrence of extreme weather events has increased during recent decades and these events are projected to be more frequent and intense in the future (Meehl and Tebaldi 2004, Goodess 2013). Extreme weather events have the potential to negatively affect bird reproduction.

Short term extreme weather events such as cold snaps can cause direct mortality to birds if the extremes are beyond birds' physiological tolerance, or can cause indirect mortality, for example by negatively affecting the abundance of insects and other prey items (Becker et al. 1997, Winkler et al. 2013). In addition, if precipitation occurs during cold days, nest abandonment, egg and nestling mortality may occur (Decker and Conway 2009). For example in southeastern Arizona, an unseasonable late May snow storm caused almost 70% of actively nesting Red-faced Warblers to abandon their nests (Decker and Conway 2009). Furthermore, consecutive cold days can affect the availability of insects, resulting in lack of food supply for chicks that can also cause mortality (Winkler et al. 2013). For example, Tree Swallow nestling mortality was explained by the occurrence of 1 to 3-day cold snaps, where the threshold (maximum daily temperature equal or below 18.5°C) was defined according to the flying insect activity (food availability) in Ithaca, New York (Winkler et al. 2013).

Similarly, extreme heat during summer can also affect bird reproduction through direct or indirect mortality, especially when several consecutive days above a temperature threshold occur (Cunningham et al. 2013). For Common Terns, higher mortality and lower fledgling body mass occurred after heat waves in Wilhelmshaven, Germany (Becker et al. 1997). Although nestlings are not able to thermoregulate properly, the mortality of chicks was not attributed directly to the heat, but to the food shortage produced by the heat waves (Becker et al. 1997).

Longer term extreme events such as droughts can also affect the availability of food and water resources, impacting bird´s fitness and survivorship (Bolger et al. 2005, Langin et al. 2009). When droughts occur before and during the breeding season, food resources decrease and within bird populations fewer pairs may attempt to breed or breeding pairs can respond by laying fewer eggs than normal (Bolger et al. 2005, Langin et al. 2009). For example, during the drought that occurred in 2002 in San Diego, California, the number of nesting attempts and the number of fledglings produced per pair were significantly lower during the drought than in a normal year for the four species under study (Bolger et al. 2005). Similarly, during a drought that occurred in 2007 in Santa Catalina Island, California, only 11% of female Orange-crowned Warblers built a nest, and none of them successfully fledged young, therefore no reproductive output was recorded for this season (Langin et al. 2009). In both of these droughts, food availability seemed to be the proximal cause of the reproductive failure.

Extreme cold weather during winter can cause direct or indirect mortality of birds (Altwegg et al. 2006) contributing to a decrease in the population density. Lower density of birds can be associated with higher productivity due to less intra-specific competition. For instance, when the number of breeding pairs of Black-throated Blue Warblers in New Hampshire was artificially reduced, bird productivity was significantly higher because males spent more time feeding their young, than in sites with higher population density (Sillett et al. 2004).

When extreme weather events occur, some species may perform better in certain habitat types where the effects of extreme events are less pronounced. For example in eastern England, Great Tits and Blue Tits breeding in riparian and urban areas during an extremely wet and cold breeding season had higher nestling body size and brood mass than those breeding in mixed deciduous forest (Whitehouse et al. 2013). While riparian and urban areas had lower productivity than the mixed deciduous forest in normal years, during this extreme event birds breeding in the forest were affected more strongly because clutch sizes were larger and they experienced higher nestling mortality due to starvation (Whitehouse et al. 2013).

Landscape pattern may influence bird species' vulnerability to extreme weather events (Foppen et al. 1999, Thomas et al. 2004, Wingfield et al. 2011). In highly fragmented forest, nests are more exposed to extreme weather, predation and parasitism than in the forest interior (Matlack 1993, Robinson et al. 1995, Flaspohler et al. 2001, Driscoll and Donovan 2004). For species adapted to forest interior, this can affect reproductive success. For instance, in fragmented forest, Wood Thrush daily survival rate was significantly lower near the edge than in the forest interior (Driscoll and Donovan 2004) due to nest predation. High temperatures can have direct and indirect impact on nest predation in continuous forest by increasing predator activity (snakes) or increasing bird nest visitation rates due to increasing food demands for nestlings, making the nest easier to find by predators (Cox et al. 2013). For instance, while the overall productivity of Acadian Flycatchers is consistently lower in fragmented forest in Missouri, occurrence of high temperatures in unfragmented forests reduces the overall productivity of this species to rates even lower than those documented in fragmented forest, because of increased nest predation especially by snakes, while in fragmented forest bird productivity was not significantly affected by high temperature (Cox et al. 2013).

Overall the existing body of literature suggests that extreme weather events affect birds, but the effects on bird productivity at regional scale are not well understood. Most studies have been conducted at local scale (Decker & Conway, 2009; Langin et al., 2009; Whitehouse et al., 2013) and in the case of short term extreme weather like cold snaps and heat waves, effects on season-long productivity have received little attention.

The main aim of my study was to investigate the effects of extreme weather events on bird productivity at regional scale in the Northeastern United States. My hypotheses were that (1) episodes of extremely cold weather during the breeding season, i.e., cold snaps, are associated with low bird productivity likely due to nestling mortality or nest abandonment, (2) periods of extremely hot weather, i.e., heat waves, are associated with low bird productivity, likely due to egg and/or nestling mortality, (3) severe droughts during the breeding season are associated with low productivity, likely because an important proportion of the population do not attempt breeding, (4) extremely cold winters are associated with high productivity of resident species. This may occur because high mortality of resident birds leads to low intra-specific competition during the subsequent breeding season, and adults are therefore able to raise more juveniles as a result of density dependence. Finally, I hypothesize that (5) there is an interaction between extreme weather events and habitat characteristics, where birds in suboptimal habitats would have a greater impact than in their preferred habitats. This effect is expected because birds that breed in optimal habitats have more resources to cope with extreme weather events.

Material and Methods

Study area

The study area includes 9 states in the Northeastern United States. I obtained banding data from 94 banding stations in this area (Figure 1). Most of the stations (~80%) were located mainly in forested areas and also included minor amount of wetlands, old fields and shrub cover (Table 1). Approximately 30% of the stations were located within 15 km of the Atlantic Ocean.

Bird data

As an index of bird productivity I calculated the proportion of juveniles to total captured, by species (Peach et al. 1996), using banding data from the Monitoring Avian

Productivity and Survivorship (MAPS) program (DeSante et al. 2013). I used data from 1992 through 2012.

I defined “juveniles” as all birds aged as hatch year (HY) or local birds (fledglings), and “adults” as all birds aged as second year (SY), after hatch year (AHY) and after second year (ASY). Each bird was counted once per year (first capture of the year) and those birds whose age was not recorded were excluded from calculations.

I analyzed 8 commonly captured species, including the resident Black-Capped Chickadee (BCCH, *Poecile atricapillus*), a cavity-nesting species affiliated with forest, the short distance migrants American Robin (AMRO, *Turdus migratorius*) which has flexible habitat requirements and Song Sparrow (SOSP, *Melospiza melodia*), a ground and shrub-nesting species. I also analyzed five long distance migrants. These included Common Yellowthroat (COYE, *Geothlypis trichas*), a species that nests in shrubs in moist habitat, Gray Catbird (GRCA, *Dumetella carolinensis*), which nests in dense shrubs, Veery (VEER, *Catharus fuscescens*), a ground nesting species of rich deciduous forest, Wood Thrush (WOTH, *Hylocichla mustelina*), a species of deciduous and mixed forests and Yellow Warbler (YEWA, *Setophaga petechia*), a species of shrubby thickets in moist areas. With this set of species it was possible to test the effect of extreme weather events on bird productivity in different habitats.

In the MAPS program protocol, the breeding season is divided into ten 10-day periods starting on May 1st and finishing on August 8th. Each MAPS station is within a study area of at least 20 ha and the nets are located within the central 8 ha (DeSante et al.

2013). Once per period, ten 12-meter nets are operated (i.e. open) for 6 hours. In order to avoid migrant or transient birds during the breeding season, different starting dates are designated, depending on latitude of the station (DeSante et al. 2013). For this reason some (more northerly) locations may operate less than 10 periods in the season. In my study area mist netting starts in period 4 (beginning of June) completing 7 sample periods in total.

Although the MAPS Program was created with the goal of constant-effort mist netting, in practice, the effort is not always the same. Lack of availability of volunteers or adverse weather conditions can reduce the sample effort in terms of number of nets open during a given period, or may result in a reduced number of sample periods, generating different sample effort among different stations or years. In the set of banding stations I considered, almost 50 stations had at least one missing period during their years of operation, and years with missing periods accounted for the 20% of the records (Table 2). To understand how missing periods affects the index of bird productivity I selected data from stations that had years with complete and standard effort, experimentally extracted data from each of the periods, and I used a t-test to see if there were differences in the estimation of the index. I did this analysis for two common species, Gray Catbird and American Robin. I found that the estimated index of productivity for Grey Catbird was very sensitive to missing periods; when period 4, 5, 6, 7, 9 or 10 were missed the index was significantly different from the index derived from the complete effort data set. In contrast, American Robin was sensitive only to missing periods 4 and 10 (Table 3).

In my study area "period 4" accounted for more than 50% of the occasions that had missing periods (Table 2). Therefore, taking into account the variation among species in sensitivity of the index of productivity to effort, and with the goal of including as many stations' data as possible in my study I considered only periods 5 through 10 in my analysis. When netting had occurred during period 4, but period 5 or 6 were missed or had been assessed with incomplete sampling (defined here as less than 70% of the standard effort) I used period 4 to replace the missing period. When in a given station one or more years were missing periods 7, 8, 9 or 10, those years were not considered in the analysis. Some stations included sub-periods (meaning that they sampled more than once each period) but in order to make the analysis comparable, I removed sub-period data, retaining only the first net day in each period. The minimum number of nets accepted was 7. Finally, in order to have a better estimation of the index of productivity, I only considered stations where on average more than 4 total individuals per year of a given species were captured. Due to natural variability in abundance and distribution of the selected species, there was a unique subset of stations and years (station-years) for each one, which means that the station-years considered in the models varied depending on the species (Table 4).

Weather data

To assess the effect of extreme weather on bird productivity I used DAYMET weather data (Thornton et al. 1997). I used two different approaches to define extreme weather events. One approach characterized extreme conditions for the entire breeding season based on low frequency of occurrences (season-long conditions that occurred in

≤10% of the station-years I analyzed) and the second approach aimed to characterize potential acute stress due to weather, based on both meaningful biological thresholds and low frequency of occurrence.

When I considered the conditions during the entire breeding season, I defined an extreme event as one which was ≥1.5 standard deviation above or below the mean, based on the historical record for each station from 1980 through 2012. This approach allowed me to assess the effect of extreme cold during breeding seasons (hereafter referred to as ECBS) and extreme hot breeding seasons (hereafter, EHBS), both based on April-July mean temperature. To assess the effect of an extremely cold winter season (hereafter, ECWS) included only those January through February maximum temperatures that were ≤ 1.5 standard deviations from the mean value for those two months.

Similarly, for drought, I used the Standardized Precipitation Index (SPI, Allstadt et al., *in prep*). To calculate SPI, I selected the time period of interest, i.e., the breeding season (April to July), and for each year, fitted the total precipitation during this time period to a Pearson-III distribution. I selected this distribution to account for the skewness common in precipitation totals (Guttman 1999). The base period that I used for the calculations was 1981 to 2010. I converted the precipitation totals into percentiles, which were then transformed to be standard deviations from a standard normal distribution (McKee et al. 1993, Guttman 1999). Thus, I defined extreme dry breeding seasons (hereafter, EDBS) as those events that were ≥ 1.5 standard deviations from the mean to the left side of the SPI distribution (Figure 2). In addition, I also defined a dry season those which had high frequency of dry days, i.e. when no precipitation occurred, in 92 or more days during the breeding season (hereafter, HFDD), which occurred ≤10% of the time.

The second approach I used to define extreme weather events was based on daily weather data. I used this approach when I expected that reaching a threshold of a given weather event might affect avian productivity, for example when experiencing minimum or maximum temperatures for a relatively brief period could conceivably cause direct or indirect mortality. I defined cold snaps during winter season (hereafter, CSWS) as a period of 4 or more consecutive days with maximum temperature ≤ -10°C during January-February. I defined cold snaps during breeding season (hereafter, CSBS) as period of 4 or more consecutive days ≤ 0°C during May. Additionally, I hypothesized that extreme cold and wet weather might negatively affect bird productivity, and I defined instances when 2 or more rainy days coincided with minimum temperatures ≤ 0°C (hereafter, RBZC) and when 10 or more rainy days coincided with minimum temperatures ≤ 5°C (hereafter, RB5C) during May (beginning of the breeding season). I defined heat waves as 3 or more consecutives days on which the temperature reached a given temperature threshold: ≥33°C (hereafter, 33HW), and ≥35°C (hereafter, 35HW). Although all these extreme weather conditions had, by definition, low frequency of occurrence in my study area, the exact frequency of occurrence varied depending on the species under analysis (Table 6).

All the extreme weather variables were included in models as binary data, where 1 indicated occurrence of a given extreme event and 0 indicated a normal year for that particular type of extreme event.

Landscape data

To assess the effect of landscape pattern on avian productivity, I first constructed a map of forest cover based on National Land Cover Data 2001 (NLCD; http://www.mrlc.gov/). I used this data set because most of the stations were operated during 1995 to 2005, and thus 2001 falls approximately at the midpoint of the avian datasets. I reclassified deciduous forest, evergreen forest, mixed forest and woody wetlands as forest (Driscoll and Donovan 2004). I calculated the area of core forest and the area of edge forest within 500 m of each station and within 10,000 m of each station using a Morphological Spatial Pattern Analysis (Vogt et al. 2007a, 2007b) using GUIDOS software (http://forest.jrc.ec.europa.eu/download/software/guidos/). I selected these metrics because they have previously been found to be associated with bird productivity in forested habitats, especially at broader scales (e.g., 10,000 m radius circles, Robinson et al. 1995).

In calculating forest metrics I used 8-neighbor connectivity and edge width value of one (1) pixel. MSPA output includes core, islet, bridge, loop, branch, perforation and edge area (Soille and Vogt 2009). However, the classes islet, bridge, loop, branch and perforation by themselves were not relevant for my research questions, and I reclassified them as edge.

Statistical analysis

To determine if extreme weather events influenced season-long bird productivity of the 8 species of interest, I constructed Generalized Linear Mixed Effect Models for each species. I designated the various weather variables as fixed effects and station within location as the random effect. The relationship between weather variables varied in a systematic way between coastal and interior stations (Figure 3) and for that reason I included location in the model. I assumed a binomial distribution for all the models because my independent variable was calculated as a proportion. Because the variables were binary I did not need to check for correlations.

I assumed that the estimation of bird productivity was more accurate when more individuals were caught (i.e., that a larger sample size leads to closer approximation of "true" proportion of juveniles in the area), and therefore I included the total number of individuals in models as a weighted variable. I included in the models only the extreme weather events that occurred at three or more stations within a given species' dataset, because my analysis was regionally focused. This resulted in elimination from consideration of four 35°C heat wave events distributed in four stations and two cold snaps during breeding season occurred in one station (Table 6). To determine which, if any, extreme weather variables were significantly associated with bird productivity, I did model selection using backward elimination extracting the variable with the greatest p-value from the model until all the explanatory variables were significant ($p < 0.05$). All the analyses were conducted in R (R Core Team 2014), and mixed effect models were run in the package lme4 (Bates et al. 2014a, 2014b). To check for spatial autocorrelation I used the package geoR (Ribeiro Jr and Diggle 2001, Diggle and Ribeiro Jr 2007).

To understand how landscape pattern influenced bird productivity at regional level, for each station I calculated the mean proportion of juveniles (including all the valid observations in each station) as a dependent variable to fit Simple Linear Regression Models in which the explanatory variable was percentage of core forest or percentage of edge forest. I did not include both landscape variables in the same model, because they were highly correlated, although the correlation varied depending on the spatial scale and the station that where considered that varied depending on the species under analysis. I used the average of total individuals caught in each station as a weighted variable. To test the assumptions that the errors were independent and normally distributed, I visually inspected the residual plots.

Once I had found the extreme weather variables that were associated with each species' productivity, I tested if the effect of those extreme weather events varied by forest patterns. To assess that, I selected the stations that had at least one record of the extreme weather variable of interest and calculated the average of the index of productivity for the normal years and for the extreme years. If only one extreme event of that type occurred, I considered that value as a representative index of productivity during the occurrence of this particular extreme weather event. I fit Simple Linear Regression Models for productivity during normal years and productivity during extreme years using as explanatory variables the proportion of core forest and proportion of edge forest separately for both spatial scales, weighting by the average number of total individuals. However, the previous analysis did not allowed me to compare if there were significant differences between normal and extreme years for a given extreme weather. To do so, I use Linear Mixed Effect Models with an interaction term between landscape and the occurrence of a given extreme weather using "station" as a random effect to account for the dependence that exists between the two values (normal and extreme) obtained from each station. I included the average number of total individuals as a weighted variable. This analysis allowed me to test for significant differences between extreme and normal years and to determine if there was an interaction between the occurrence of extreme weather and landscape characteristics.

Finally, I used Simple Linear Regression Models to understand the station-level association between bird productivity and weather. I did this analysis for stations that had a high number of records (years of operation). In all these models I considered the weather variables as continuous variables.

Results

With regard to the season-long measures of extreme weather that I analyzed (EDBS, EHBS, ECBS, and HFDD; see table 5 for definitions), the most frequent event over the 20 years of my study was EHBS (extremely hot breeding season), which occurred in 174 different station-years. The season-long event that was most rare was ECBS (extremely cold breeding season), which occurred in 130 station-years. Extremely cold winter seasons (ECWS) affected 142 station-years.

From the set of shorter term extreme events I analyzed, (35HW, 33HW, CSBS, RBZC, RB5C, and CSWS), 33HW (heat waves ≥33°) occurred most frequently, affecting 386 different station-years. The short term event that was most rare was 35HW (heat waves ≥35°C), which occurred in 25 station-years. The frequency of occurrence of these events varied according to the species and the subset of stations at which they were captured, thus species with more records usually had higher frequency of extreme events (Table 6).

In the 84 stations that I included in my analysis, the proportion of core forest in the local 500-m radius area ranged from 0% to 100%, and the proportion of edge forest ranged from 0% to 39% (Figure 4). At the landscape scale of the surrounding 10,000-m radius area, proportion of core forest ranged from 0% to 88%, and the proportion of edge forest ranged from 1% to 24% (Figure 5).

I found that bird productivity was explained by some extreme weather events in 4 of the 8 studied species. Low productivity of Gray Catbirds and Song Sparrows coincided with heat waves (35HW and 33HW, respectively) and low productivity in Common Yellowthroat coincided with extremely hot breeding seasons (EHBS). Extremely cold breeding season (ECBS) and extremely cold and wet beginning of the breeding season (RB5C) explained low productivity of Gray Catbird and Black-capped Chickadee respectively. Drought during breeding season, as represented by high frequency of dry days during the breeding season (HFDD) and extremely cold winter season (ECWS) were associated with high Black-capped Chickadee productivity (Table 7).

The amount of edge forest was associated with productivity of one species, Black-capped Chickadee (Table 8). Higher proportion of edge forest at both local (500-m radius) and landscape (10,000-m radius) scales was related to lower Black-capped Chickadee productivity (Figure 6). Similarly, Yellow Warbler productivity was negatively explained by the proportion of edge at the local spatial scale (Figure 7). In contrast, the proportion of edge at local spatial scale positively explained Common Yellowthroat productivity (Figure 8). Landscape variables by themselves were not associated with productivity of American Robin, Song Sparrow, Veery or Wood Thrush.

Landscape pattern influenced bird productivity differently depending on the extreme weather considered in the model (Table 9). Black-capped Chickadee productivity in years with high frequency of dry days (HFDD) was significantly lower at stations with a low proportion of core forest in the surrounding 10,000-m radius area ($p < 0.001$) however this relation was not significant for normal years (Figure 9). Similarly, Black-capped Chickadee productivity was also significantly lower at stations with a low proportion of core forest in the surrounding 500-m radius ($p = 0.043$) in years in which the beginning of the breeding season was wet and cold (RB5C), but during normal years this relation was not significant (Figure 10). In contrast, when I compared years with extreme cold winter season versus normal years, I found that during normal years, Black-capped Chickadee productivity was significantly lower when the proportion of edge forest was high at both spatial levels, while during extremely cold winters this relation was significant only at landscape level (Figure 11 and 12).

Gray Catbird productivity during extreme cold breeding season (ECBS) was significantly lower at stations with a high proportion of core forest in the 10,000-m radius neighborhood ($p = 0.028$, Figure 13), while this relation was not significant during normal years.

When I compared years of normal and extreme weather using Linear Mixed Effects Models, I found that there was a significant interaction effect between landscape patterns and the occurrence of extreme weather for Black-capped Chickadee. Extreme weather, in terms of wet and cold beginning of the breeding season (RB5C), interacted with proportion of core forest at 500-m radius ($p = 0.011$), suggesting that there is a different effect of this extreme weather condition depending on the amount of core forest in the surrounding 500-m radius area. During normal years, productivity of Black-capped Chickadee was not significantly explained by proportion of core forest, however during years with this extreme condition, productivity was significantly lower when proportion of core forest was low (Figure 10).

Although effects of some extreme weather events were not detected when all the stations were analyzed together, when I analyzed stations separately I found that for some species productivity was associated with weather at the station level. In almost all cases in which I found that productivity was associated with weather at the station level, the stations had more than 10 years of data available. For example, for American Robin bird productivity was negatively associated with the number of dry days in the breeding season (Figure 14). Productivity of both Common Yellow-throat and Yellow Warbler was positively associated with April-July SPI (Figure 15 and 16, respectively). These patterns, associations between bird productivity and weather were much more apparent at stations where the data set was most complete. The fact that these associations were apparent in only the longest time series, and where effort level most closely approached the standard protocol, suggests that the lack of associations between productivity and weather for other species may have as much to do with available data as with any ecological reason. In that sense it is really important to guarantee the existence of long term and nation-wide monitoring programs such as MAPS which provide a great opportunity to understand the effect of regional and local drivers on bird reproduction and population trend.

Overall, my results indicate that the interplay of extreme weather events and landscape pattern affects productivity in some species. Extreme weather events were associated with an overall decrease in bird productivity, and the less fragmented forests during extreme weather conditions were associated with higher productivity in the forest associated Black-capped Chickadee.

Discussion

Effects of extreme events on bird productivity

To prove conclusively that extreme weather affects bird productivity is a big challenge because extreme events are rare and there are other threats such as land-use change, habitat loss, and biotic interactions that also affect bird reproduction success

(Fauth 2000, Fort and Otter 2004, Balogh et al. 2011). Despite this, I found that in some species extreme weather events are associated with productivity.

Extreme weather events related with high temperatures had the greatest impact on bird productivity. Three of eight species were negatively affected by the occurrence of heat waves or extreme hot breeding seasons. Those species were Common Yellowthroat, Gray Catbird and Song Sparrow. Yellow Warbler was also affected by the occurrence of heat waves, although its negative trend was not significant (p-value = 0.063, Table 7). This finding is important given current global warming and the projected increase in frequency of heat waves in the future (Meehl and Tebaldi 2004). All these four species are associated with similar breeding habitat (early successional forest, riparian corridors, forest edges, shrubs) and their open-cup nests, although protected by vegetation, are exposed to weather. None of these species construct highly-insulated nests (Skowron and Kern 1980), a factor in their vulnerability to extreme temperatures.

During hot and sunny days, females Common Yellowthroat may stand on the nest with wings outspread, protecting nestlings from direct sun radiation (Stewart 1953). Similarly, Gray Catbird females spend a large proportion of their time protecting the eggs and chicks during hot days (Johnson and Best 1982). When high temperatures occur, females must choose between spending longer time protecting the nest from the direct sun or provisioning their young. If chicks are not fed adequately they are likely to have poor body condition, making them more susceptible to mortality (Becker et al. 1997). For Grey Catbird, both parents feed nestlings, however when females have to spend more time shading the nest, nestlings' energy and water requirements may not be fully satisfied when only the male is providing food, potentially leading to mortality of chicks (Becker et al. 1997). Another negative consequence of extreme heat during breeding season is that higher temperatures are associated with higher levels of predation, especially by snakes, which are more active during high temperatures (Morrison and Bolger 2002, Sperry et al. 2008) and this is especially important for Common Yellowthroat and Song Sparrows because they place their nest close to the ground where a wide variety of snake species have relatively easy access.

Another important factor to consider is the number of broods per season that each species typically has. Common Yellowthroats have 1-2 broods per season depending on the location within their range (Stewart 1953, Guzy and Ritchison 1999). In those places where they have only one brood per season, increased predation events due to increasing predator activity will contribute to low reproductive success. Although breeding pairs can re-nest after a nest failure, they probably will not have enough time to complete more than one brood per season. Gray Catbirds can produce 2-3 broods per season depending on the location (Smith et al. 2011) and if their first nesting attempt fails they quickly re-nest. However when they lose their second brood in July, when heat waves often occur, they do not attempt to re-nest (Scott et al. 1987) which may affect their season-long productivity.

The patterns of association of Common Yellowthroat, Song Sparrow, and Gray Catbird productivity with high heat contrasts with the patterns of House Sparrow association with temperature in Europe, where temperatures ≥ 31°C were associated with higher nest hatching success and had no association with fledgling success (Pipoly et al. 2013). However, House Sparrow is a cavity nester and thus patterns may not be directly comparable with the open cup nesting species that I studied.

Black-capped Chickadee productivity was negatively associated with the occurrence of 10 or more rainy days that coincided with minimum temperatures ≤ 5°C during May (i.e. a cold wet May). Similar results were found in Europe, where extremely cold and wet breeding season negatively affected Great Tit and Blue Tit reproduction (Whitehouse et al. 2013) due to starvation caused by low food availability. It is important to consider that Black-capped Chickadees have a strong social hierarchy (Ratcliffe et al. 2007). High-ranking birds have higher nest success than low-ranking birds (Otter et al. 2007). Low-ranking birds are usually in poorer body condition and they have higher nest abandonment when the weather conditions are not favorable (Fort and Otter 2004). They are less able to invest their energy to breed because they have to assure their own survival first.

Black-capped Chickadee productivity was positively affected by the occurrence of extreme cold during the previous winter season. Since this species is a resident bird, winter weather conditions can have an indirect impact on reproduction. Occurrence of an extremely cold winter may cause high mortality (Brittingham and Temple 1988), decreasing the population density in the following breeding season. Lower population density is associated with less intraspecific competition which can explain higher productivity after extremely cold winter. My results are similar to those found in Northern

British Columbia, where low density of Black-capped Chickadee breeding pairs was associated with high fledgling success (Otter et al. 2007).

Black-capped Chickadee productivity was also positively associated with years when high frequency of dry days occurred, a measure of drought. This result was unexpected, because drought is known to negatively affect bird productivity (Bolger et al. 2005, Langin et al. 2009).Over the course of my study, there were 33 station-years during which high frequency of dry days occurred during April-July (Table 6). While it is possible that the result is spurious there is a potential ecological explanation as well. An important proportion of this extreme weather condition (42%) occurred during La Niña years (NOAA 2014), which are associated with precipitation above normal during winter. That can cause high mortality of resident birds generating low population density during the subsequent breeding season and higher productivity (Otter et al. 2007).

Effects of landscape pattern on bird productivity

In examining how habitat pattern influenced each species' productivity, I found that only proportion of edge forest was associated with bird productivity. This relation was found only for 3 of the 8 species: Black-capped Chickadee, Common Yellowthroat and Yellow Warbler (Table 8). Black-capped Chickadee productivity decreased when proportion of edge forest increased at local (500-m radius) and landscape (10,000-m radius) levels. Although this species is a forest generalist, it has a poorer performance in fragmented forest habitats (Fort and Otter 2004). In highly fragmented forest, where only small patches are available, this species has large territory sizes that includes more than one patch, which implies higher energy investment and risk of predation when moving between them (Desrochers and Belisle 2007). It has been observed that Black-capped Chickadee reproductive success is lower in fragmented habitats , mainly because high nest abandonment by low-ranking birds (Fort and Otter 2004). Low-ranking birds in fragmented habitats face the breeding season in a poorer body condition, because they spent the winter in a low habitat quality with few food resources and more exposure to harsh weather conditions (wind, snow, etc.). On the other hand, since this species nests in cavities, it is probable that in landscapes with higher proportion of edge forest, non-forest cavity nesting species may compete with Black-capped Chickadee for the available cavities. Species including House Wren (*Troglodytes aedon*) and House Sparrow (*Passer domesticus*) can usurp nests and destroy eggs and kill nestlings of Black-capped Chickadee, which may cause low productivity in fragmented forest habitat (Belles-Isle and Picman 1986, Weisheit and Creighton 1989, Olson and Grubb 2007).

Common Yellowthroat productivity was higher in more fragmented habitats, possible because edges promote the shrubby edges that this species uses, when they occur in moist or riparian habitat (Peak and Thompson 2006), and riparian habitat naturally has a greater proportion of edge habitat than upland forest. I was surprised to find that Yellow Warbler productivity was low in areas with a high proportion of edge forest in the surrounding 500 m, because this species' preferred breeding habitat includes disturbed and early successional habitats (Dunn and Garret 1997). This result may reflect the high risk of nest failure in this types of habitats, due to predation and brood parasitism (Scott 1977, Ortega and Ortega 2000, Flaspohler et al. 2001, Poulin and Villard 2011).

I found that productivity of the forest specialists Veery and Wood Thrush, in the Northeastern US area was not explained either by proportion of core forest nor proportion of edge forest. This result was not expected because reproductive success of both species is higher in unfragmented forest due to high predation and brood parasitism close to edges in fragmented landscapes (Burke and Nol 2000, Fauth 2000, Driscoll and Donovan 2004). However these findings of sensitivity to edge are based on nest monitoring, not capture data. It is possible that juvenile movement and dispersal are causing this confounding result when mist nets are used. On the other hand, these species had low presence in terms of number of stations where they were found, which could explain why no association between productivity of this species and extreme weather events or landscape metrics was found. In other words it could be due to small sample size.

Effects of extreme events and landscape pattern on bird productivity

When extreme weather events occurred during the breeding season, Black-capped Chickadee productivity was significantly lower in less forested habitats, while no difference in productivity was observed in years with normal weather during the breeding season. The difference observed in fragmented sites may be related to the energy cost of moving between patches in more fragmented landscapes (Desrochers and Belisle 2007), which can be even more difficult during years with extreme weather conditions. The resulting physiological stress can result in smaller clutch size or an increase in nest abandonment (Fort and Otter 2004). Opposite results were found for Great and Blue Tits in Europe (Whitehouse et al. 2013), where birds in more forested landscapes had significantly lower productivity when an extreme cold and wet breeding season occurred. Bird reproduction was traditionally greater in woodlands, however, high mortality of chicks due starvation exacerbate the negative effect of this extreme event in woodlands compared with the other habitats (Whitehouse et al. 2013). In my study, I found that the influence of forest cover on Black-capped Chickadee productivity at local spatial scale was significantly different between extreme and normal years.

Productivity of Black-capped Chickadee was lower at sites with high amounts of edge forest following both extremely cold winter season and normal winter season, although this pattern was not significant for extremely cold winter at the local spatial scale, only at the landscape scale. These findings give some support to the idea that birds in more fragmented habitat may suffer higher mortality during winter and productivity may be higher as a result of density dependence.

According to my results, occurrence of extreme cold breeding season negatively affects Gray Catbird productivity, and during these extreme years, areas that were more forested showed lower productivity. In more forested areas, the availability of suitable habitat for this species is reduced, however it may be that during normal years this reduced area still provide enough food resources (insects and fruits) for breeding birds. When an extremely cold breeding season occurs the same areas may provide insufficient food resources (Winkler et al. 2013), forcing Gray Catbirds to use larger territories, and parents to leave the nest unattended for longer periods increasing the risk of predation or mortality due to weather. On the other hand, Gray Catbird nests have moderate insulation (Skowron and Kern 1980) and when it is extremely cold, females have to spend more time brooding the eggs and chicks (Johnson and Best 1982), and it may force the female to stay in the nest brooding longer than normal, making both female and young dependent on the male for provisioning, affecting body condition, and ultimately increasing the potential for nest abandonment. Catbirds are also exposed to more predation in fragmented habitats (Flaspohler et al. 2001, Balogh et al. 2011). Predation is an important cause of nest failure and mortality of fledgling Gray Catbirds (Balogh et al. 2011).

Methodological issues

Some factors not related with extreme weather that likely influenced my results are those related to the approach that I used to calculated the index of bird productivity. For each species, I included only data from stations where on average more than 4 individuals per year were captured, which allowed me to keep in the analysis all the records when 1, 2 or 3 individuals were caught in some years, only if at that station the species was usually captured and was relatively abundant. I did this to maximize the time series for each station. However when the number of individuals captured is low, the estimation of the index has high uncertainty. For example, when only one individual is caught at a station and that individual is an adult, the value of the productivity index is 0. When the individual is a juvenile the value of the productivity index is 1.

The level of certainty is completely different when 20 individuals are caught and only one of them is a juvenile. In this case the estimated index of productivity is 0.05, and the estimation has more certainty because the sample size is bigger. In some cases, I observed that during years when an extreme weather event occurred, the number of individual caught was lower than in normal years making the estimation less certain (see for example bottom right plot in Figure 16).

The proportion of juveniles in the catch has been used in several studies as an index of productivity because it is highly correlated with nest productivity (Nur and Geupel 1993, Bart et al. 1999). However several issues may affect this relationship depending on the species. First, post-fledgling dispersal to different habitat types may generate a bias in the estimation of the index of productivity. Juveniles can move to areas that are not suitable for breeding, and then high rate of capture of juveniles in these areas may generate an overestimation of the index of productivity (Akresh et al. 2009). Second, mist net placement may contribute to bias in the estimation of the index of productivity. At MAPS stations the operators place the mist nets in strategic sites (DeSante et al. 2013), for example where birds are likely to cross a small opening in the vegetation, and where bird's capture probability is higher. Therefore, although the productivity of these species may be lower in fragmented habitats, high mobility of fledgling during dispersal combined with the strategic placement of nets may artificially increase juvenile catchability in more fragmented areas. Finally, it is possible that some birds avoid being captured, leading to an estimate that is different than the true estimate.

I think that the proportion of juveniles to total individuals may be a closer approximation of breeding season productivity in the vicinity of a given banding station. It is important to consider that when banders determine the age of a bird, they classify juveniles as “local” birds or “hatch year” birds. The first category is used only when the individuals have some characteristic that are typical for birds that are still dependent on their parents (there is certainty that they were born in the immediate area), for example some plumage features (i.e. growing feathers), soft parts, etc. The “hatch year” designation is used when the individual is a juvenile but is not dependent on its parents. Up to 60% of mortality can occur in the first week post-fledgling (Balogh et al. 2011) when the birds are still dependent on their parents. However in the banding data I used, young birds were classed mostly as hatch year birds and there were few local birds. Therefore, the index of productivity in my study was calculated based on birds that had already survived the most critical phase of the post-fledgling stage. This suggests that the index of productivity I used is perhaps a more accurate estimate of annual productivity of the local site than the estimation of bird productivity based on nest monitoring.

Conclusion

Extreme weather events are projected to be more frequent and intense in the future. If we are to be good stewards and managers of natural resources, is important to understand how weather affect bird reproduction and in which circumstances these effects can be modified by landscape pattern. In my study I found that productivity of some species was negatively affected by extreme weather events, mainly those related with temperature, during the breeding season. I also found that productivity of a resident species, the Black-Capped Chickadee, was associated with extreme weather conditions outside of the breeding season. Extremely cold winters can cause high mortality and in my study extreme cold in winter was associated with higher productivity in the following summer, perhaps as a result of the resulting low population density. Finally, I found that landscape pattern influenced productivity of Black-capped Chickadees. In extreme weather conditions, this species had greater productivity in unfragmented than in fragmented forest. Understanding the effect of both weather and landscape pattern, and their interactive effects, is necessary for planning effective future habitat management that can mitigate the effects of climate change on birds, especially species of conservation concern. I did not find associations between extreme weather events and productivity of Wood Thrush and Veery. These two species had lower sample size in my data set than the other species. I recommend therefore that an effort be made to target the placement of new MAPS banding stations at sites that contain greater amounts of forested habitat to increase the capture rate for these species. Increasing sample size will allow the estimation of the effects of extreme weather on these species' productivity.

Literature cited

Akresh, M. E., K. Dinse, J. Foufopoulos, S. C. Schubel, and T. Kowalczyk. 2009. Passerine Breeding and Post-Fledgling Habitat Use in Riparian and Upland Temperate Forests of the American Midwest. Condor 111(4):756–762.

Altwegg, R., A. Roulin, M. Kestenholz, and L. Jenni. 2006. Demographic Effects of Extreme Winter Weather in the Barn Owl. Oecologia 149:44–51.

Balogh, A. L., T. B. Ryder, and P. P. Marra. 2011. Population Demography of Gray Catbirds in the Suburban Matrix: Sources, Sinks and Domestic Cats. Journal of Ornithology 152(3):717–726.

Bart, J., C. Kepler, P. Sykes, and C. Bocetti. 1999. Evaluation of Mist-Net Sampling as an Index to Productivity in Kirtland ' s Warblers. Auk 116(4):1147–1151.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014a. lme4: Linear Mixed-effects Models Using Eigen and S4. ArXiv e-print; submitted to Journal of Statistical Software, http://arxiv.org/abs/1406.5823.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014b. lme4: Linear Mixed-effects Models Using Eigen and S4. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.

Becker, P. H., T. Troschke, and A. Behnke. 1997. Starvation of Common Tern Sterna hirundo Fledgling During Heat Waves. Journal of Ornithologie 138(2):171–182.

Belles-Isle, J.-C., and J. Picman. 1986. House Wren Nest-destroying Behavior. Condor 88(2):190–193.

Bolger, D. T., M. a Patten, and D. C. Bostock. 2005. Avian Reproductive Failure in Response to an Extreme Climatic Event. Oecologia 142(3):398–406.

Brigode, P., Z. Mićović, P. Bernardara, E. Paquet, F. Garavaglia, J. Gailhard, and P. Ribstein. 2013. Linking ENSO and Heavy Rainfall Events Over Coastal British Columbia Through a Weather Pattern Classification. Hydrology and Earth System Sciences 17:1455–1473.

Brittingham, M. C., and S. A. Temple. 1988. Impacts of Supplemental Feeding on Survival Rates of Black-Capped Chickadees. Ecology 69(3):581–589.

Burke, D. M., and E. Nol. 2000. Landscape and Fragment Size Effects on Reproductive Success of Forest-Breeding Birds in Ontario. Ecological Aplications 10(6):1749–1761.

Cox, W. A., F. R. Thompson, J. L. Reidy, and J. Faaborg. 2013. Temperature Can Interact with Landscape Factors to Affect Songbird Productivity. Global Change Biology 19(4):1064–1074.

Cunningham, S. J., R. O. Martin, C. L. Hojem, and P. a R. Hockey. 2013. Temperatures in Excess of Critical Thresholds Threaten Nestling Growth and Survival in a Rapidly-warming Arid Savanna: a Study of Common Fiscals. PLoS ONE 8(9):e74613.

Decker, K. L., and C. J. Conway. 2009. Effects of an Unseasonable Snowstorm on Red-Faced Warbler Nesting Success. Condor 111(2):392–395.

DeSante, D. F., K. M. Burton, P. Velez, D. Froehlich, and D. Kaschube. 2013. MAPS Manual. 2013 Protocol. The Institute for Bird Populations. Contribution Number 127. 79 pages.

Desrochers, A., and M. Belisle. 2007. Edge, Patch, and Landscape Effects on Parid Distribution and Movements. Pages 243–262 *in* K. Otter, editor. Ecology and Behavior of Chickadees and Titmice. An Integrated Approach. Oxford University Press, New York.

Diggle, P. J., and P. J. Ribeiro Jr. 2007. Model Based Geostatistics. Springer, New York.

Driscoll, M. J. L., and T. M. Donovan. 2004. Landscape Context Moderates Edge Effects: Nesting Success of Wood Thrushes in Central New York. Conservation Biology 18(5):1330–1338.

Dunn, J. L., and K. L. Garret. 1997. A field Guide to Warblers of North America. Houghton Mifflin Co, Boston.

Fauth, P. T. 2000. Reproductive Success of Wood Thrushes in Forest Fragments in Northern Indiana. Auk 117(1):194–204.

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Species-specific Edge Effects on Nest Success and Breeding Bird Density in a Forested Landscape. Ecological Aplications 11(1):32–46.

Foppen, R., C. Ter Braak, J. Verboomi, and R. Reijnen. 1999. Dutch Sedge Warblers Acrocephalus Schoenobaenus and West-african Rainfall: Empirical Data and Simulation Modeling Show Low Population Resilience in Fragmented Marshlands. Ardea 87(1):113–127.

Fort, K. T., and K. A. Otter. 2004. Effects of Habitat Disturbance on Reproduction in Black-Capped Chickadees (Poecile atricapillus) in Northern British Columbia. Auk 121(4):1070–1080.

Goodess, C. M. 2013. How is the Frequency, Location and Severity of Extreme Events Likely to Change up to 2060? Environmental Science and Policy 27S:S4–S14.

Guttman, N. 1999. Acception the Standardized Precipitation Index: A Calculation Algorithm. Journal of the American Water Resources Association 35(2):311–322.

Guzy, M., and G. Ritchison. 1999. Common Yellowthroat (Geothlypis trichas), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/448.

Johnson, E. J., and L. B. Best. 1982. Factors Affecting Feeding and Brooding of Gray Catbird Nestlings. Auk 99(1):148–156.

Langin, K. M., T. S. Sillett, J. Yoon, H. R. Sofaer, S. A. Morrison, and C. K. Ghalambor. 2009. Reproductive Consequences of an Extreme Drought for Orange-crowned Warblers on Santa Catalina and Santa Cruz Islands. Pages 293–300 *in* C. C. Damiani and D. K. Garcelon, editors. Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA.

Matlack, G. R. 1993. Microenvironment Variation Within and Among Forest Edge Sites in the Eastern United States. Biological Conservation 66:185–194.

McKee, T. B., N. J. Doesken, and J. Kleist. 1993. The Relationship of Drought Frequency and Duration to Time Scales. Pages 179–183 Eighth Conference on Applied Climatology. Anaheim, California.

Meehl, G. a, and C. Tebaldi. 2004. More Intense, More Frequent, and Longer Lasting Heat Waves in the 21st Century. Science 305:994–997.

Morrison, S., and D. T. Bolger. 2002. Variation in a Sparrow’s Success with Rainfall : Food and Predator-mediated Processes. Oecologia 133(3):315–324.

NOAA. 2014. National Oceanic and Atmospheric Administration. http://www.cpc.noaa.gov.

Nur, N., and G. R. Geupel. 1993. Evaluation of Mist-netting , Nest-searching and Other Methods for Monitoring Demographic Processes in Landbird Populations. Pages 237–244 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds: September 21-25, 1992, Estes Park, Colorado. Gen. Tech. Rep. RM-GTR-229, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Olson, J. R., and T. C. J. Grubb. 2007. Winter Adaptations in Chickadees and Titmice and the Added Effect of Habitat Fragmentation. *in* K. A. Otter, editor. Ecology and Behavior of Chickadees and Titmice. An Integrated Approach. Oxford University Press, New York.

Ortega, J. C., and C. P. Ortega. 2000. Effects of Brown-Headed Cowbirds and Predators on the Nesting Success of Yellow Warblers in Southwest Colorado. Journal of Field Ornithology 71(3):516–524.

Otter, K., H. Van Oort, and K. T. Fort. 2007. Habitat Quality and Reproductive behavior in Chickadees and Tits: Potential for Habitat Matrix Use in Forest Generalist. Pages 277–291 *in* K. A. Otter, editor. Ecology and Behavior of Chickadees and Titmice. An Integrated Approach. Oxford University Press, New York.

Peach, W. J., S. T. Buckland, and S. R. Baillie. 1996. The Use of Constant Effort Mist-netting to Measure Between-year Changes in the Abundance and Productivity of Common Passerines. Bird Study 43:142–156.

Peak, R. G., and F. R. Thompson. 2006. Factors Affecting Species Richness and Density in Riparian Areas. Journal of Wildlife Management 70(1):173–179.

Pipoly, I., V. Bókony, G. Seress, K. Szabó, and A. Liker. 2013. Effects of Extreme Weather on Reproductive Success in a Temperate-breeding Songbird. PLoS ONE 8(11):e80033.

Poulin, J.-F., and M.-A. Villard. 2011. Edge Effect and Matrix Influence on the Nest Survival of an Old Forest Specialist, the Brown Creeper (Certhia americana). Landscape Ecology 26:911–922.

R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ratcliffe, L., D. J. Mennill, and K. A. Schubert. 2007. Social Dominance and Fitness in Black-capped Chickadees. Pages 131–150 *in* K. A. Otter, editor. Ecology and Behavior of Chickadees and Titmice. An Integrated Approach. Oxford University Press, New York.

Ribeiro Jr, P. J., and P. J. Diggle. 2001. geoR: a package for geostatistical analysis. R-NEWS 1:14–18.

Robinson, S. K., F. Thompson, T. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional Forest Fragmentation and Nesting of Migratory Birds. Science 267:1987–1990.

Schubert, S. D., Y. Chang, M. J. Suarez, and P. J. Pegion. 2008. ENSO and Wintertime Extreme Precipitation Events over the Contiguous United States. Journal of Climate 21:22–39.

Scott, D. M. 1977. Cowbird Parasitism on Gray Catbird at London, Ontario. Auk 94:18–27.

Scott, D. M., R. E. Lemon, and J. A. Darley. 1987. Relaying Interval after Nest Failure in Gray Catbirds and Northern Cardinals. Wilson Bulletin 99:708–712.

Sillett, T. S., N. L. Rodenhouse, and R. Holmes. 2004. Experimentally Reducing Neighbor Density Affects Reproduction and Behavior of a Migratory Songbird. Ecology 85(9):2467–2477.

Skowron, C., and M. Kern. 1980. The Insulation in Nests of Selected North American Songbirds. Auk 97(4):816–824.

Smith, R., M. Hatch, D. Cimprich, and F. Moore. 2011. Gray Catbird (Dumetella carolinensis), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/167.

Soille, P., and P. Vogt. 2009. Morphological Segmentation of Binary Patterns. Pattern Recognition Letters 30:456–459.

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake Activity Affects Seasonal Variation in Nest Predation Risk for Birds. Journal of Avian Biology 39:379–383.

Stewart, R. E. 1953. A Life History Study of the Yellow-Throat. Wilson Bulletin 65(2):99–115.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction Risk from Climate Change. Nature 427:145–148.

Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating Surfaces of Daily Meteorological Variables over Large Regions of Complex Terrain. Journal of Hydrology 190:214–251.

Vogt, P., K. H. Riitters, C. Estreguil, J. Kozak, T. G. Wade, and J. D. Wickham. 2007a Mapping Spatial Patterns with Morphological Image Processing. Landscape Ecology 22:171–177.

Vogt, P., K. H. Riitters, M. Iwanowski, C. Estreguil, J. Kozak, and P. Soille. 2007b. Mapping Landscape Corridors. Ecological Indicators 7:481–488.

Weisheit, A. S., and P. D. Creighton. 1989. Interference by House Sparrows in Nesting Activities of Barn Swallows. Journal of Field Ornithology 60:323–328.

Whitehouse, M. J., N. M. Harrison, J. Mackenzie, and S. a Hinsley. 2013. Preferred Habitat of Breeding Birds may be Compromised by Climate Change: Unexpected Effects of an Exceptionally Cold, Wet Spring. PLoS ONE 8(9):e75536.

Wingfield, J. C., J. P. Kelley, and F. Angelier. 2011. What are Extreme Environmental Conditions and how do Organisms Cope with them? Current Zoology 57(3):363–374.

Winkler, D. W., M. K. Luo, and E. Rakhimberdiev. 2013. Temperature Effects on Food Supply and Chick Mortality in Tree Swallows (Tachycineta bicolor). Oecologia 173:129–38.

Table 1. Habitat description of MAPS banding stations in Northeastern United States included in this study. Each station was classified according to the description provided. Data source: http://www.birdpop.org/maps.htm. Accessed June 2014.

Station	State	Habitat description	Riparian	Forest/Woods	Shrub	Wetland	Field/Grassland
ASRP	NH	riparian deciduous	x	x			
ATOS	CT	northern hardwood/hemlock/beaver pond		x		x	
ATRE	ME	mixed conifer/deciduous forest		x			
BALT	NY	deciduous riparian woodland	x	x			
BEAR	NJ	mixed deciduous forested		x			
BEAV	CT	marsh edge w h.hornbeam & white birch		x		x	
BFSW	NY	wetland/fields/forest/plantation		x		x	x
BING*	NY	successional swamp				x	
BKBR	VT	mixed conifer forest		x			
BLHI	MA	oak/pine (low density)		x			
BLUE	ME	balsam-red spruce forest/riparian/alder	x	x			
BMNC	NY	red maple, cherry		x			
BORF	CT	mature deciduous forest/riparian/grassland	x	x			x
BORR	CT	mature forest/grassland		x			x
BRAV	NY	scrub-shrub			x		
BUHO	NY	forest/secondary growth		x			
CAHI	NY	mixed deciduous with meadow/ scrub		x	x		
CBWP*	PA	lowland deciduous riparian forest	x	x			
CHRO	ME	maple-oak deciduous forest/riparian	x	x			
CLDC	NY	shrubland/old field			x		x
CLHI	PA	deciduous other/deciduous forest		x			
CMS1	NY	tidal wetland/alder swamp/mixed deciduous forest		x		x	
CORS*	NY	no info					
CUVA	PA	deciduous forest		x			

Station	State	Habitat description	Riparian	Forest/Woods	Shrub	Wetland	Field/Grassland
DCVT	VT	agricultural/clay-plain oak-hickory forest		x			x
DEVD	CT	deciduous forest		x			
EANY	NY	open field/mixed deciduous forest/riparian	x	x			x
FHSP	NY	lakeshore scrub/mixed hardwood		x	x		
FL--*	NJ	old-field/edge					x
FTTI	NY	second growth		x			
GIFA	ME	deciduous forest/mixed shrubland		x	x		
GMFI	CT	mixed forest/other		x			
GOCO	ME	balsam fir/deciduous forest/boggy areas		x		x	
GTSW	NJ	mixed hardwood/scarlet oak		x			
HAZD	RI	upland oak-red maple forest		x			
HELM	NY	shrub/pioneer tree on forest edge		x	x		
HGHL	ME	stunted balsam-red spruce forest/boggy		x		x	
HIHO	MA	pine (high density)		x			
HOFF	NY	mixed woodland/grassland in sub		x			x
HTAC*	NJ	mixed deciduous forest		x			
HUBB*	NH	northern hardwood forest		x			
HUNT	VT	marsh/forest/old-field		x		x	x
INDI	NY	deciduous forest		x			
IPLO	MA	lawn/garden/swamp				x	x
KAIS	NY	young ash forest/fallow fields		x			x
KANE	CT	swamp woodland/pasture		x			x
KETT	PA	riparian and upland mixed forest	x	x			
KSMA	NH	fragmented riparian corridor/ag fields/suburbia	x				x
LAUR	NY	deciduous woods/ponds/stream/swamp		x		x	
LNER	ME	Saturated Woodland/Shrubland/herbaceous		x		x	x
LOBE	MA	oak (high density)		x			

Station	State	Habitat description	Riparian	Forest/Woods	Shrub	Wetland	Field/Grassland
LONG	PA	deciduous forest/hemlock forest		x			
MABE	MA	pine (low density)		x			
MAP1	CT	mixed deciduous-conifer/open meadows		x	x		
MAP2	CT	oak-hickory-red maple forest		x			
MASH	NY	deciduous woodland/tidal		x		x	
MBBS	NH	pine/oak, hay field		x			x
MERD	MA	mixed deciduous-white pine		x			
MISS	VT	maple-ash bottomland forest/edge		x			
MOWO	NY	oak/beech/locust		x			
MWSF	CT	mixed-deciduous forest/wetlands		x		x	
NAMP*	NY	shrubby trees/woods/field		x	x		x
NASC	MA	oak/pine (high density)		x			
NINI	RI	coastal scrub-shrub			x	x	
OADU	MA	oak (low density)		x			
PEMA	ME	deciduous shrubland/mixed woodland		x	x		
PONU	ME	mixed deciduous-evergreen forest/shrubland		x	x		
POWD	NY	overgrown field					x
PRCK	NY	low scrub/young deciduous forest		x	x		
PUNK	MA	mixed woodland riparian corridor	x	x			
RACK	CT	upland transitional hardwoods/pine swamp		x		x	
RAKE	PA	secondary deciduous woods		x			
REPO	ME	mixed deciduous-evergreen forest/pond		x		x	
ROIS	ME	evergreen forest/mixed shrubland		x	x		
SACE	CT	old pasture/2nd growth forest/pond		x		x	x
SACF	CT	2nd-grwth forest/wetland/old pasture		x		x	x
SCPO	ME	evergreen woodland/mixed shrubland		x	x		
SIDN	ME	mixed hardwood-softwood forest		x			

Station	State	Habitat description	Riparian	Forest/Woods	Shrub	Wetland	Field/Grassland
SKYT	PA	riparian deciduous forest w/ norway spruce	x	x			
SPNE	ME	mixed forest/mixed woodland		x			
SPRG	NY	old-field/young woods		x			x
SSNC*	NY	upland oak-hickory/red maple-tupelo swamp		x		x	
STRM	PA	eastern deciduous forest/riparian zone	x	x			
TASW	NY	mixed deciduous forest/swamp/brushy area		x	x	x	
THWO	CT	mixed deciduous forest		x			
TODD*	PA	deciduous forest		x			
TRUS	RI	red maple swamp		x		x	
TWOM	PA	boreal bog				x	
UETE	ME	mixed hardwood-coniferous		x			
VINS	VT	old field/pond edge/hedgerow		x		x	x
WAWO	NY	moist deciduous forest		x		x	
WIBR*	NY	floodplain forest		x		x	
WOBO	ME	mixed hardwood-softwood forest		x			
WPNT	NY	oak-hickory forest		x			

* Stations not included in the analysis

Table 2. Number of Monitoring Avian Productivity and Survivorship (MAPS) stations with missing periods in the Northeastern United Stated from 1992 through 2012. MAPS protocol divides the breeding season in 10 sample periods, with different starting dates depending on the location. MAPS stations located in the Northeast start in period 4.

		Period							Number of missing periods			
Year	Stations	P4	P5	P6	P7	P8	P9	P10	≥1	1	2	≥3
1992	24	4	1	3	3	4	1	1	6	2	2	2
1993	26	3	0	1	1	0	0	0	4	3	1	0
1994	26	1	1	1	0	0	0	0	2	1	1	0
1995	26	1	2	1	0	0	0	0	3	2	1	0
1996	28	2	0	1	0	0	0	0	2	1	1	0
1997	39	5	4	2	1	2	1	2	7	3	2	2
1998	40	4	1	1	0	3	1	2	7	3	3	1
1999	44	1	0	1	0	1	0	0	2	1	1	0
2000	47	4	3	2	2	1	2	2	9	5	3	1
2001	55	4	2	2	2	0	2	0	7	4	2	1
2002	57	5	2	2	2	1	1	2	11	8	3	0
2003	64	5	4	4	4	7	7	4	17	8	4	5
2004	53	6	1	3	3	3	1	2	13	8	4	1
2005	49	6	3	3	2	0	4	1	11	6	2	3
2006	51	9	1	4	2	4	2	1	14	6	7	1
2007	46	11	5	2	3	4	2	2	17	8	6	3
2008	34	9	3	2	2	3	2	2	13	8	2	3
2009	18	2	1	1	1	3	1	3	6	3	2	1
2010	10	0	0	0	0	0	0	1	1	1	0	0
2011	1	0	0	0	0	0	0	0	0	0	0	0
2012	1	0	0	0	0	0	0	0	0	0	0	0
Total	739	82	34	36	28	36	27	25	152	81	47	24
%	100	11.1	4.6	4.9	3.8	4.9	3.7	3.4	20.6	11.0	6.4	3.2

Table 3. Sensitivity of the index of productivity to missing mist netting periods. T-tests were used to determine the effect of missing periods on the index of productivity, simulating each missing period in turn, for two species, by removing data from the complete set. Stars indicate that the index calculated from missing data differed significantly from the index calculated using the complete dataset. Station-years with complete effort but no records of these species were not used.

Species	Period 4	Period 5	Period 6	Period 7	Period 8	Period 9	Period 10
Gray Catbird (n = 37)	***	***	***	*		***	***
American Robin (n = 21)	**						*

*** < 0.001 **<0.01 *<0.05

Table 4. Summary of total observations and number of stations considered in the analysis for each species.

Species	Acronym	Observations	Stations
American Robin (*Turdus migratorius)*	AMRO	164	25
Black-capped Chickadee (*Poecile atricapillus)*	BCCH	270	41
Common Yellowthroat (*Geothlypis trichas*)	COYE	234	38
Gray Catbird (*Dumetella carolinensis*)	GRCA	336	49
Song Sparrow (*Melospiza melodia*)	SOSP	185	29
Veery (*Catharus fuscescens*)	VEER	270	31
Wood Thrush (*Hylocichla mustelina*)	WOTH	180	21
Yellow Warbler (*Setophaga petechia*)	YEWA	118	20

Table 5. Explanatory variable acronyms and definitions.

Variable	Description
EDBS	Extremely dry breeding season. SPI values ≤ -1.5 standard deviation from the mean during breeding season (April-July).
EHBS	Extremely hot breeding season. Mean temperature anomalies ≥ 1.5 standard deviation from the mean during breeding season (April-July).
ECBS	Extremely cold breeding season. Mean temperature anomalies ≤ -1.5 standard deviation from the mean during breeding season (April-July).
35HW	35°C heat waves. Occurrence of at least 3 consecutive days with maximum temperature ≥ 35°C, during breeding season (April-July).
33HW	33°C heat waves. Occurrence of at least 3 consecutive days with maximum temperature ≥ 33°C during breeding season (April-July).
HFDD	High frequency of dry days. Occurrence of 92 or more dry days (no precipitation) during breeding season (April-July, 122 total days).
CSBS	Cold snap breeding season. Occurrence of at least 4 consecutive days with minimum temperature ≤ 0°C during May.
RBZC	Rain below 0°C. Occurrence of at least 2 rainy days with minimum temperature ≤ 0°C during May.
RB5C	Rain below 5°C. Occurrence of at least 10 rainy days with minimum temperature ≤ 5°C during May.
ECWS	Extremely cold winter season. Minimum temperature anomalies ≤ -1.5 standard deviation from the mean during winter season (January-February).
CSWS	Cold snaps winter season. Occurrence of at least 4 consecutive days with maximum temperature ≤ -10°C during winter season (January-February).

Table 6. Tally of occurrence of extreme weather events that intersected MAPS data used in the models. Cell values in "events" rows show number of times that a particular type of extreme weather event overlapped a given species' data set, and cell values in "stations" rows show the number of stations where those events occurred. See table 5 for variable definitions.

		Extreme weather variables										
		EDBS	EHBS	ECBS	35HW	33HW	HFDD	CSBS	RBZC	RB5C	ECWS	CSWS
AMRO	events	20	5	9	7	33	10	8	8	8	15*	11
	stations	14	4	7	4	14	9	6	5	5	13	7
BCCH	events	25	8	12	5	34	33	20	17	16	23	22
	stations	16	8	9	4	16	19	12	11	10	19	12
COYE	events	23	10	15	2	24	20	14	15	15	23	19
	stations	15	9	11	2	12	13	11	11	9	19	13
GRCA	events	35	11	23	11	65	33	14	15	14	29	17
	stations	21	10	18	7	25	21	11	11	9	25	11
SOSP	events	16	6	15	4	22	13	12	11	13	19	15
	stations	11	5	11	1	9	9	9	8	8	15	10
VEER	events	24	13	14	4	31	12	18	20	18	19	23
	stations	15	11	11	1	14	10	11	13	11	17	12
WOTH	events	22	8	13	12	54	15	3	7	4	18	7
	stations	12	6	11	6	14	11	2	4	3	17	4
YEWA	events	12	4	10	1	17	10	4	7	5	11	7
	stations	9	3	7	1	8	8	3	5	3	8	6

*Gray cells indicate variables that were not included in the model for a given species, either because the species was not resident or because of small sample size.

Table 7. Association of different extreme weather events with bird productivity based on Generalized Linear Mixed Effects Models, in which extreme weather variables were the fixed effects and station within location was the random effect. Backward elimination was used to keep in the model only the extreme variables that explained bird productivity (cut-off p-value>0.05). Columns show the variable acronyms (see table 5 for definitions), rows "effect" show if the effect was negative (-) or positive (+) and "p-value" rows show the statistical significance for the extreme weather variables for each species.

		Extreme weather variables										
		EDBS	EHBS	ECBS	35HW	33HW	HFDD	CSBS	RBZC	RB5C	ECWS	CSWS
AMRO	effect											
	p-value											
BCCH	effect						+			-	+	
	p-value						0.006			0.037	0.019	
COYE	effect		-									
	p-value		0.032									
GRCA	effect			-	-							
	p-value			0.008	0.001							
SOSP	effect					-						
	p-value					0.010						
VEER	effect											
	p-value											
WOTH	effect											
	p-value											
YEWA	effect											
	p-value											

Table 8. Regional relationship between bird productivity and proportion of edge at two spatial scales (500-m radius and 10,000-m radius area). Columns "effect" show if the relation was negative (-) or positive (+) and columns "p-value" show the statistical significance for the different spatial scales by species. No significant associations were found between productivity and proportion of core forest (not shown).

	Edge forest			
	500 m		10 km	
Species	effect	p-value	effect	p-value
AMRO				
BCCH	-	0.04	-	0.03
COYE	+	0.04		
GRCA				
SOSP				
VEER				
WOTH				
YEWA	-	0.01		

Table 9. Comparison of the effect of landscape variables on bird productivity during extreme and normal years. These results are based on Simple Linear Regression Models. Non significant values are shown for comparison purposes. Columns "effect" show if the relation was negative (-) or positive (+) and columns "p-value" show the statistical significance for the different spatial scales by species

			Core forest				Edge forest			
			500 m		10,000 m		500 m		10,000 m	
Species	variable	weather	effect	p-value	effect	p-value	effect	p-value	effect	p-value
BCCH	HFDD	extreme			+	0.00				
		normal			+	0.42				
	RB5C	extreme	+	0.04						
		normal	-	0.75						
	ECWS	extreme					-	0.37	-	0.05
		normal					-	0.04	-	0.04
COYE	EHBS	extreme								
		normal								
GRCA	ECBS	extreme			-	0.03				
		normal			-	0.29				
	35HW	extreme								
		normal								
SOSP	33HW	extreme								
		normal								

Figure 1. Study area. Spatial distribution of MAPS banding Stations in the Northeastern United States (red dots). ME=Maine, NH=New Hampshire, VT=Vermont, MA=Massachusetts, RI=Rhode Island, CT=Connecticut, NY=New York, PA= Pennsylvania, NJ=New Jersey. Only stations considered in the analysis are shown.

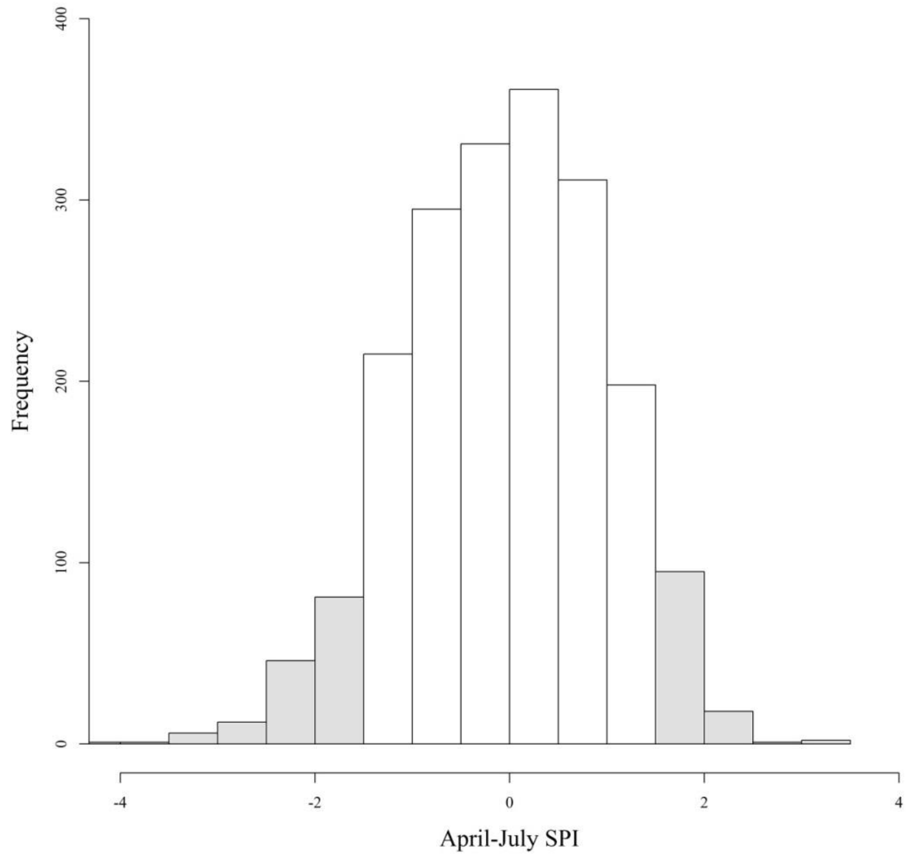

Figure 2. Histogram of the breeding season (April-July) Standardized Precipitation Index values considering all 94 stations from 1992 to 2012. In gray are the weather events considered extreme (i.e. more than 1.5 standard deviations from the mean, after standardizing the data). Extreme dry events are those located to the left side of the frequency distribution.

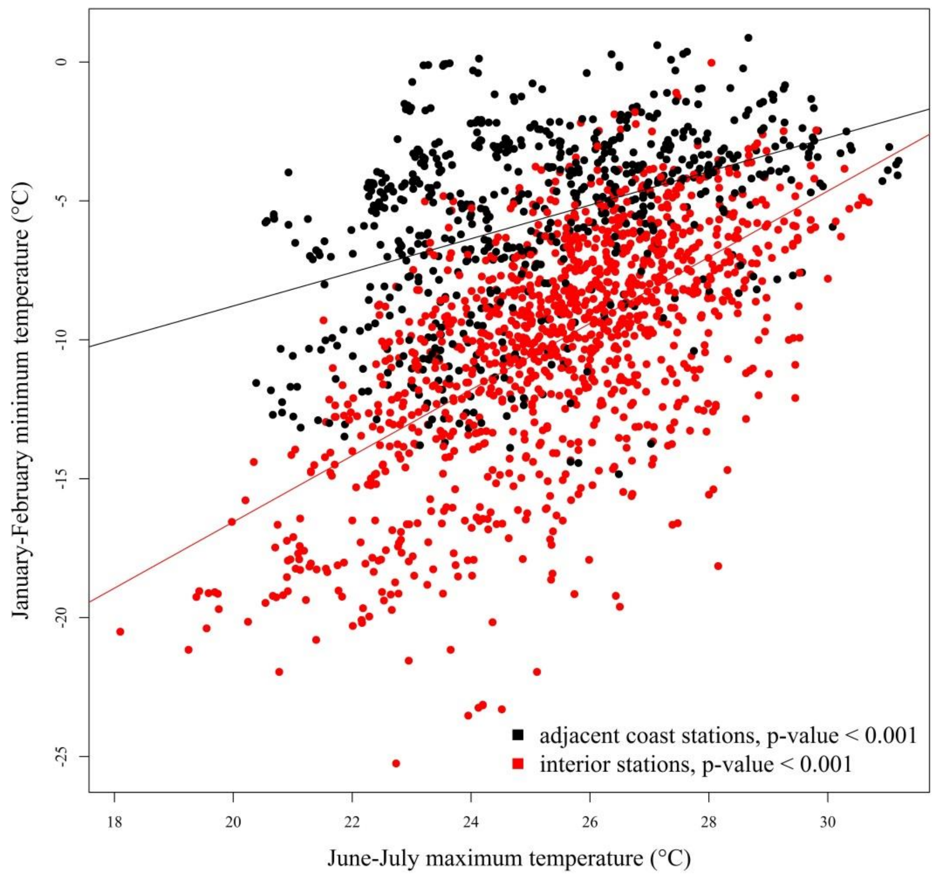

Figure 3. Example of correlation between weather variables. This plot shows the linear relationship between minimum temperature in January-February and maximum temperature in June-July from 1992 through 2012 in the 94 MAPS stations. Independent linear models for coastal and interior stations showed stronger significant relation for the interior located stations, suggesting potential different weather effect on bird productivity depending on the location.

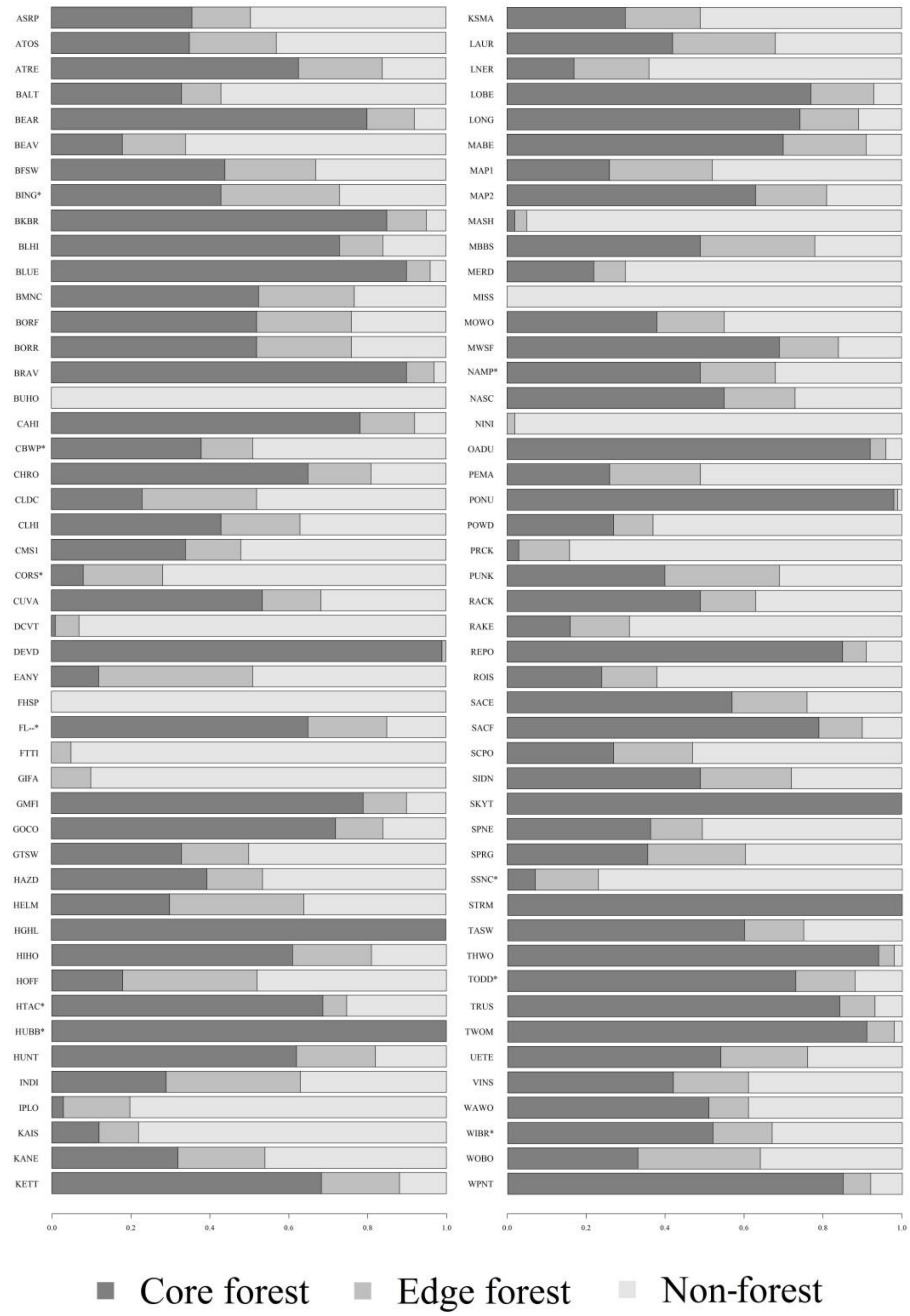

Figure 4. Proportion of core forest, edge forest and non-forest based on Morphological Spatial Pattern Analysis, 500-m radius buffer around each MAP banding stations. Stations not included in the analysis are marked with asterisk (*).

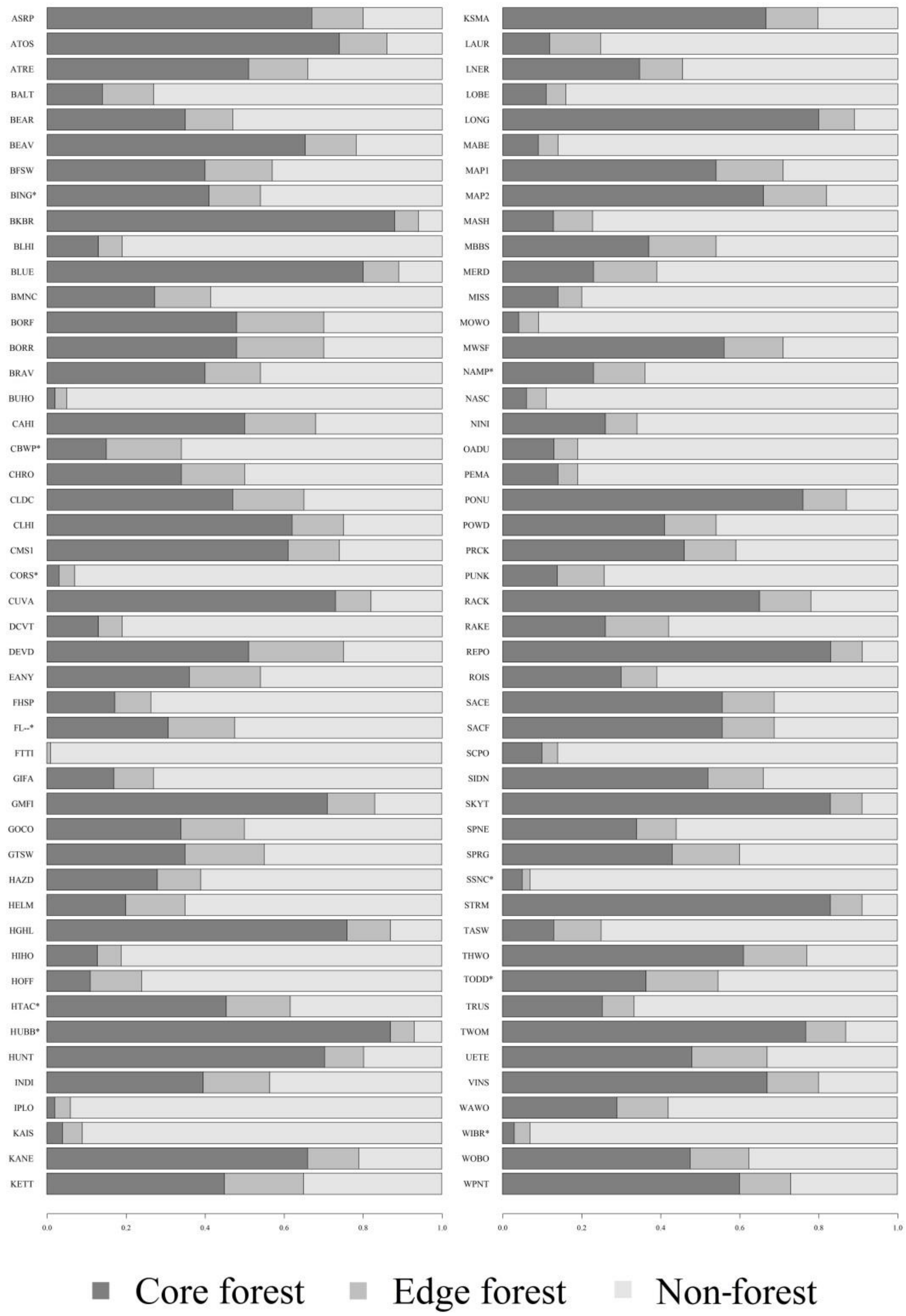

Figure 5. Proportion of core forest, edge forest and non-forest based on Morphological Spatial Pattern Analysis, 10,000-m radius buffer around each MAP banding stations. Stations not included in the analysis are marked with asterisk (*)

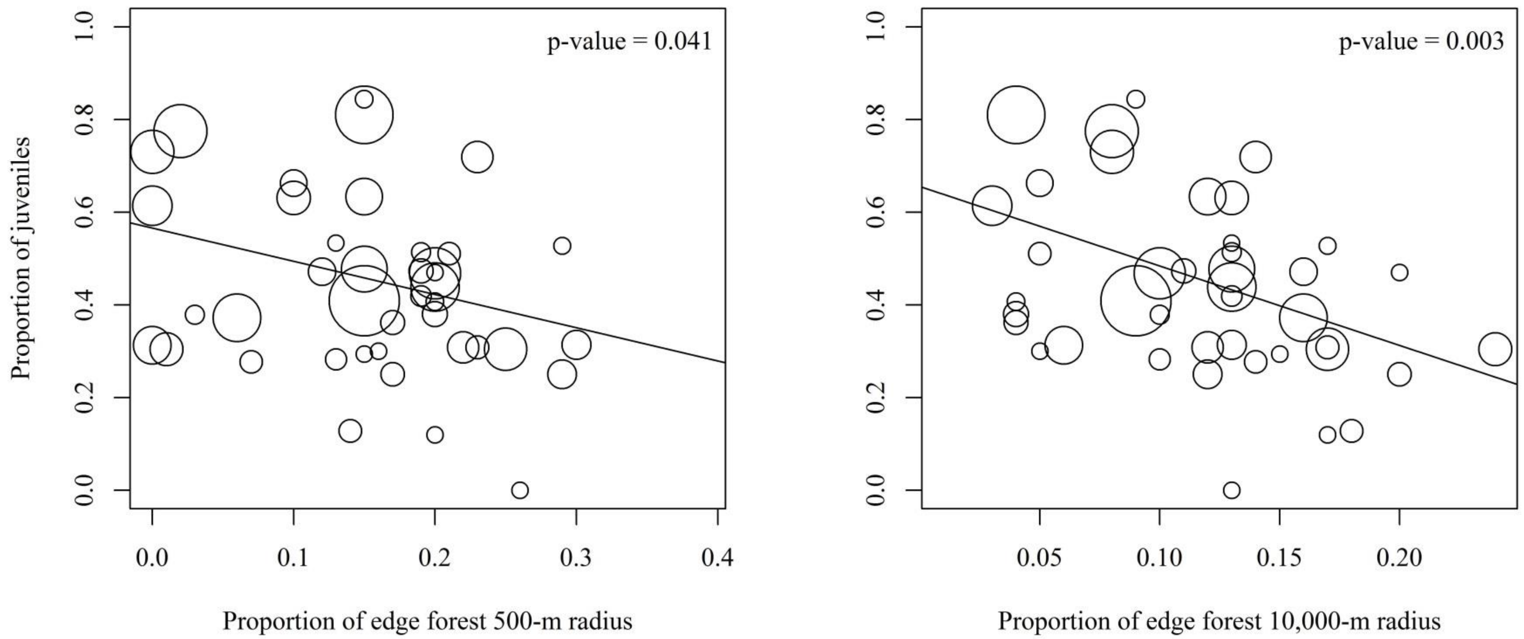

Figure 6. Black-capped Chickadee productivity versus edge forest at local (left) and landscape (right) scale. Analysis was made at regional scale using Simple Linear Regression Models. The station average of total individuals was included in the model as a weighted variable. Each circle represents the average productivity for each station. The circles' size indicates the average number of total individuals captured in each station.

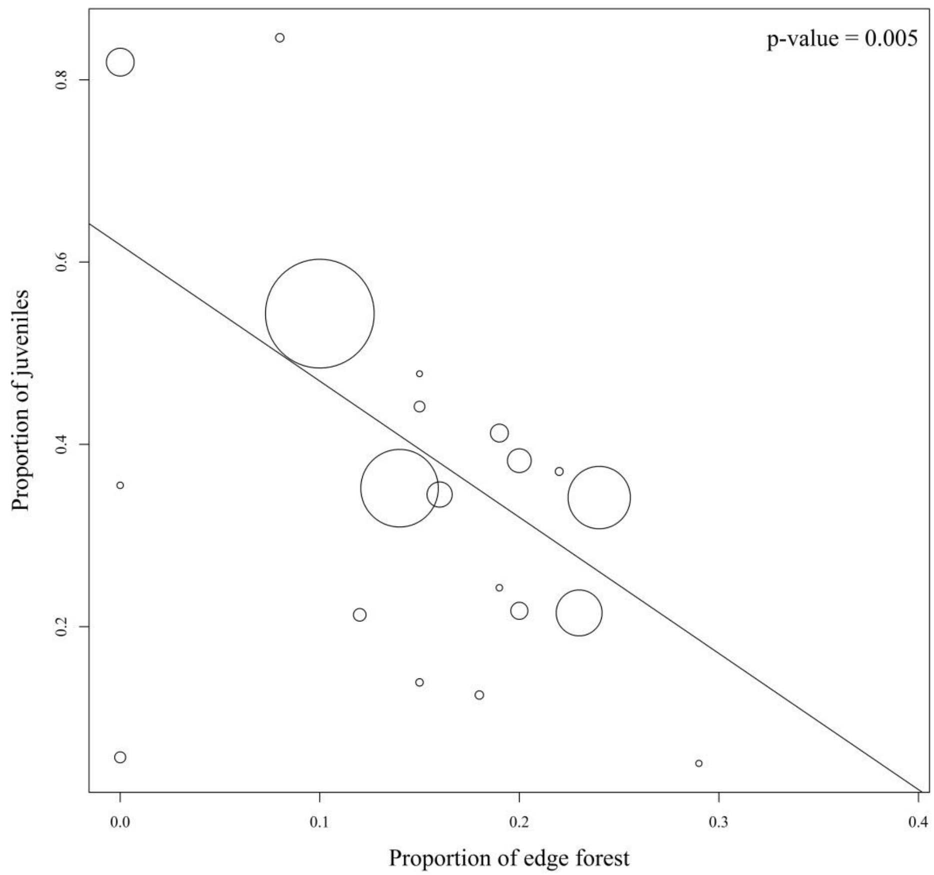

Figure 7. Yellow Warbler productivity versus edge forest at local scale (500-m radius). The station average of total individuals was included in the Simple Linear Regression Model as a weighted variable. Each circle represents the average productivity for each station. The circles' size indicates the relative average number of total individuals captured in each station.

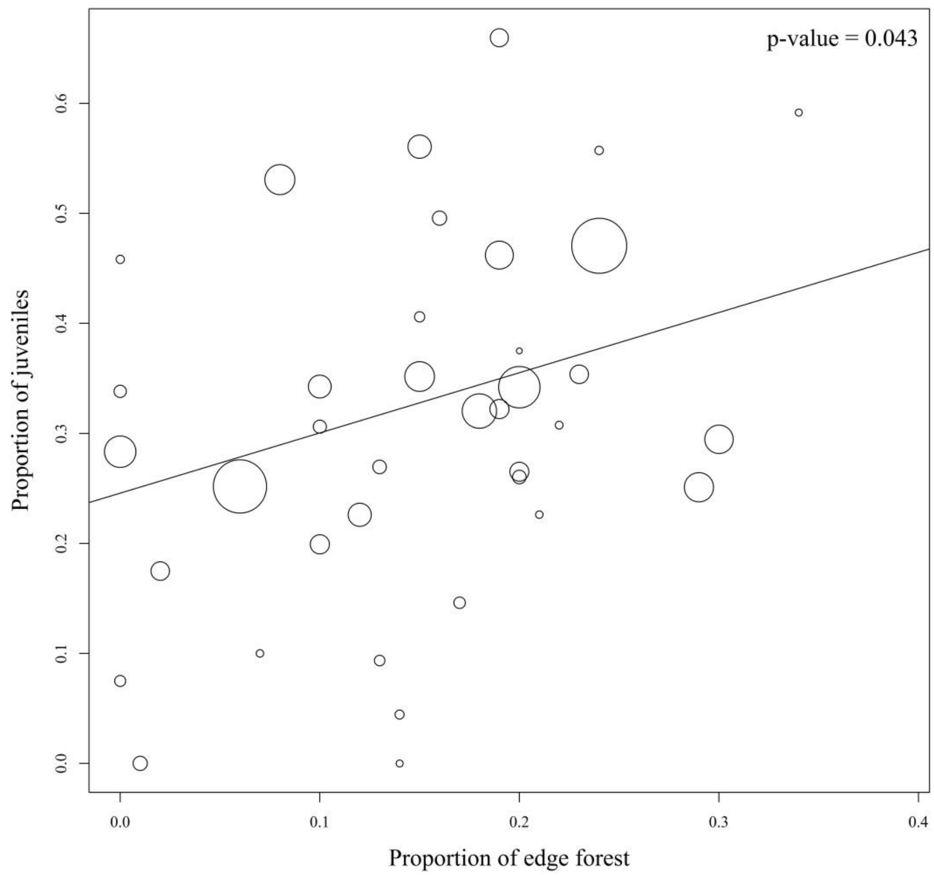

Figure 8. Common Yellowthroat productivity versus edge forest at local scale (500-m radius). The station average of total individuals was included in the Simple Linear Regression Model as a weighted variable. Each circle represents the average productivity for each station. The circles' size indicates the relative average number of total individuals captured in each station.

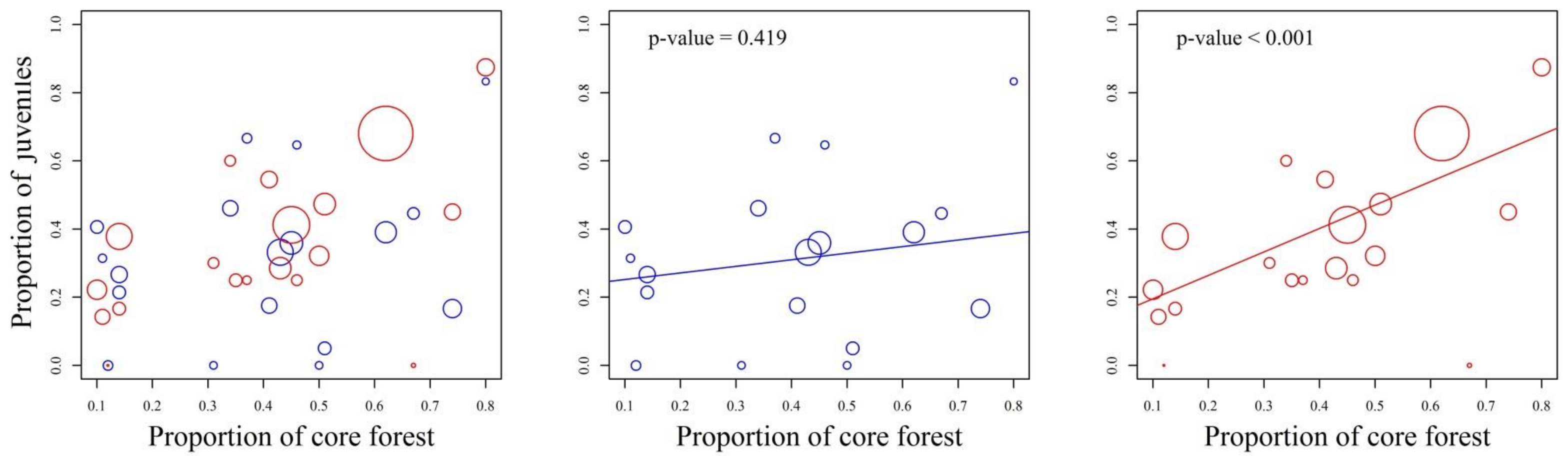

Figure 9. Black-capped Chickadee proportion of juveniles versus proportion of core forest (10,000-m radius) at stations where high frequency of dry days (HFDD) occurred at least once. Left panel shows both extreme (years with high frequency of dry days, HFDD) and normal years, middle panel shows only normal years and right panel shows extreme years. Each circle represents the average productivity for one station (blue for normal years and red for extreme years). The circles' size indicates the average number of total individuals through the years considered in each case.

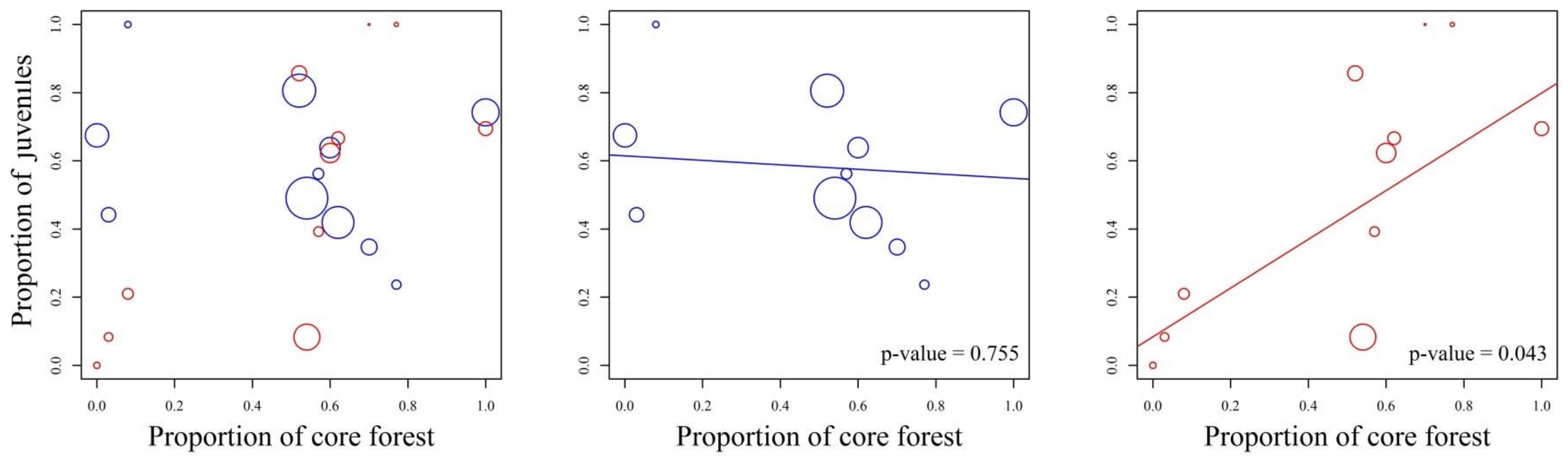

Figure 10. Black-capped Chickadee proportion of juveniles versus proportion of core forest (10,000-m radius) at stations where 10 or more rainy days coincided with minimum temperatures below or equal to 5°C (RB5C) occurred at least once. Left panel shows both extreme (RB5C) and normal year, middle panel shows only normal years and right panel shows extreme years (RB5C). Each circle represents the average productivity for one station (blue for normal years and red for extreme years). The circles' size indicates the average number of total individuals through the years considered in each case.

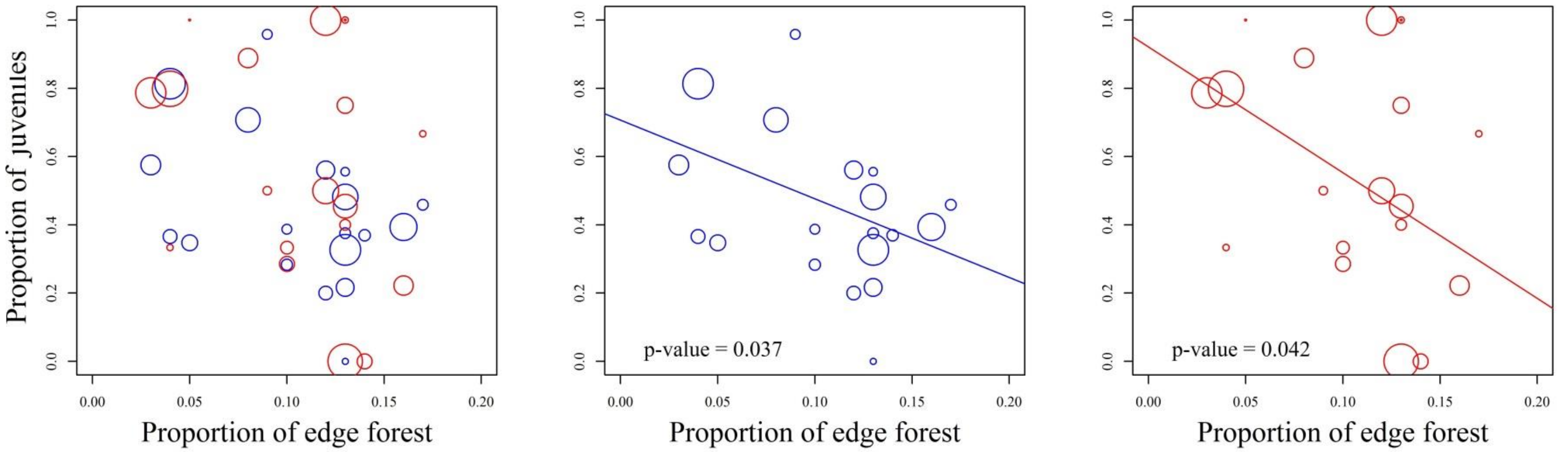

Figure 11. Black-capped Chickadee proportion of juveniles versus proportion of edge (10,000-m radius) at stations where extremely cold winter season (ECWS) occurred at least once. Left panel shows both extreme (ECWS) and normal year, middle panel shows only normal years and right panel shows extreme years (ECWS). Each circle represents the average productivity for one station (blue for normal years and red for extreme years). The circles' size indicates the average number of total individuals through the years considered in each case.

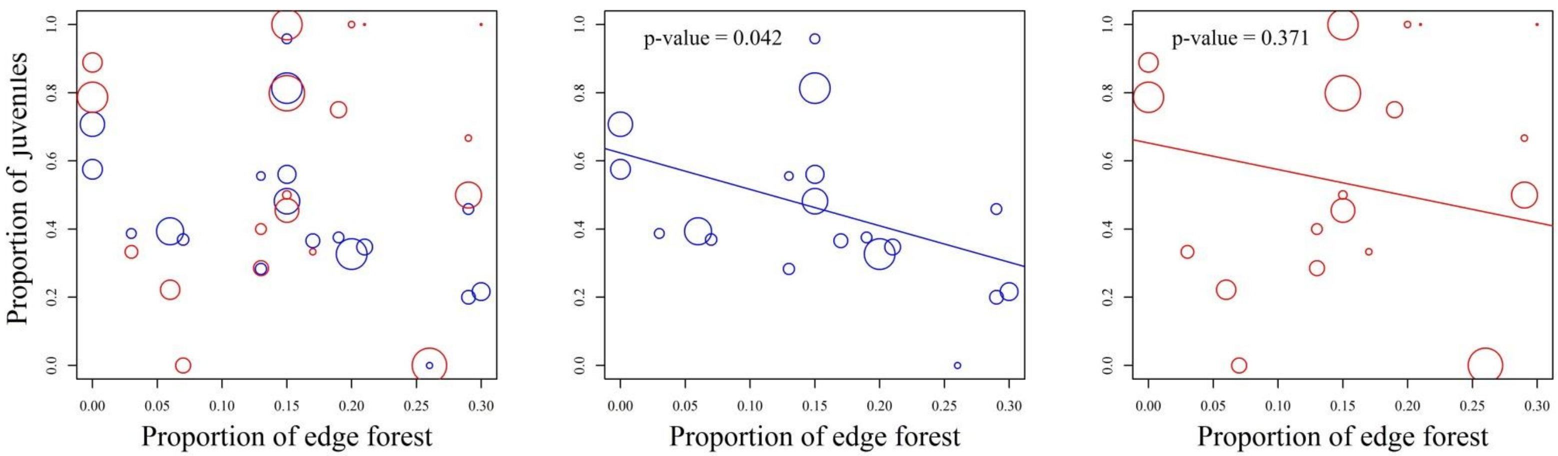

Figure 12. Black-capped Chickadee proportion of juveniles versus proportion of edge forest (500-m radius) at stations where extremely cold winter season (ECWS) occurred at least once. Left panel shows both extreme (ECWS) and normal years, middle panel shows only normal years and right panel shows extreme years (ECWS). Each circle represents the average productivity for one station (blue for normal years and red for extreme years). The circles' size indicates the average number of total individuals through the years considered in each case.

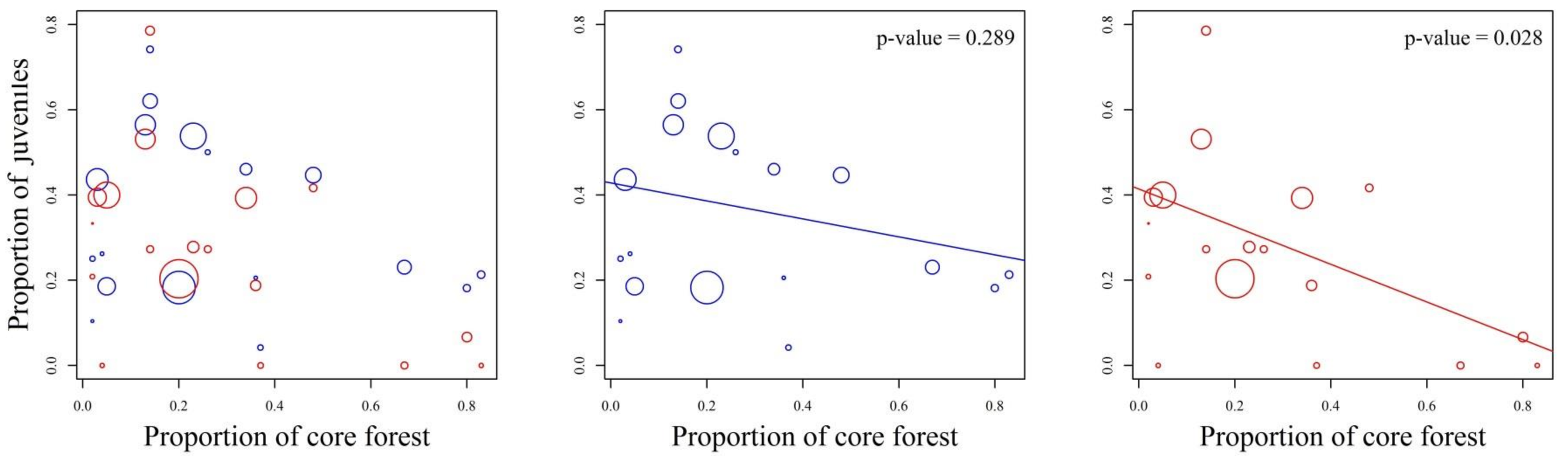

Figure 13. Gray Catbird proportion of juveniles versus proportion of core forest (10,000-m radius) at stations where extreme cold breeding season (ECBS) occurred at least once. Left panel shows both extreme (ECBS) and normal years, middle panel shows only normal years and right panel shows extreme years (ECBS). Each circle represents the average productivity for one station (blue for normal years and red for extreme years). The circles' size indicates the average number of total individuals through the years considered in each case.

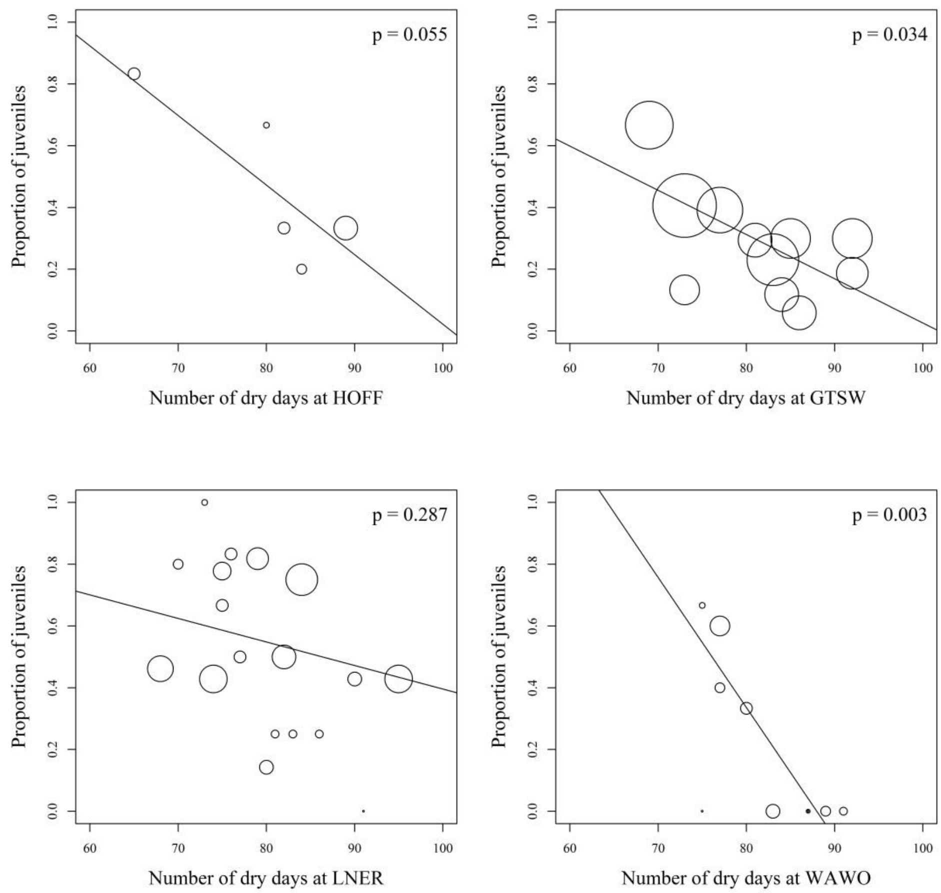

Figure 14. Productivity of American Robin versus the number of dry days during the breeding season at 4 MAPS banding stations. Analyses were made at station level. The number of total individuals captured each year was included in the model as a weighted variable. Each circle represents one year of data. The circles' size indicates the relative number of total individuals captured each year at a given station.

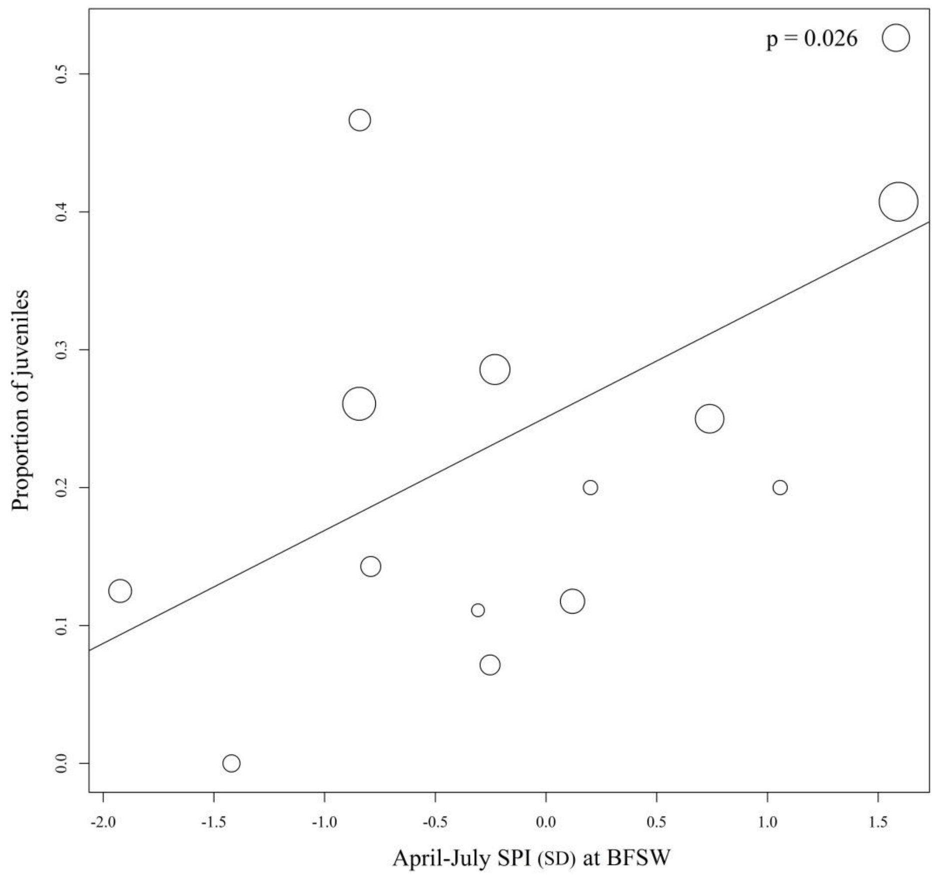

Figure 15. Productivity of Common Yellowthroat versus April-July SPI at Buttercup Farm MAPS banding station (BFSW). The number of total individuals captured each year was included in the model as a weighted variable. Each circle represents one year of data. The circles' size indicates the relative number of total individuals captured each year at a given station.

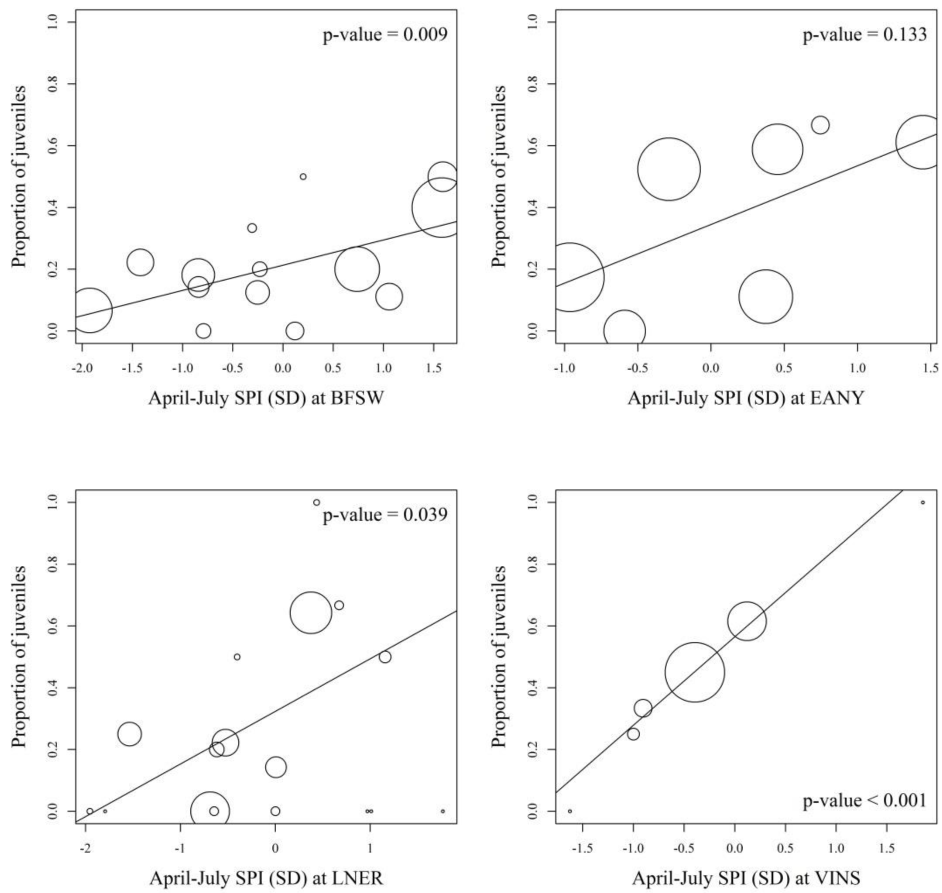

Figure 16. Productivity of Yellow Warbler versus the April-July SPI at 4 MAPS banding stations. Analyses were made at station level. The number of total individuals captured each year was included in the model as a weighted variable. Each circle represents one year of data. The circles' size indicates the relative number of total individuals captured each year at a given station.