Extreme variations in spring temperature affect ecosystem regulating services provided by birds during migration

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Abstract. Extreme weather is becoming more pronounced, making phenological patterns less predictable. Among the potential consequences, extreme weather may alter relationships of migratory birds with their seasonal food resources and thus impact valuable ecosystem regulating services (e.g., bird predation of herbivorous insects). Our goal was to quantify the effect of an extremely warm spring on these relationships in a U.S Midwest oak savanna. Average regional temperatures in the spring of 2009 coupled with record highs in 2010 (8°C warmer) were the basis of a natural experiment for addressing our goal. In both springs we documented tree flowering and leaf-out phenology, related these to arrival and foraging behavior of the three most abundant migratory wood-warbler species (*Parulidae*), and quantified the effects of migratory bird foraging on insect density, size, and herbivory using a branch exclosure experiment. In 2009, the dominant tree species at our study site, eastern black oak (*Quercus velutina*), flowered in mid-May and the wood warblers foraged heavily in the savanna during this time. Branches from which birds were excluded exhibited a trend toward higher insect density, larger Lepidopterans, and greater flower damage than control branches. In 2010, tree phenology was four weeks earlier than in 2009 and the wood warblers were nearly absent from the savanna (83% fewer), likely because peak food availability preceded their arrival in mid-May. Insect density was 83% greater in 2009 than 2010. However, in 2010, 81% of sampled leaves exhibited substantial damage (>25% of leaf-area removed) compared with 27% of leaves in 2009, presumably due to a lack of herbivorous insect regulation by birds. Our results suggest that the extremely warm spring of 2010 altered linkages between migratory birds and their invertebrate prey that are typical during years of average weather, which likely affected habitat use and the delivery of ecosystem regulating services.

Key words: arthropod; asynchrony; climate change; insect; mismatch; oak savanna; *Parulidae*; phenology; stopover; synchrony; weather; wood warbler.

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INTRODUCTION

Extreme variations in spring weather in the Northern Hemisphere are becoming more pronounced (Meehl and Tebaldi 2004). Extreme weather affects many biological processes (e.g., phenology, survival; Parmesan 2006, Ellwood et al. 2013), and migratory animals are particularly at risk as they encounter a diversity of conditions throughout their journeys (Winkler et al. 2014). A particular concern is that large deviations in weather from typical conditions may alter formerly synchronous phenological relationships (Parmesan 2006, Johansson et al. 2015, Rafferty et

al. 2015), such as coincidence between the arrival of migratory birds at stopover and breeding habitats and peak abundance of ephemeral food resources (Visser and Both 2005, McKinney et al. 2012). If the degree of asynchrony is large, there is potential for reduced individual and population-level fitness (Both et al. 2006, Møller et al. 2008, McKinney et al. 2012, Day and Kokko 2015). Thus, shifts in species phenologies due to extreme weather and climate change have potentially deleterious consequences for biodiversity (Parmesan 2006).

Globally, each spring, billions of migratory birds depart poleward from their nonbreeding habitats closer to the equator to temperate breeding grounds. The arrival of migratory birds at stopover sites (i.e., habitats used for resting and refueling during migration) typically matches peaks in herbivorous insect abundance (Graber and Graber 1983, Alerstam et al. 2003, McGrath et al. 2008). There are at least two immediate benefits of synchronized arrival at stopover sites with insect abundance. First is improvement of migratory bird body condition, which increases a bird's ability to cope with migration and breeding season demands (Moore and Kerlinger 1987, Sandberg and Moore 1996). Second, insectivorous migratory birds also provide a substantial ecosystem service by regulating the abundance of herbivorous insects located on trees and other plants (Moore and Yong 1991, Whelan et al. 2008, Wenny et al. 2011). Therefore, phenological synchrony between avian migrants and herbivorous insects likely has broader implications for ecosystem function than solely improved body condition (Bauer and Hoye 2014).

The ecological and economic benefits provided by bird regulation of insect herbivores has been demonstrated during both the breeding and nonbreeding periods when birds are relatively stationary (e.g., Marquis and Whelan 1994, Van Bael et al. 2003, Kellermann et al. 2008). However few studies have quantified this benefit during spring migration (Moore and Yong 1991, Strode 2015), a period of high insect abundance in temperate regions of the world (Forkner et al. 2004). Further, it remains unclear how extreme weather may interact with migratory bird regulating services. This is an important gap in knowledge given the global scale of avian spring migration, the apparent pattern of synchrony between migratory songbird arrival at stopover sites and herbivorous insect emergence, and the current and predicted increase in frequency of extreme weather.

We studied variation in migratory bird habitat use relative to habitat phenology at a black oak (*Quercus velutina*) savanna in two spring seasons with very different weather—one average, the other anomalously warm—with two objectives in mind. Our first objective was to determine patterns of coincidence in arrival and foraging behavior of three migratory wood-warbler species (*Parulidae*) with that of tree phenology. Although studies in other systems of North America have identified important tree phenophases that overlap with migratory bird stopover (e.g., Rodewald and Brittingham 2007, McGrath et al. 2008, Strode 2009, Kellermann and van Riper III 2015, Wood and Pidgeon 2015), these relationships remain unclear in the oak savanna system of this study. Our second objective was to quantify the effect of the extreme difference in spring temperature on potential ecosystem regulating services that migratory birds provide. In a branch exclosure experiment, we sought evidence for three hypotheses about this regulatory effect: (1) a no effect hypothesis which posits that migratory birds provide little to no regulating service under any temperature regime; (2) a regulation hypothesis, wherein migratory birds consistently provide regulating services regardless of temperature regime; and (3) a temperature-mediated regulating service hypothesis which asserts that avian regulation of insect density, size, and vegetation damage varies according to temperature regime.

METHODS

Study area and sampling design

We collected all data in 1,200 ha of oak savanna (hereafter savanna) embedded within a matrix of grassland and woodland that is part of 24,281 ha Fort McCoy Military Installation, in southwestern Wisconsin, USA (Fig. 1). Eastern black oak is the most common tree species in the savanna, accounting for approximately 92% of tree basal area. Within the savanna, we randomly selected 61 50-m radius sample points using Hawth's tools in ArcGIS 9.1, spaced >275 m
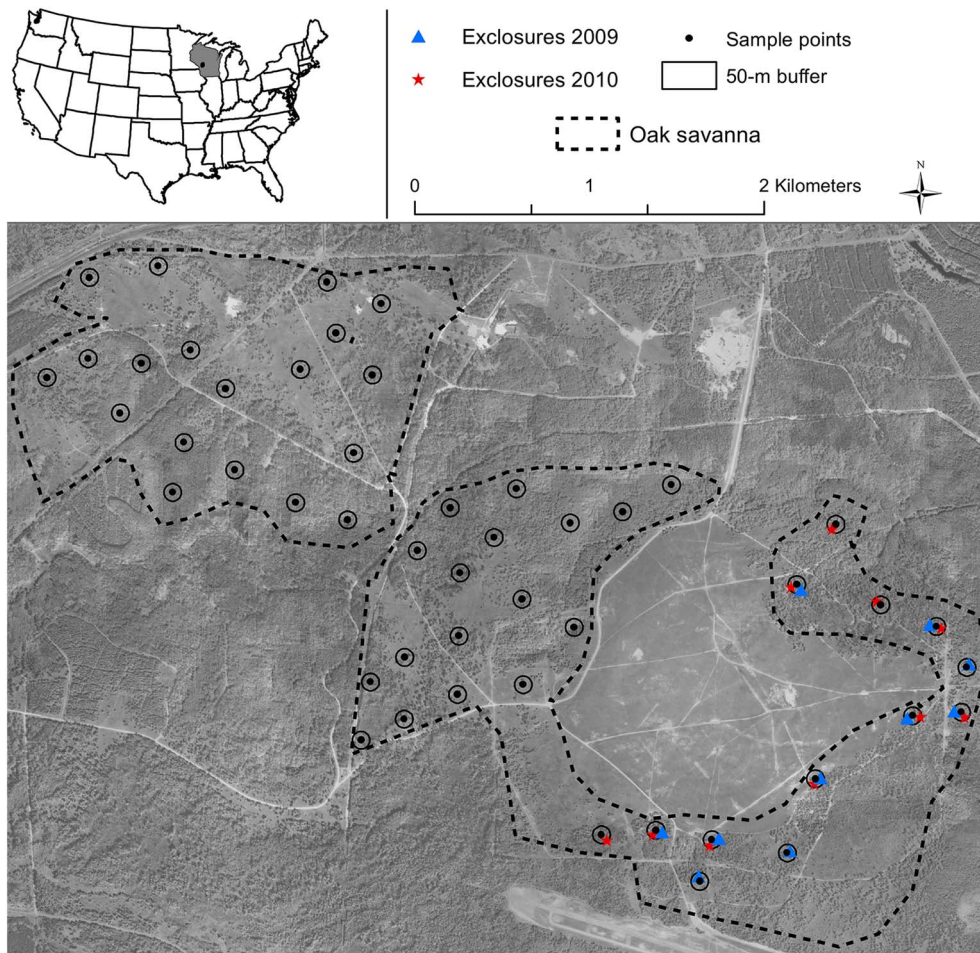
Fig. 1. Fort McCoy Military Installation (black point), located in southwest Wisconsin (shaded gray), USA, and depiction of sampling design, overlaid on a 1-m resolution infrared air photo. Circles indicate locations of the 61, 50-m radius sample points. We collected foraging observations of three wood-warbler species within the boundaries of the oak savanna (dashed lines). Blue triangles (2009) and red stars (2010) indicate locations of 20 branch exclosures.

apart, where we collected tree phenology and bird count and foraging data (Fig. 1). We conducted the branch exclosure experiment at a subset of 13 sample points (Fig. 1). We chose these 13 sample points, located in the eastern-most section of the study, because military training activity in this portion of the Installation was light and thus risk of accidental damage from these activities was low relative to other areas. In addition to black oak, other tree species in our study area include northern pin oak (*Quercus ellipsoidalis*), jack pine (*Pinus banksiana*), black cherry (*Prunus serotina*), and bur oak (*Quercus macrocarpa*); the dominant shrub is

American hazelnut (*Corylus americana*) and the dominant grass species is little bluestem (*Schizachyrium scoparium*).

We collected field data over two years, 2009 and 2010. The temperature patterns during March and April of 2009 were similar to the long-term average (1950–2008) of southwestern Wisconsin (Wood and Pidgeon 2015). However, in March and April of 2010 the average daily temperature of the region was approximately 8°C warmer than the long term average (www.noaa. gov; Wood and Pidgeon 2015). The 2010 record extreme weather was accompanied by greatly advanced vegetation phenology in the region

(Wood and Pidgeon 2015). Thus, the contrast in weather between 2009 and 2010 provided a natural experimental design that allowed us to test the regulatory effect of migrant passerines on invertebrate herbivores under average and extremely warm temperature conditions. Throughout the manuscript, we refer to 2009 as the 'average' year and 2010 as the 'warm' year.

Tree phenology measurements

At each of the 61 sample points, we selected four mature black oak trees as replicate sample units for all tree phenology measurements. We included the tree nearest to the center of the sample point and the nearest tree to a randomly generated distance (between 5 and 45 m) in each quadrant, demarcated by the angles of 1°–120°, 121°–240°, and 241°–360°. We characterized phenology of trees on the same days that point counts were conducted (see *Methods: Avian point counts and foraging observations*) between April 20 and June 6, which is the approximate period of wood warbler migration in southern Wisconsin (Temple et al. 1997). During each visit, we recorded the percentage of the tree crown that was in a given phenophase: (1) budding, (2) bud burst, (3) catkins (flowering), (4) emerging leaf (incomplete, pre-summer condition, light green coloration), and (5) mature leaf (summer condition, dark green coloration).

Avian point counts and foraging observations

We conducted five-minute point counts, recording distances to all birds seen and heard within 50 m, starting at sunrise and continuing for about 3.5 hours (Ralph et al. 1995). While we set out to conduct point counts twice a week to correspond with average migrant turnover at stopover sites (Moore and Kerlinger 1987, Seewagen et al. 2010), military training schedules and weather prevented several planned counts resulting in thirteen counts at each point in 2009 and 10 counts at each point in 2010. Each observer conducted at least two counts at each sample point in each year.

We examined patterns of coincidence between tree phenology and arrival and habitat use by three migratory wood-warbler species: the Tennessee Warbler (*Oreothlypis peregrina*), the Palm Warbler (*Setophaga palmarum*), and the Yellow-rumped Warbler (*Setophaga coronata*) (Table 1).

Portions of the Palm and Yellow-rumped Warbler populations winter as far north as the southern U.S, and we categorized these species as short-distance migrants (Poole 2005). The Tennessee Warbler winters in the tropics and we categorized this species as a long-distance migrant (Poole 2005). We predicted that Palm and Yellow-rumped Warblers would more flexibly adapt their arrival and use of the savanna to the conditions in a given spring than Tennessee Warblers because their more temperate wintering location might allow them to better track plant and food resource phenology influenced by the same general weather patterns that were affecting habitat phenology in Wisconsin.

Male wood warblers migrate earlier than females (Francis and Cooke 1986). During our counting period, we noticed that when only males were present there appeared to be less singing than when females were also present. This coupled with the changing tree phenology likely led to variable detection probabilities both within and between years. However, we were not able to account for imperfect detection for each sampling date due to low sample sizes (especially Tennessee and Palm Warblers in 2010; Table 1). Therefore, the extent of our inferences is limited to the unadjusted raw count data.

To explore the relationships between different phenophases of trees and foraging by the three wood-warbler species, we recorded their behavior in black oak trees at different stages of phenological development. Our protocol was to opportunistically search for foraging birds while walking between sample points. Once we found an individual of a target species, we followed and documented its foraging activities and movements for as long as possible, up to five minutes (Wood et al. 2012). We observed that most individuals used multiple black oak trees during foraging bouts. We included data from each tree used for >30 seconds (82% of observations) to understand the relationship between foraging and tree phenophase. We recorded few individuals foraging in trees other than black oak (6%), and we did not include these observations in our analyses. We documented the following data: date, time, bird species, tree species used, bird search effort (number of hops, walks, flights), and type of attack (bud glean, flower glean, leaf glean, bark glean, hover, or sally). We

Table 1. Three wood-warbler species studied during spring migration in 2009 and 2010 at Fort McCoy Military Installation, Wisconsin, USA.

Species	Scientific classification	Migration distance to WI	n 2009	n 2010
Tennessee Warbler	*Oreothlypis peregrina*	longer	394[128,12554]	8[7,347]
Palm Warbler	*Setophaga palmarum*	shorter	39[2,342]	29[20,1884]
Yellow-rumped Warbler	*Setophaga coronata*	shorter	121[46,3023]	59[33,2507]

Note: Numbers in superscript following counts are the (1) unique foraging bouts and the (2) cumulative seconds we observed species during foraging observations.

recorded data by speaking into a digital recorder with a built in timer (Sony ICD-PX720 Digital Voice Recorder), while constantly watching the bird through binoculars.

Exclosure experiment

To quantify ecosystem regulating services provided by insectivorous migratory birds, and how these services may have varied between the average and warm year, we conducted a branch exclosure experiment on 10 black oak trees in 2009 and 10 different black oak trees in 2010. There are three reasons why we attribute the main predation effect of herbivorous insects at our study site during the months of April and May to migratory birds. First, there are only two arboreal foliage-gleaning species that are common in the savanna: Baltimore Oriole (*Icterus galbula*) and Orchard Oriole (*Icterus spurius*; Wood et al. 2011), but territory establishment of these species typically occurs in late May. Second, resident species that would use trees for insect food resources, such as the Black-capped Chickadee (*Poecile atricapillus*) are uncommon in the savanna (Wood 2011). Third, bats, which also eat herbivorous insects from tree substrates (Williams-Guillen et al. 2008), were detected infrequently in the savanna in a recent bat-acoustic survey of Fort McCoy (T. Wilder, *unpublished data*).

In the portion of the Installation with lighter military training, we chose 10 sample points in which we selected a tree that had suitable branching architecture (i.e., large branches that were not intermingled with adjacent branches) within the 50-m circle of a sample point. On each tree, in mid-April during both years, which is prior to wood-warbler arrival in our study area (Temple et al. 1997), we installed an exclosure in the middle to upper-portion of the tree crown. We used this portion of the crown because this is

where we observed the majority of wood-warbler species foraging during pilot work for this study. At the same crown height on the tree, we selected a control branch, where birds were free to forage. We selected exclosure and control branches that were exposed to similar light and wind conditions.

The average height of trees in which we applied our experiment was 9.9 m, which was similar to the average canopy height within the savanna, and to the trees that we observed for phenological change ($\bar{x} = 10.2$ m). Each exclosure covered approximately 3 m of branch and encompassed multiple smaller branches on which the majority of flowers and leaves occurred. We surrounded branches with monofilament netting (1.5×3.8 cm mesh size; Memphis Net and Twine Company) and secured overlapping segments with twist ties. The mesh size was large enough for smaller arthropods (e.g., caterpillars, spiders) to freely move in and out, while excluding birds. We used rope and twine, tied to adjacent branches or trees, to keep the mesh at least one meter from all enclosed vegetation to minimize any difference in the local environmental conditions due to the exclosure. All portions of the branches were covered, and we diligently monitored exclosures during set-up and throughout the experiment, removing occasionally discovered spider webs on the netting to guard against the potential bias of favoring arthropod predators (Forkner and Hunter 2000).

We set out to clip vegetation, from both the exclosure and the control branch, at two time points to estimate regulatory effects by insectivorous migratory birds during and immediately following migration. Our planned clippings were aligned with the usual migrant arrival and departure dates in our study system (Temple et al. 1997; T. Wilder, *personal communication*) and were not related directly to plant and insect

phenology. Our first clipping on 16 May was timed to overlap peak abundance of wood-warbler migrants (Temple et al. 1997). Our second clipping on 31 May was timed for after wood-warbler migrants typically depart the region (Temple et al. 1997). In 2009, after the first clipping, a severe storm disabled two of our nets. Thus, we were only able to clip vegetation from eight trees on May 31 in 2009. In 2010 along with the advanced plant phenology, we also detected insects on flowers and emerging leaves of some branches we put exclosures around. The mid-May branch analysis of 2009 had focused primarily on differences in flower and emerging leaf damage associated with bird predation pressure on insect herbivores. In 2010, with the advanced tree phenology we were not able to analyze differences among flowers and emerging leaves, and thus omitted the mid-May clipping.

To clip vegetation, we carefully opened exclosures and used tree pruners and shears to clip two, two-gallon sized bags of vegetation after first enclosing the majority of the intended branch in the bag. We gathered approximately 20% of live vegetation during each clipping. In 2009, during our first clipping, the vegetation consisted of emerging leaves and oak flowers, while in the second clipping, in both years, the vegetation was primarily mature leaves. After clipping vegetation, we sealed the bags and placed them in a freezer within approximately one hour.

After vegetation had been frozen for at least 24 h, we sorted all insects, flowers, and leaves from each bag. To do this we thawed the bags for approximately one hour, and then carefully placed the contents onto a clean white-paper-covered table. We tallied the number of insects, identified them to taxonomic Order, measured their length (mm), and sorted them by the vegetative substrate on which they were found (flower, leaf, or woody). For insects not found on vegetation after freezing, we listed substrate as unknown.

We stored insect specimens in glass vials of 30% ethanol, and later verified identifications with a University of Wisconsin-Madison entomologist (D. Young, *personal communication*). We sorted all flowers ($n = 6,929$) and leaves ($n = 16,279$) from each clipping. During our first clipping in 2009, we examined leaves and flowers under a stereomicroscope to determine whether flowers and emerging leaves exhibited any evidence of insect damage (e.g., yes or no from chewing and/or eating). We frequently observed a group of catkins clumped together with a caterpillar in the center of the group, and noticeable absence of catkin tissue was evident on the side of catkins that were proximate to the caterpillar. During clipping at the end of May in both years, the effect of insect herbivory was so great that we sorted leaves based on the proportion of leaf area that had been eaten. We tallied herbivory in three categories: light (<25%), moderate (25–50%), and heavy (>50%) leaf-area removal. We used sketched diagrams as models of leaf damage to inform sorting leaves into categories. After sorting vegetation and insects from the two plastic bags of an exclosure or control branch, we dried all vegetative material in an oven (200°C) for approximately one hour. We then weighed flowers and leaves, separately, from our first clipping in 2009 (May 16), and all leaf material from our clippings on May 31, in both years. We scaled flower damage by 100 flowers, leaf damage by 100 leaves, and total insect, Lepidoptera, and Hemiptera abundance (the two most common Orders) by 10 g of dry vegetation weight. We refer to the adjusted insect values as density measurements because these accounted for abundance per standard mass of dry vegetation.

Statistical analysis

To address our first objective of exploring patterns of coincidence in arrival and foraging behavior of the wood-warbler species with tree phenology, we (1) determined the average proportion of trees in each tree phenology category; (2) relativized counts for each bird species by dividing the counts for a given Julian date by the number of observations totaled over both years; (3) calculated the total foraging attacks directed at leaves, flowers, and aerial maneuvers (hovers and sallies), scaled per minute, and relativized each attack type in turn, as described in #2; and (4) calculated the attack index, a measure of foraging success, which is defined as the ratio of total attacks over total search maneuvers, scaled per minute (Wood et al. 2012). We relativized the attack index values as in #2. We calculated all metrics for six dates in

both 2009 and 2010 (Julian dates 105, 115, 125, 135, 145, 155). The average tree phenology scores, bird counts, and foraging calculations included surveys ranging from four days prior to five days after the six specified Julian dates.

Additionally, we quantified whether Lepidoptera larvae, which are a preferred food resource for spring migrating birds (Graber and Graber 1983), found on oak flowers differed in size from those found on leaf surfaces. This analysis was intended to determine if there was evidence supporting possible mechanisms influencing wood-warbler arrival and foraging patterns in relation to tree phenology. We used size as a proxy for food quality assuming larger prey items have higher caloric content (Griffiths 1975). We used Lepidoptera length data from our first branch clipping in May 2009 from exclosure branches rather than controls, because we assumed migratory birds consumed the larger food items on un-netted control branches. We used a two-sample t-test, with the substrate (i.e., flower or leaf) on which caterpillars were found as our grouping variable.

To address our second objective of quantifying the effect of extreme variations in annual spring temperature on ecosystem regulating services provided by migratory birds, we conducted three analyses. First, to understand the effect of migratory bird foraging on insect density and vegetation damage within each season, we fit a series of paired, two-sample t-tests. We compared (a) density and (b) size of all insects, plus Lepidoptera and Hemiptera, separately, between the netted and un-netted branches at each time point when branches were clipped; and (c) flower and leaf damage, at the time of first clipping in 2009 (16 May), and substantial leaf damage (>25%) at the time of the second clipping on 31 May, in 2009 and 2010, between netted and un-netted branches. We used one-tailed tests for significance because we assumed that branches covered with netting would only have higher or equal values, but not lower values, than controls.

Second, to quantify the relationship of insect density and size with flower and leaf damage we fit correlations using either Pearson's product-moment correlation (r) or Spearman's rank correlation coefficient (ρ) depending on whether outliers were absent (in which case we used Pearson's product-moment correlation) or pre-sent (in which case we used Spearman's rank correlation). We performed this analysis to understand relationships between each insect metric and vegetation damage.

Third, we quantified between-year differences in Lepidoptera density and size, and substantial leaf damage. We constructed three two-tailed, non-paired Wilcoxon signed-rank tests, using data from the control branches clipped on 31 May, in both years (grouping variable). We used data from the control branches because we wanted to determine the integrative result of bird depredation and extreme weather on insect herbivore abundance and leaf damage.

For all analyses, we assessed the assumptions of each test by constructing histograms and fitting normal QQ-plots. We also inspected the variance structure of residuals and searched for outliers in the data. If data were non-normal, we applied log-transformations. If data met assumptions for parametric analyses, we calculated t-tests. If parametric tests were not appropriate due to violations in model assumptions, we used a non-parametric, paired Wilcoxon signed-rank test. Because of the modest sample sizes of our exclosure experiment, we used an alpha threshold of 0.10 to assess significance for all t-, Wilcoxon signed-rank tests, and correlation analyses. We performed all analyses in the R statistical software package (R Core Team 2014).

RESULTS

Patterns of phenological synchrony

We observed strong differences in the timing of tree phenology and patterns of wood-warbler foraging behavior and success between the average and warm year (Fig. 2). In the average year, leaves began to emerge, and flowering occurred in mid-May, and the Tennessee Warbler heavily used the savanna at this time (Fig. 2). Additionally, this species departed the savanna coincident with the end of oak flowering (Fig. 2). We did not detect associations between Tennessee Warblers and other tree phenophases (Fig. 2). We found weaker patterns of synchrony between Palm and Yellow-rumped Warblers with oak tree phenology (Fig. 2). Though, a consistent pattern between years was that these species departed the savanna before trees were in summer condition (Fig. 2). In the average year, oak
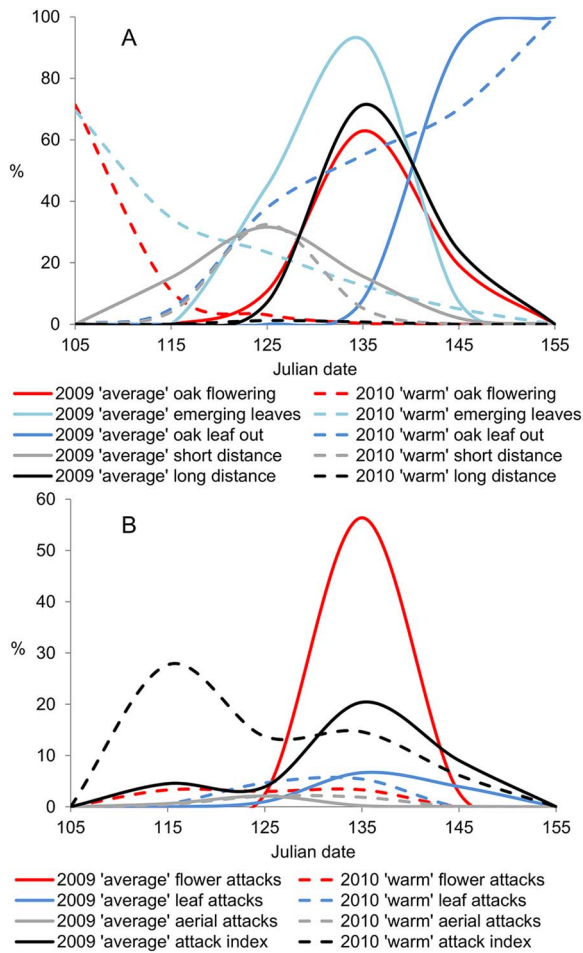
Fig. 2. (A) Proportional abundance of three wood-warbler species, the Tennessee Warbler (longer distance migrant), the Palm Warbler, and the Yellow-rumped Warbler (latter two are shorter distance migrants), grouped by migration distance, and percent flowering, emerging leaf, and leaf-out of 244 black oak trees, from April 14 to June 3 (Julian day: 105–155), 2009 and 2010. (B) Proportion of flower and leaf attacks, and aerial foraging maneuvers (hover and sallies), by the three wood-warbler species, scaled per minute, and attack index, which is a measure of foraging success (total attacks/total searches). 2009 late winter and spring temperatures were similar to the long-term (1950–2008) average temperatures, whereas 2010 was significantly warmer over this period. We refer to these as the average (2009) and warm (2010) years.

flowers were the dominant foraging substrate for Tennessee Warblers, and the peak of foraging success coincided with the peak of oak flowering (Fig. 2).

In contrast, in the warm year, oak tree leaf-out and flowering began approximately in early-to mid-April, 30 days earlier than in the average year (Fig. 2). The Palm and Yellow-rumped Warblers arrived at the savanna approximately two weeks earlier in the warm year, though the Tennessee Warbler arrived at similar times in both years (Fig. 2). In the warm year, we observed far fewer individuals of the three wood-warbler species (83% fewer) than in the average year, despite similar survey effort (Table 1). More specifically, we detected 98% fewer Tennessee Warblers, 51% fewer Yellow-rumped Warblers, and 26% fewer Palm Warblers in the warm year (Table 1). The few Tennessee Warblers that we observed in the warm year departed the habitat at a similar time as Palm and Yellow-rumped Warblers, which was coincident with the end of oak flowering, in contrast to the average year when they persisted longer at the site (Fig. 2). After oak flowering in both years, the three species shifted foraging substrates from flowers to leaves before the leaves had matured to summer condition (Fig. 2). We found that Lepidopterans on flowers were significantly larger than those on leaves ($t_{641} = 4.49$, $p < 0.01$; Fig. 3; 10% larger), highlighting a plausible mechanism for the heavy use of oak flowers by the wood-warbler species.

Ecosystem regulating services

We collected 2,223 insect specimens from five Orders (Table 2). We found few arachnids in our clippings ($n = 5$), and thus we did not include them in final tallies. We collected 1,405 insects from the clipping on 16 May 2009, 496 on 31 May 2009, and 322 on 31 May 2010 (Table 2). The composition of the insects varied dramatically among these periods. Hemiptera, dominated by treehopper nymphs (family *Membracidae*), were the most common insects in mid-May 2009, and were 72% and 99% more abundant during black oak flowering than during leaf out in 2009 and 2010, respectively. We collected 54% and 81% more Lepidoptera larvae during black oak flowering in 2009 than during leaf out in 2009 and 2010, respectively. Overall insect density was
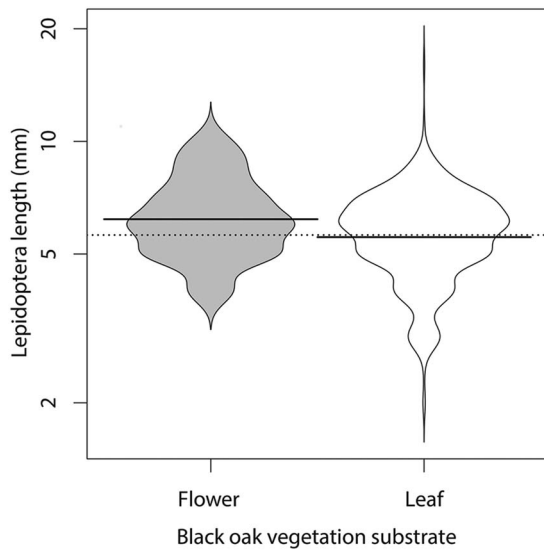
Fig. 3. Bean plot of the length of Lepidopterans (mm) collected on oak flowers ($n = 65$) or leaf surfaces ($n = 578$) from clipped black oak (*Quercus velutina*) vegetation, 16 May 2009 (Julian day 137). The shape of the bean represents a one-dimensional scatter plot and its distribution as a density shape, and the solid black lines represent the mean value, and the dotted line represents the average length of all individuals measured. We excluded birds from these branches for three weeks. The color scheme indicates a significant difference in length, based on a two-tailed, two-sample *t*-test ($t_{641} = 4.49$, $p < 0.01$).

far lower in 2010 with the exceptions of Coleoptera, which were 95% and 98% more common than in 2009, and Hymenoptera, which were 18% and 81% more common than in 2009 (Table 2).

During oak flowering and the emerging leaf phenophase, which coincided with the 16 May branch clipping in the average year, our evidence

Table 2. Sample sizes of five insect orders collected from three clippings during a branch exclosure experiment.

Insect order	2009 16 May	2009 31 May	2010 31 May
Coleoptera	8	3	148
Diptera	2	0	6
Hemiptera	754	209	4
Hymenoptera	47	11	57
Lepidoptera	594	273	107

suggests that foliage-gleaning migratory birds contributed to limiting insect ($t_9 = -1.42$, $p = 0.09$, 17% higher density within exclosures) and Hemiptera density ($t_9 = -1.52$, $p = 0.08$, 24% higher density within exclosures), depredated larger Lepidopteran larvae ($t_9 = -1.43$, $p = 0.09$, 3% larger average Lepidopteran size within exclosures), and lowered herbivory on oak flowers ($w_{20} = 7$, $p = 0.02$, 32% greater flower damage within exclosures; Table 3, Fig. 4). Hemiptera density was negatively, though not significantly, correlated with flower damage ($r_{18} = -0.36$–0.26, $p > 0.12$). On the other hand, density of Lepidoptera was positively correlated with vegetation damage, though not significantly ($r_{18} = 0.36$, $p = 0.12$). Insect size was positively correlated with flower damage ($r_{18} = 0.47$, $p = 0.04$), and this pattern was driven by the average size of Lepidoptera ($r_{18} = 0.49$, $p = 0.03$; Fig. 5), suggesting the depredation effect of migratory songbirds on larger Lepidoptera larvae may limit herbivory (Fig. 5). We did not find evidence that migratory birds limit damage to emerging leaves during oak flowering ($t_9 = 0.83$, $p = 0.21$; Table 3).

Once oak tree leaves matured to summer condition by May 31, we did not find support that migratory songbirds limit density of insects, and, in turn, substantial leaf damage (Table 3). The only exception was density of Lepidoptera, which was surprisingly higher on control rather than exclosure branches ($t_9 = 1.46$, $p = 0.09$; Table 1). This variable was positively, but not significantly, correlated with substantial leaf damage ($r_{14} = 0.24$, $p = 0.37$). A plausible reason why we did not detect a depredation effect during the summer leaf-out period in 2009 was due to wood warbler foraging behavior (i.e., heavier use of flowers as foraging substrates rather than leaves). The exception was in 2010, when we surprisingly detected higher substantial leaf damage on control branches ($t_9 = 1.68$, $p = 0.06$). We also found the average length of Lepidoptera larvae was larger on control than exclosure branches ($t_9 = 1.63$, $p = 0.07$), and this variable was positively correlated with substantial leaf damage ($\rho = 0.56$, $p = 0.01$; Fig. 5). Similar to the clippings from 2009, Lepidoptera density was positively correlated with substantial leaf damage ($r_{18} = 0.38$, $p = 0.09$).

We found strong between-year differences, based on the May 31 clippings, of Lepidoptera

Table 3. Mean insect, Hemipteran, and Lepidopteran density (number/10 g of dry vegetation), size, as represented by average length (mm), and amount of insect-induced damage to flowers and leaves (per 100 flowers or leaves) on exposed and bird-excluded branches of black oak trees (*Quercus velutina*).

Variable	Exposed branch	Bird-excluded branch	t	df	p
2009 flowering phase					
Insect density	28.89	35.13	−1.50	9	0.084
Hemiptera density	15.53	20.35	−1.52	9	0.082
Lepidoptera density	12.31	12.37	−0.04	9	0.484
Insect length mm	4.45	4.33	0.75	9	0.235
Hemiptera length mm	3.26	3.41	−1.05	9	0.161
Lepidoptera length mm	5.78	5.98	−1.43	9	0.094
Flower damage†	5.45	8.07	7	20	0.019
Leaf damage	53.32	51.80	0.83	9	0.212
2009 leaf-out phase					
Insect density	8.43	6.52	1.14	7	0.147
Hemiptera density	3.66	4.00	0.69	7	0.258
Lepidoptera density	4.34	2.38	1.46	7	0.094
Insect length mm	8.28	8.15	0.30	7	0.388
Hemiptera length mm	5.61	5.61	0.06	7	0.477
Lepidoptera length mm	9.88	12.25	−1.07	7	0.160
Leaf damage, >25%	27.85	28.60	−0.13	7	0.451
2010 leaf-out phase					
Insect density	1.46	1.57	−1.05	9	0.161
Hemiptera density	. . .	. . .	. . .	. . .	. . .
Lepidoptera density	0.59	0.43	0.90	9	0.196
Insect length mm	8.87	8.44	0.41	9	0.345
Hemiptera length mm	. . .	. . .	. . .	. . .	. . .
Lepidoptera length mm	9.61	8.16	1.63	9	0.071
Leaf damage, >25%	81.01	78.24	1.68	9	0.063

Notes: We sampled branches during the flowering phase on 16 May 2009 (Julian day 137) and the mature leaf-out phase, May 31 (Julian day 152), in both years, and we report summaries from *t*-test and Wilcoxon signed-rank tests from May 2009 (average weather) and 2010 (extremely warm). Blank cells are due to few Hemipterans being collected during this branch clipping and thus not subjected to analysis.

† We display the median values between treatments, the associated *w*-test statistic, and the *p-value* from a paired, one-tailed, Wilcoxon signed-rank test, because we could not meet assumptions necessary for *t*-tests. The degrees of freedom for this test are the total sample size.

densities ($w_{18} = 73$, $p = 0.02$; Fig. 6), and the amount of substantial leaf damage ($w_{18} = 0$, $p < 0.01$; Fig. 6), but not in the size of Lepidopterans ($w_{18} = 42$, $p = 0.90$). Density of Lepidoptera larvae, as well as Hemipterans, was far greater in the average year during migration (mid-May), which may have contributed to heavier use of the study area by migrants that year (Table 3, Fig. 6). However, substantial leaf damage was far greater in the warm year (81%) compared with the average year (28%; Table 3, Fig. 6). Although flower surfaces were the primary foraging substrate, all three wood-warbler species foraged for insects on leaves as well (Fig. 2), and thus likely contributed to reducing insect herbivores on leaf surfaces. Even though leaf surfaces in 2010 were exposed to insect herbivores for approximately three weeks longer than in 2009 (due to the far earlier tree phenology and the timing of our branch clipping at the end of May), the extremely large differences in leaf herbivory

between years provides evidence of the substantial negative effect the unusual warm spring may have had on the delivery of ecosystem regulating services by migratory birds.

DISCUSSION

Our results suggest that prolonged extreme spring temperatures altered relationships of spring migratory birds and their seasonal food resources, which in turn affected habitat use and the delivery of ecosystem regulating services. In a year when late winter and spring temperatures were similar to the long-term average, we observed patterns of coincidence between presence of both short- and long-distance migratory wood warblers and black oak tree flowering and leaf emergence. In this same year we found support for the regulation hypothesis. Insectivorous migratory birds appeared to have reduced the density of herbivorous insects, including
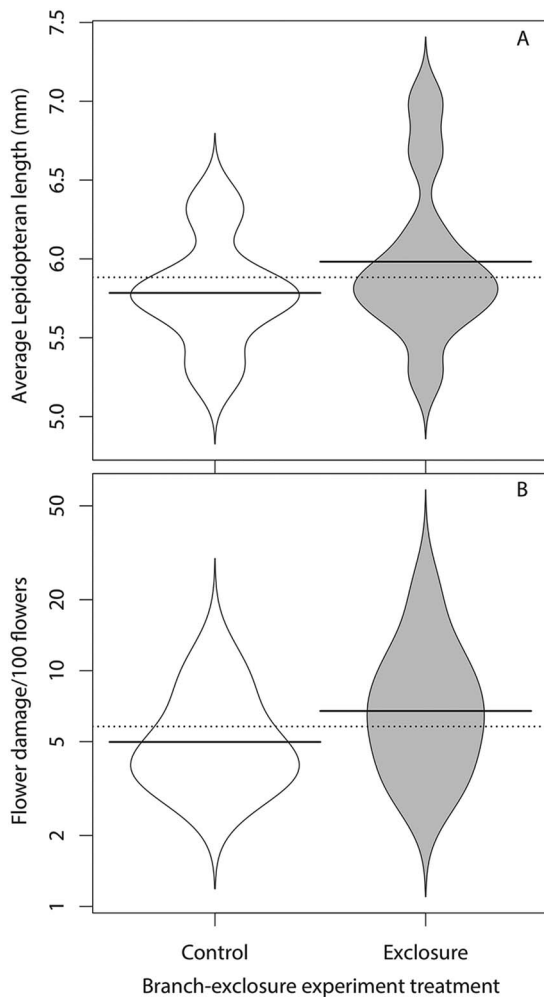
Fig. 4. (A) Average Lepidopteran length (mm) and (B) flower (catkin) damage/100 flowers, between control and exclosure branches on 16 May 2009 (Julian day 137). The color scheme indicates a significant difference between pairs, based on a paired t-test for Lepidopteran length (mm), $t_9 = -1.42$, $p = 0.09$, and a Wilcoxon signed-rank tests for flower damage, $w_{20} = 7$, $p = 0.02$, at the alpha-value of 0.10.
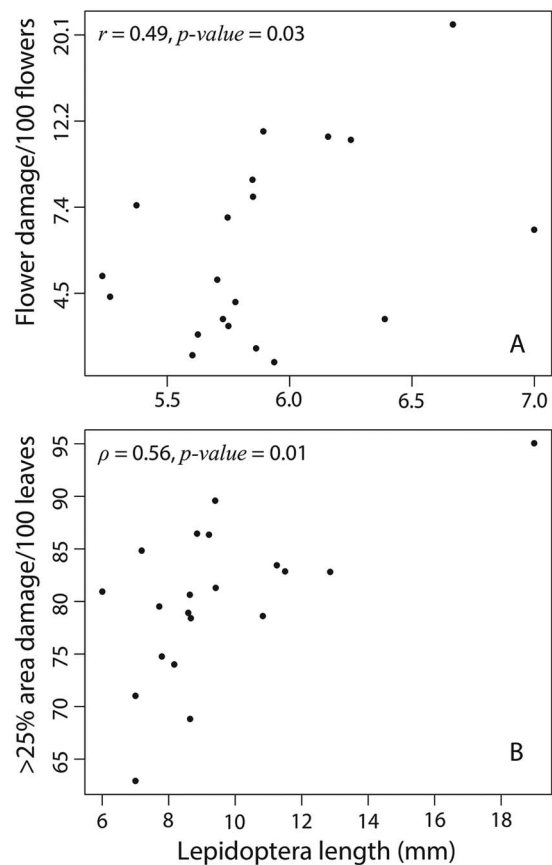

Fig. 5. Scatterplots of (A) Lepidoptera length (mm) versus flower damage (number of flowers with damage/100 flowers) on 16 May 2009 (Julian day 137) and the associated Pearson's correlation coefficient (r), and (B) Lepidoptera length (mm) versus leaf damage (number of leaves with >25% leaf area damage/100 leaves) on 31 May 2010 (Julian day 152) and the associated Spearman's rank correlation coefficient (ρ).

large Lepidopterans, thus limiting vegetation damage. In contrast, we found that in a year of extremely warm late winter and spring temperatures, tree phenology was greatly advanced while the timing of migrant bird arrival varied slightly (short-distance migrants) or not at all (long-distance migrant) from the average year. Yet abundance and foraging activity of birds were far lower and their presence was not associated with a reduction in insect densities or vegetation damage. We speculate that the extremely advanced phenology of the black oak trees in the warm year was accompanied by advanced insect phenology, which likely resulted in a mismatch between peak insect abundance and migratory bird arrival. With less prey available to foraging birds, migrants may have moved out of the habitat, and possibly the region, quickly. We were not able to explore hypotheses related to between-year weather variability (e.g., temperature mediated regulating service hypothesis), and these remain to be
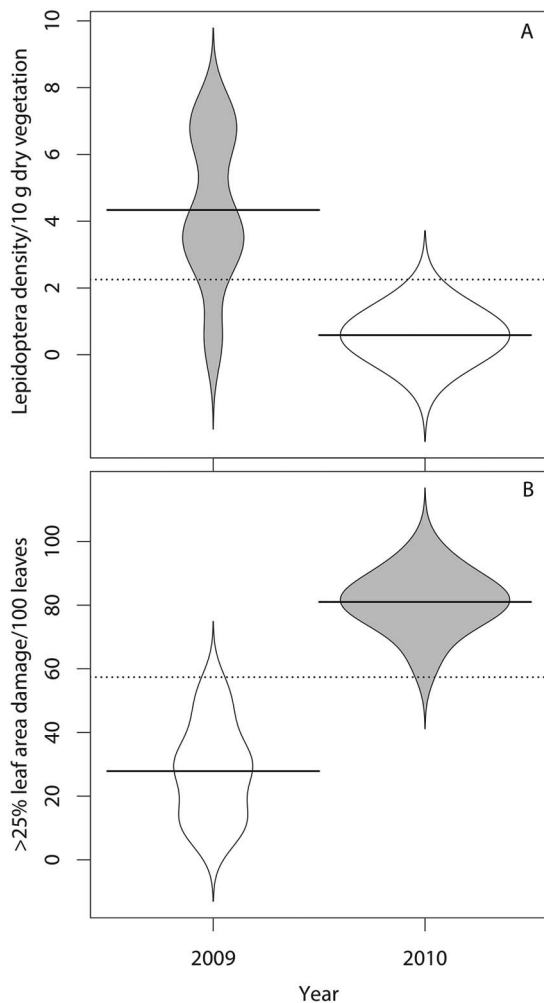
Fig. 6. (A) Lepidoptera density (number/10 g dry leaf material) and (B) number of leaves with substantial leaf damage (number of leaves with >25% leaf area damage/100 leaves) for exposed oak branches between 2009 and 2010. Although, the theoretical density shape of the Lepidoptera bean plot extends below 0, and the leaf damage plot extends below 0 and to 120, we note the spread of data does not exceed 0, for both beans, and 100 for the leaf damage bean. Color scheme indicates a significant difference between pairs, based on a Wilcoxon signed-rank tests for Lepidoptera density $w_{18} = 73$, $p < 0.01$ and leaf damage, $w_{18} = 0$, $p < 0.01$.

tested. Nonetheless, the strong between-year difference we found in herbivory suggests that the relationship between bird migration and insect abundance was severed by the extreme

spring temperature, which resulted in an apparent breakdown of ecosystem regulating services provided by migratory birds.

Food availability and accessibility are two mechanisms that influence synchrony of spring migratory birds with tree phenophases at stopover locations (Graber and Graber 1983, McGrath et al. 2008, Wood et al. 2012). In an Illinois woodland, spring migratory wood-warbler habitat use was coincident with the abundance of Lepidoptera larvae (Graber and Graber 1983), and in an Arizona riparian area, spring migratory birds heavily predated arthropods that were abundant on flowering Honey Mesquite (*Prosopis glandulosa*; McGrath et al. 2008). In our system, black oak trees had far higher insect densities during the flowering and emerging leaf phases than during subsequent phenophases. Insect emergence and abundance during the flowering and emerging leaf phenophases of oaks coincides with a period of high plant palatability, prior to strong increases of chemical compounds (Forkner et al. 2004). This high abundance of insects underscores the importance of timing of spring migratory bird arrival at stopover sites when both Lepidopteran and Hemipteran prey densities appear to be at their peak for the spring season. Moreover, we found Lepidoptera larvae were significantly larger on black oak flowers than on leaves, providing more evidence to the importance of the oak flowering phenophase to wood warblers (Wood and Pidgeon 2015). In addition to Lepidoptera larvae, migrants appeared to predate Hemiptera nymphs during the flowering and leaf-out time of oaks. During this development stage, the nymphs are less mobile than as adults and likely are a valuable food resource for birds (D. Young, *personal communication*). These results support those from Arizona, where Hemipterans were an important food resource for spring migrating Nashville Warblers (*Oreothlypis ruficapilla*; McGrath and van Riper III 2005). Our methodology did not quantify the effect of Hemiptera feeding (i.e., sucking), and thus it is possible that we underestimated the vegetation damage caused by the spring insect community at our black oak savanna location. In addition to food availability, the accesibility of insects for migrant gleaners was greatest in a Wisconsin decidous forest during the early spring when short leaf petioles

and the location of flowers on branches made them physically accessible (Wood et al. 2012). Taken together, synchronization of migratory bird arrival at stopover sites with peak food abundance and accessibility likely benefits refueling rates (Graber and Graber 1983) and ultimately positively affects migration success (Moore and Kerlinger 1987).

Migratory birds departing their wintering grounds in the tropics have seemed unable to detect climatic and phenological conditions on their temperate stopover and breeding grounds and thus rely mainly on endogenous (Holberton and Dufty 2005, Tonra et al. 2011) and exogenous cues (Studds and Marra 2011, McKellar et al. 2013) at wintering locations to initiate departure. We observed that the Palm and Yellow-rumped Warblers, which are shorter-distance migrants, arrived two weeks earlier in the warm year, but still likely missed the peak of food availability by nearly two weeks. The Tennessee Warbler, which is a long-distance migrant, arrived at similar times in 2009 and 2010, suggesting that for long-distance migratory birds any adjustment in arrival date is a gradual process, unlikely to respond to extremes in a given year (Hurlbert and Liang 2012). It has been suggested that for every 1°C increase in temperature in eastern North America, the phenology of common lilac (*Syringa vulgaris*), a proxy for broad plant phenological patterns, advances by three days (Marra et al. 2005). Yet, the median capture dates for migratory birds at bird banding stations has advanced only one day for every 1°C increase in temperature (Marra et al. 2005), suggesting an increasing phenological mismatch between plant phenology and bird migration. In our study, temperatures were approximately 8°C warmer in the early spring of 2010 than at the same time in 2009. As a result, oak tree phenology (and presumably insect phenology) was nearly 30 days earlier in 2010, which is similar to the predicted 24 day mismatch based on projections made by Marra et al. (2005). This is concerning because record hot spells are predicted to become more pronounced in temperate regions of the Northern Hemisphere (Meehl and Tebaldi 2004), potentially exacerbating mismatch between food resource phenology and bird migration at stopover sites during abnormally warm springs. Our findings suggest that migratory birds—particu-

lary long distance migrants—will likely be unable to adjust their migration timing to match peak food availabilty at stopover sites during record early springs, which could negatively affect migratory bird body condition.

While the differing bird abundance patterns we witnessed in a warm year compared to an average year are clear indications that birds shifted their behaviors and habitat use in response to the altered local phenology, it is unknown whether such mismatch events at stopover sites have broader population-level effects. There are, however, clear links between conditions migratory birds experience on the wintering grounds with breeding success (Webster et al. 2002, Norris et al. 2004). Thus, it is highly plausible that conditions migratory birds experience at stopover sites are also linked to breeding season outcomes (Sandberg and Moore 1996). Yet, this remains unclear. Nevertheless, the fitness contribution of stopover sites will likely become increasingly unpredictable among years as weather exhibits more extreme variability (Winkler et al. 2014). This variability may lead to greater mortality during migration (Newton 2007), to different spatial patterns of migration (Streby et al. 2015), or to lower reproductive effort (e.g., number of eggs laid; Winkler et al. 2002). Therefore, in addition to understanding the relationship between conditions a migratory bird experiences on the wintering grounds and their breeding season success, our results suggest that quantifying environmental conditions and bird fitness at stopover sites may provide further insights into the effects of extreme weather and climate change on avian populations.

Birds reduce insect herbivores during the breeding and wintering periods, which benefits plant growth and ecosystem function (e.g., Marquis and Whelan 1994, Van Bael et al. 2003, Kellermann et al. 2008). Our study extends the findings from the stationary periods of the annual cycle by describing important regulating services that migratory birds provide during spring stopover when late winter and early spring temperatures were similar to the long-term average. Further, we provide empirical evidence that extremely warm spring temperatures altered linkages between migratory birds and their invertebrate prey, which likely resulted in a disruption of the delivery of ecosystem

regulating services that migratory birds provide.

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