COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Detecting mismatches of bird migration stopover and tree phenology in response to changing climate

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Abstract Migratory birds exploit seasonal variation in resources across latitudes, timing migration to coincide with the phenology of food at stopover sites. Differential responses to climate in phenology across trophic levels can result in phenological mismatch; however, detecting mismatch is sensitive to methodology. We examined patterns of migrant abundance and tree flowering, phenological mismatch, and the influence of climate during spring migration from 2009 to 2011 across five habitat types of the Madrean Sky Islands in southeastern Arizona, USA. We used two metrics to assess phenological mismatch: synchrony and overlap. We also examined whether phenological overlap declined with increasing difference in mean event date of phenophases. Migrant abundance and tree flowering generally increased with minimum spring temperature but depended on annual climate by habitat interactions. Migrant abundance was lowest and flowering was highest under cold, snowy conditions in high elevation montane conifer habitat while bird abundance was greatest and flowering was lowest in low elevation riparian habitat under the driest conditions. Phenological synchrony and overlap were unique and complementary metrics and should both be used when assessing mismatch. Overlap declined

due to asynchronous phenologies but also due to reduced migrant abundance or flowering when synchrony was actually maintained. Overlap declined with increasing difference in event date and this trend was strongest in riparian areas. Montane habitat specialists may be at greatest risk of mismatch while riparian habitat could provide refugia during dry years for phenotypically plastic species. Interannual climate patterns that we observed match climate change projections for the arid southwest, altering stopover habitat condition.

Introduction

Migration is a complex phenomenon exhibited globally by thousands of species to take advantage of seasonal variation in resources. Many species, particularly small-bodied (6–12 g) passerine songbirds, cannot complete their migratory journey in a single flight (Moore and Kerlinger 1987). Long-distance migratory passerines must make regular stopovers to replenish fat reserves which are critical for meeting the intense physiological demands of migration (McWilliams and Karasov 2001; Seewagen and Guglielmo 2010).

Passerines must coordinate the timing of their migration and stopover to synchronize with the phenology of food resources along their migration route (Marra et al. 2005). Herbivorous invertebrates are a critical prey item for many species during stopover (Moore and Yong 1991; Carlisle et al. 2012), and their emergence is in-turn synchronized with the phenology of emerging leaves and flowers (Visser and Holleman 2001; Elzinga et al. 2007; Forkner

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et al. 2008). Selection of foraging substrates by migrants at stopover sites along the lower Colorado River in southwest Arizona was synchronized with flowering of willow and mesquite (Kellermann and van Riper 2015), and they preferentially foraged in mesquite trees with more flowers which contained a greater abundance of preferred invertebrate prey (McGrath et al. 2009). If the timing of stopover by migrants is not synchronized with plant phenology at stopover sites, they will also be out of synch with important food resources at those sites.

Phenological mismatch between migratory birds and seasonal resources due to climate change is resulting in population declines in some regions (Both and Visser 2001; Both et al. 2009; Thackeray et al. 2010). The directionality, magnitude, and duration of phenological responses to climate differ by species as well as latitude and biogeography (Parmesan 2007; Fontaine et al. 2009). Climate-driven changes in phenology can impact migration timing, speed, and route selection of birds (Both 2010; Tottrup et al. 2010) with carry-over effects later in the season (Norris and Marra 2007), including reduced reproductive success and population declines (Both et al. 2006; Rockwell et al. 2012). Therefore, knowledge of climate-related patterns of phenological mismatch across the large annual ranges encompassed by migratory bird species is important for their conservation (Faaborg et al. 2010). However, the phenology of migration and stopover habitat remains poorly understood in many regions.

The arid southwestern United States provide important stopover sites in western North America; however, most research has been limited to riparian habitats (e.g., Skagen et al. 2005; Paxton et al. 2008; Strode 2009), while the stopover habitat ecology of upland and montane habitats in this region remain relatively unknown. The Madrean region of southeastern Arizona is comprised of large isolated mountains recognized for their biodiversity, including many plant and animal species that are endemic, at the northern limits of their range, or only exist locally at high elevations (Whittaker and Niering 1964; Coblentz and Riitters 2004). The large elevational gradients of more than 2400 m in the "Sky Island" Mountains represent rare oases of forest and woodland habitats encompassed by the larger Sonoran Desert landscape. Climate change projections indicate increasingly hotter and drier conditions for the American Desert Southwest (Seager et al. 2007; Garfin et al. 2010). Significant upslope shifts in the range of vegetation communities in response to climate change and variation have already been documented in arid mountain regions of California and New Mexico (Allen and Breshears 1998; Kelly and Goulden 2008), while greater winter precipitation in southeast Arizona since the 1970s is driving dramatic changes in ecological community composition (Brown et al. 1997). The potential for climate-driven stopover habitat loss along elevation gradients in the Madrean region (Brown et al. 1997; Sekercioglu et al. 2008) emphasizes the need for a better understanding of the current dynamics of avian stopover habitat ecology in the desert southwest.

The goals of our study in the Madrean Archipelago of southeastern Arizona were to (1) examine patterns of bird and tree phenology, (2) quantify potential phenological mismatch occurring between avian stopover and tree flowering in terms of phenological synchrony and overlap, and (3) assess potential influence of interannual climate variation during our study and how this relates to documented climate change. A fourth goal is described below.

Detecting phenological responses to climate can be sensitive to the analytical methodology used (Parmesan 2007; Miller-Rushing et al. 2008; Gullett et al. 2013). Therefore, we used two closely related but distinct metrics to assess mismatch: phenological synchrony and phenological overlap (Miller-Rushing et al. 2010). Both metrics are derived from the coincidence of the temporal distributions of two phenological events over time, rather than the commonly used metric of onset (e.g., first record for the year) which can yield biased assessment of species' phenological responses to climate (Miller-Rushing et al. 2008; Gullett et al. 2013). We use synchrony as a measure of temporal co-occurrence of particular phenophases of at least two species. Overlap is the shared area of the plotted distributions of these species phenologies. Overlap directly takes into account the magnitude of a species phenology, for example the percent of a tree that is flowering over time. Changes in synchrony, as well as magnitude will affect the degree of species overlap (Miller-Rushing et al. 2010). We used both synchrony and overlap metrics because, theoretically, two distributions could remain relatively synchronized in time from year to year (e.g., bird abundance and flowering peak at the same time), while the amount of overlap could change due to reductions in magnitude (e.g., lower bird abundance or less flowering in 1 year). Miller-Rushing et al. (2010) predicted that overlap of the phenology of a species and species comprising its habitat should decline as the difference in the mean event date of the phenophases increases. We are unaware of studies that have directly tested this prediction, therefore a fourth goal of our study was to test for this relationship between overlap and mean event timing of migratory bird and tree flowering phenology.

Materials and methods

Study sites

We established study sites in the Santa Catalina, Santa Rita, and Huachuca Mountain ranges, and in the Patagonia

Creek, Santa Cruz, and San Pedro River riparian corridors. These mountains were selected for their proximity to Tucson, Arizona, and their relative ease of access. Riparian areas were selected that had perennial surface water flow and contiguous reaches of cottonwood-willow woodlands at least 5 km long. One exception was Tanque Verde Wash in Tucson, which only had surface water flow during 2009 and 2010.

To select individual survey sites, we first reclassified Southwest ReGAP land cover maps (Lowry et al. 2005) into five vegetation types: riparian cottonwood-willow, mesquite woodland, oak-juniper woodland, pine-oak woodland, and montane conifer (see descriptions below), based on Whittaker and Niering (1964) and Nature Serve (Comer et al. 2003), using ArcGIS 9.3.1 (ESRI 2009). For oak-juniper, pine-oak, and montane conifer habitats, we next demarcated polygons of contiguous habitat and then identified polygons that met a series of criteria. Polygons needed to be within 500 m of an access road or trail and large enough to contain two point-line or "point count" transects (Reynolds et al. 1980) that were at least 1.25 km long and at least 500 m apart while remaining 500 m from all polygon boundaries. We then selected the largest polygon for each habitat type and the second largest polygon that was not bordering the first in order to assure better spatial coverage of each mountain. Next, we randomly selected "seed" points within each polygon and created point count transects (see below). Points were 250 m apart and at least 500 m from polygon edges.

We initially established two 10-point transects per polygon per habitat for oak-juniper, pine-oak, and montane conifer habitats. However, these habitat types are typically located in steep, rugged, and inaccessible mountain terrain and many of our randomly selected points were not accessible due to cliffs and canyons. These points were either moved to the nearest accessible trail or road or deleted if no access was possible in that area. Ultimately, we established 12 routes in each of these three habitats (4 per mountain range) with an average of eight points per route, comprising 99 total points in oak-juniper, 93 points in pine-oak, and 90 points in montane conifer. Ultimately, 40 % of points were located on maintained trails or dirt roads.

Mesquite woodland often borders riparian cottonwood-willow habitat in the American southwest. Our mesquite habitats were located out in the valleys, 20–30 km from the mountain ranges where the previous three habitats were located. Due to this flat and open terrain, we created one 20-point transect per polygon for mesquite and riparian habitats resulting in six mesquite and six riparian routes. Due to access and private land development (housing and cattle grazing) in mesquite habitat and large gaps in riparian forest, we limited route length, especially in mesquite. Thus, we ultimately established 63 mesquite points with an average of 11 points per route and 89 riparian points with 15 points per route on average. Our sites ranged in elevation from 675 to 2775 m with riparian being the lowest and montane conifer the highest.

Bird surveys and focal bird species

We performed 5-min variable-radius point counts at each point (Reynolds et al. 1980) and included all birds within 100 m of the point center. A team of five highly trained biologists surveyed all five habitat types during each survey day (2 routes each of oak-juniper, pine-oak, and montane conifer and one mesquite and riparian route), and observers rotated through sites and habitat types daily. We surveyed each point count route once every 10 days between 10 March and 15 May 2009 and 2010 for a total of eight surveys of each route. We did not survey during heavy rain or winds. We had reduced effort in 2011 between 10 March and 3 April; we surveyed one-third of upland routes, but all riparian routes.

We selected 10 focal species of migratory birds in the order Passeriformes that have been included in other studies in the region (Hutto 1985; Skagen et al. 2005; McGrath et al. 2009) and had sufficient numbers of detections for analyses (Table 1). All species are small-bodied, primarily insectivorous species that commonly forage by gleaning invertebrate prey from vegetation, and only Bell's Vireo (*Vireo bellii*), Lucy's Warbler (*Oreothlypisluciae*), and Blue-gray Gnatcatcher (*Polioptilacaerulea*) are known to breed in our study area, the rest are exclusively through-migrants (Poole 2005).

Tree phenology and focal tree species

We selected one focal tree species from each habitat type (Table 1). These predominant species were the most common, abundant, and representative of each habitat type (Whittaker and Niering 1964), and known to be an important substrate for migratory birds based on published literature (Hutto 1985; McGrath et al. 2009; Paxton et al. 2008; Strode 2009), expert opinion in the region, and personal observations (Kellermann, unpublished data). We estimated flowering phenology for deciduous and semi-deciduous trees and pollen cone (microstrobilus) production for conifers as they are pollen-producing floral structures, and we collectively refer to this phenophase across all focal tree species as "flowering". We surveyed 100 individual trees along each point count transect on each day of bird surveys and estimated their percent flowering relative to the 100 % potential for that individual (vanriper 1980). We recorded the phenology of the first 100 individuals encountered along each route. Individual trees were not marked, so the same individuals were not necessarily observed during each survey.

Table 1 Focal migratory bird and tree species in the Madrean Archipelago, Arizona, USA

	Focal species	Status	Habitat types
Bird	Bell's Vireo (*Vireo bellii*)	BM	ME, RI
	Ruby-crowned Kinglet (*Regulus calendula*)	TM	MC, PO, OJ, RI
	Black-throated Gray Warbler (*Setophaga nigrescens*)	BM	OJ
	Hermit Warbler (*Setophaga occidentalis*)	TM	MC, PO
	Townsend's Warbler (*Setophaga townsendi*)	TM	MC, PO
	Yellow-rumped Warbler (*Setophaga coronata*)	TM	MC, PO, OJ, RI
	Orange-crowned Warbler (*Oreothlypis celata*)	TM	MC, OJ, RI
	Lucy's Warbler (*Oreothlypis luciae*)	BM	ME, RI
	Wilson's Warbler (*Cardellina pusilla*)	TM	ME, RI
	Blue-gray Gnatcatcher (*Polioptila caerulea*)	BM	OJ, ME
Tree	Douglas-fir (*Psuedotsuga menzeisii*)		MC
	Silver-leaf oak (*Quercus hypoleucoides*)		PO
	Arizona oak, Emoryoak (*Quercus arizonica, Q. emoryii*)		OJ
	Velvet mesquite (*Prosopis vetulina*)		ME
	Gooding's willow (*Salix gooddingii*)		RI

Bird species were classified as locally breeding migrants (*BM*) or through-migrants (*TM*) which do not breed in the study region. Habitat types for bird species represent those where at least 5 % of annual survey detections occurred. Tree species are representative of habitat types: montane conifer (*MC*), pine-oak (*PO*), oak-juniper (*OJ*), mesquite (*ME*), and riparian (*RI*)

Climate

We assessed winter (1 December–14 March) and spring (15 March–15 May) climate conditions during the 3 years of our study using local ground-based remote automated weather stations (RAWS; NOAA 2013). Weather stations ranged in elevation from 705 to 2512 m with a mean of 1232 m (Fig. 1). Weather variables we analyzed were mean daily precipitation during winter and mean daily minimum air temperature per 10-day period of bird surveys. We did not include spring precipitation as a variable because our sites received extremely little to no precipitation during the spring survey season. We used data from weather stations within the elevational band encompassed by individual point count locations within each habitat type to calculate mean daily minimum spring temperatures per survey period.

Analysis

We used generalized linear mixed-effects models (GLMMs) to examine patterns of relative migrant abundance and percent tree flowering with mean birds per point per survey period and mean percent flowering per transect per survey period as dependent variables, respectively, year and habitat type as fixed effects, and mountain range, habitat, and transect as hierarchically nested random effects using a quasi poisson error distribution. We also used GLMMs to test for interannual differences and elevational trends in winter precipitation and spring temperature with weather station as a random factor.

To assess phenological synchrony of avian stopover with tree flowering, we used proportional migrant abundance as the dependent variable. We calculated proportional migrant abundance as the proportion of detections for each bird species made in each habitat type per 10-day survey period out of the total number of detections for that species across all habitats each year, assuming that species could potentially select any habitat for stopover. We used this proportional value as the dependent variable for bird phenology because it accounts for interannual variation in abundance (Kellermann and van Riper, in review). We used binomial generalized linear models (GLMs) to assess the linear relationship (phenological synchrony) of proportional migrant abundance with percent tree flowering.

We calculated phenological overlap as the definite integral of the area shared by the response curves of proportional migrant abundance and percent tree flowering per year for all focal birds within the habitats within which at least 5 % of their annual detections occurred (Table 1). We assessed differences in overlap among years and habitat types and the relationship between overlap and the difference in the mean timing of these phenological events (Miller-Rushing et al. 2010), which we calculated as the absolute difference between the mean date across all individual bird detections within a habitat type of each species per year and the mean date across all days each tree species was documented flowering, using GLMs.

All analyses were performed in program R 2.15.1 (2012). We ran GLMMs with the nlme package in program R.
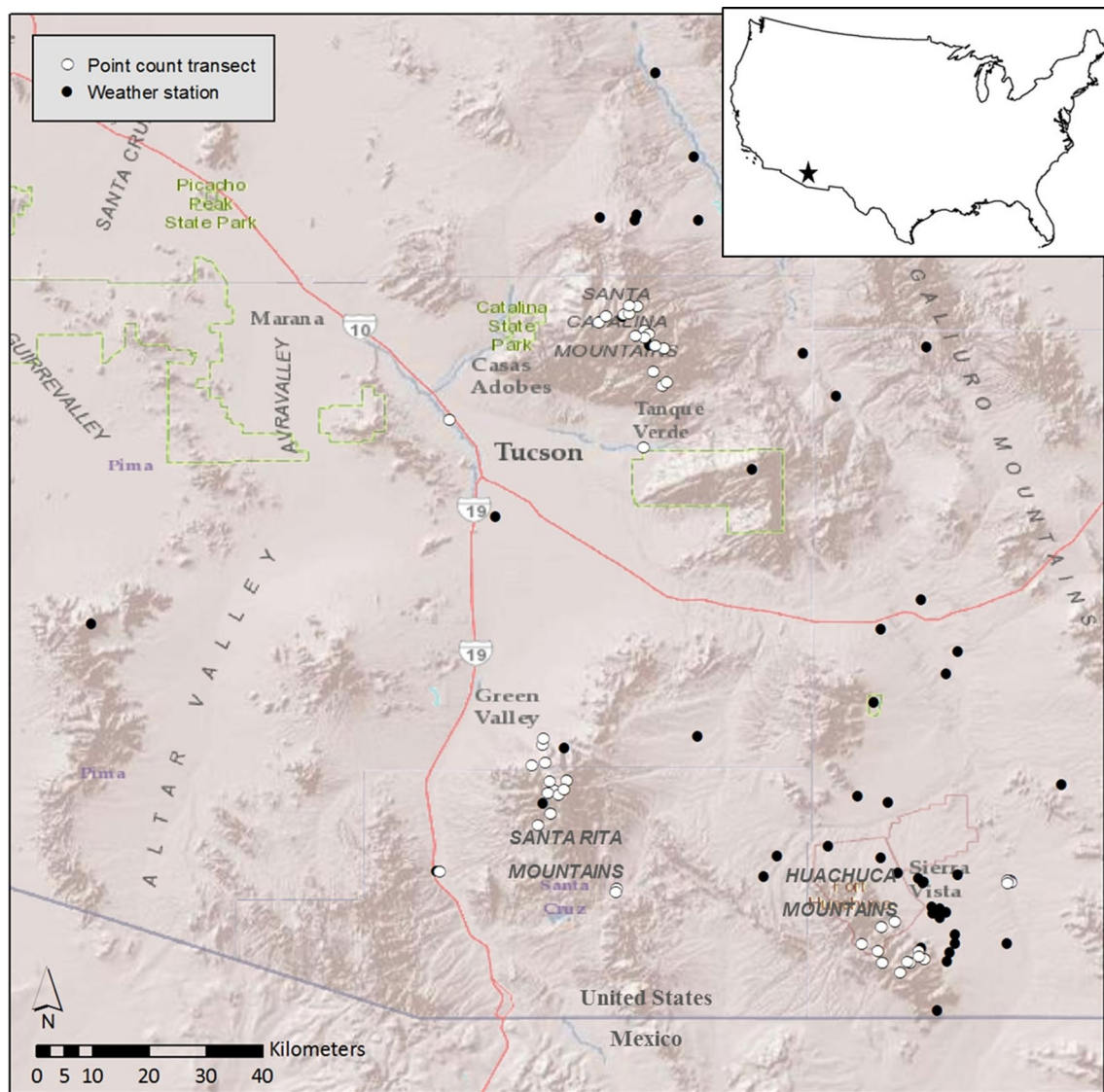
Fig. 1 Study region of the Madrean Sky Island Mountains in southeast Arizona where spring bird migration and tree flowering were surveyed along point count transects and winter weather conditions at ground-based weather stations in 2009–2011

Results

Climate

Winter daily precipitation was different among all years ($F = 118$, $df = 2$, $P < 0.0001$), with the greatest in 2010 (1.48 ± 0.1 mm), the lowest in 2011 (0.24 ± 0.03 mm) and an intermediate amount in 2009 (0.55 ± 0.04 mm). Total winter precipitation in 2009, 2010, and 2011 was 1790.4 mm, 4245.3 mm, and 806.3 respectively, and much of this precipitation fell as snow at high elevations, where total snowfall was far greater in 2010 (1090 mm) than 2009 (100 mm) or 2011 (355 mm). Winter precipitation was not significantly different across the elevational gradient

($F = 0.09$, $df = 1$, $P = 0.76$). Minimum daily spring temperatures were lower in 2010 (5.8 ± 0.1 °C) than 2009 (7.8 ± 0.1 °C) and 2011 (7.9 ± 0.1 °C). Minimum temperature decreased with increasing elevation ($F = 13$, $df = 1$, $P < 0.0001$).

Bird abundance and tree flowering

Relative abundance of all focal bird species depended on year and habitat (Fig. 2). Relative abundance was different among years for all species except Bell's Vireo; it was lowest in 2010 in 70 % of focal species and was highest in 2011 for two species, orange-crowned warbler and yellow-rumped warbler, and there was an interaction of year with

Fig. 2 Mean relative abundance of migratory birds (birds per survey point) and percent tree flowering (±1SE) during spring over 3 years in five habitat types, montane conifer (*MC*), pine-oak (*PO*), oak-juniper (*OJ*), mesquite (*ME*), and riparian cottonwood-willow (*RI*) which span over 2000 m of elevation in the Sky Island Mountains of southeastern Arizona
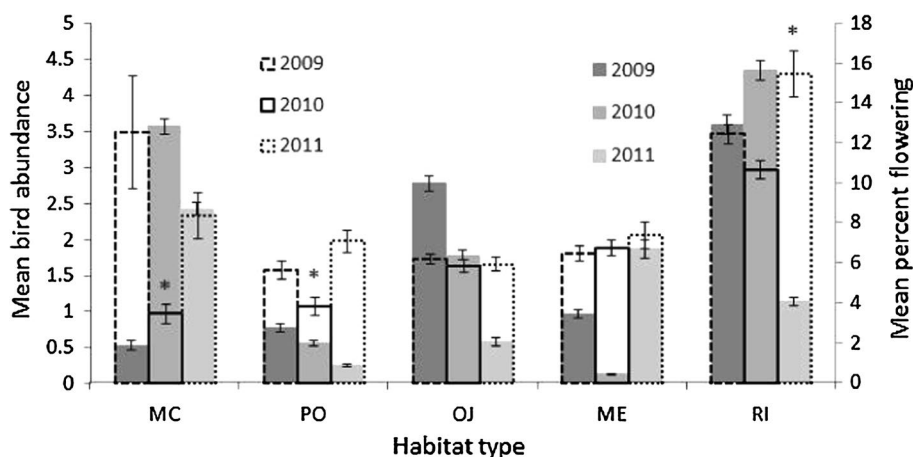
habitat ($F = 2.34$, $df = 8$, $P = 0.008$), with the greatest interannual fluctuations in montane conifer and riparian habitats, while abundance remained relatively consistent in mesquite and oak-juniper (Table 2). Tree flowering also varied among years across all focal tree species and was greatest in 2010 for Gooding's willow, Emory and Arizona white oak, and Douglas-Fir; lowest in 2011 for Gooding's willow, Emory and Arizona white oak, and silver leaf oak, and lowest in 2010 for velvet mesquite (Table 2; Fig. 2). Flowering of all tree species increased with increasing minimum temperatures except Gooding's willow, which had a negative relationship with spring temperature (Table 2).

Phenological synchrony

Proportional abundance of migratory birds within habitat types was highly synchronized with tree flowering in most years (e.g., Fig. 3) for all focal bird species, except Bell's Vireo (Table 2), and this relationship was positive for all species except ruby-crowned kinglet (Table 2). Proportional abundance increased with mean minimum temperature per period (Fig. 4) for all species except ruby-crowned kinglet, while black-throated gray warbler and blue-gray gnatcatcher both had negative interactions of tree flowering and spring temperature (Table 2).

Phenological overlap

Overall, we found a high degree of phenological overlap of migratory birds with the flowering of tree species across habitat types. Overlap was nearly 60 % lower in 2011 (0.96 ± 0.14, $z = 6.22$, $P < 0.0001$) than 2009 (1.53 ± 0.24) and 2010 (1.48 ± 0.26). Overlap in riparian habitat was almost twice that of all other habitat types (2.5 ± 0.3, $z = 6.6$, $P < 0.0001$), and there was a year by habitat interaction (Fig. 5). Overlap was lower in 2010 than both 2009 and 2011 in montane conifer ($z = 3.0$, $P = 0.004$) and mesquite habitat ($z = 3.77$, $P = 0.0006$).

Overlap was also lower in 2010 than 2009 in pine-oak habitat ($z = 2.79$, $P = 0.004$), and lower in 2011 than 2009 and 2010 in riparian ($z = 3.43$, $P = 0.03$), oak-juniper ($z = 5.0$, $P = 0.005$), and pine-oak habitats ($z = 3.77$, $P = 0.005$). Overlap was greater for species that breed in the Madrean Sky Island mountains (1.66 ± 0.2) than through-migrant species (1.16 ± 0.1, $P = 0.0003$).

Overlap and event timing

Overlap declined with increasing difference in mean event timing of bird migration and tree flowering ($p < 0.0001$, Fig. 6). Although overlap decreased with increasing difference in event timing in all habitat types, this relationship was steepest and only significant in riparian habitat ($\beta = -0.04$, $P = 0.02$, Fig. 6).

Discussion

The phenology of migratory birds and tree flowering at stopover sites in the Madrean Sky Island Mountains varied significantly over the 3 years of our study and across five habitat types, with complex year by habitat interactions. Bird migration showed strong phenological synchrony and overlap with tree flowering but varied among years and habitats in relation to interannual and elevational differences in climate. The separate metrics of phenological synchrony and overlap revealed unique and complementary insights into phenological relationships between birds, tree flowering, habitat and interannual climate conditions. For example, there were instances where peak bird abundance and flowering intensity were synchronized, while overlap was, however, greatly reduced due to lower bird abundance or flowering intensity in a given year (Fig. 3a). In other instances, reduced overlap was the result of phenological asynchrony (Fig. 3b). Therefore, phenological studies need to incorporate metrics of both synchrony and overlap when assessing potential phenological mismatch.

Table 2 Mean relative bird abundance and percent tree flowering during spring migration, 10 March–15 May, 2009–2011 (±1SE) in the Madrean Sky Islands, Arizona; the generalized linear model coefficients of proportional bird abundance with tree flowering (*Flower*), mean minimum daily temperature per 10-day survey period (*TMIN*), and their interaction; and GLM coefficients of tree flowering with TMIN

	Species	2009	2010	2011	*P*	Flower	TMIN	Interaction
Bird	Bell's Vireo	0.15 (0.01)	0.15 (0.01)	0.14 (0.01)		0.03	3.1***	
	Black-throated Gray Warbler	0.22[a] (0.01)	0.18[b] (0.01)	0.2 (0.01)	**	15.28***	7.17	−3.88**
	Blue-Gray Gnatcatcher	0.07[a] (0.01)	0.11[b] (0.01)	0.11[b] (0.01)	***	13.04	8.64*	−3.45*
	Hermit Warbler	0.15[b] (0.05)	0.02[a] (0.01)	0.16[b] (0.04)	***	0.46***	3.99**	
	Lucy's Warbler	0.17[b] (0.05)	0.06[a] (0.01)	0.15[b] (0.02)	*	0.12[1]	2.16**	
	Orange-crowned Warbler	0.03[a] (0.004)	0.01[b] (0.003)	0.09[c](0.01)	***	0.33*	5.01***	
	Ruby-crowned Kinglet	0.45[a] (0.04)	0.31[b] (0.03)	0.36[b] (0.04)	**	−0.1*	−1.36*	
	Townsend's Warbler	0.17[b] (0.05)	0.06[a] (0.01)	0.15[b] (0.2)	*	0.28*	4.94***	
	Wilson's Warbler	0.22[b] (0.02)	0.12[a] (0.01)	0.24[b] (0.02)	***	0.4***	8.54***	
	Yellow-rumped Warbler	0.71[a] (0.07)	0.53[b] (0.04)	0.88[c] (0.08)	***	0.65***	1.12*	
Tree	*Salix gooddingii*	12.9[a] (0.5)	16.2[b] (0.5)	4.1[c] (0.2)	**		−2.88***	
	Prosopis vetulina	11.4[b] (0.8)	0.9[a] (0.2)	13.6[b] (1.0)	***		4.0***	
	Quercus arizonica, Q. emoryii	6.4[a] (0.4)	6.7[b] (0.3)	2.2[c] (0.2)	**		2.93***	
	Quercus hypoleucoides	7.7[a] (0.5)	0.9[b] (0.1)	0.1[c] (0.02)	***		2.01***	
	Psuedotsuga menziesii	4.4[a] (0.2)	15.0[b] (0.4)	8.1[c] (0.3)	**		2.89***	

Superscript letters represent significantly different years with alpha level: [1] $P < 0.01$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 3 Phenological synchrony and overlap between proportional migrant abundance (*solid lines*) and mean percent flowering (*dashed lines*) for two focal bird and tree species, **a** Black-throated Gray Warbler (*BTYW*) and Arizona and Emory oak and **b** Yellow-rumped Warbler (*YRWA*) and *Salix gooddingii* (*SAGO*) during eight 10-day survey periods in 2009 (*top panels*), 2010 (*middle*), and 2011 (*bottom*)
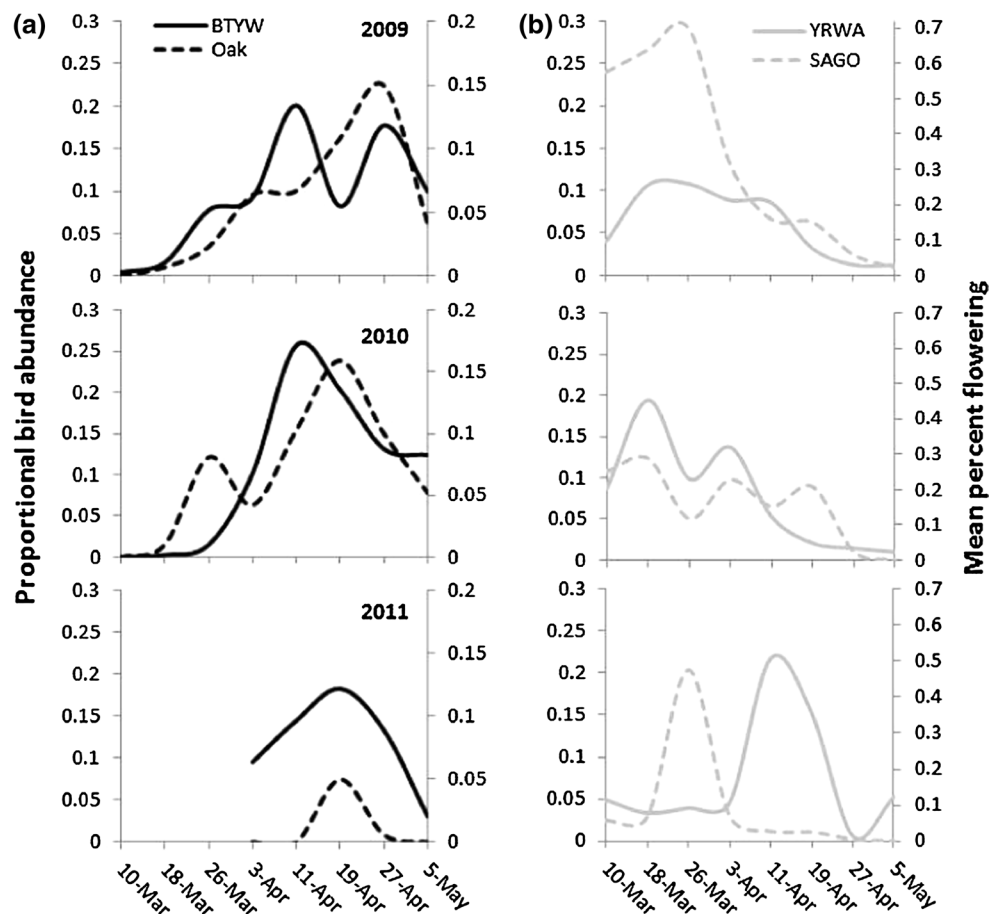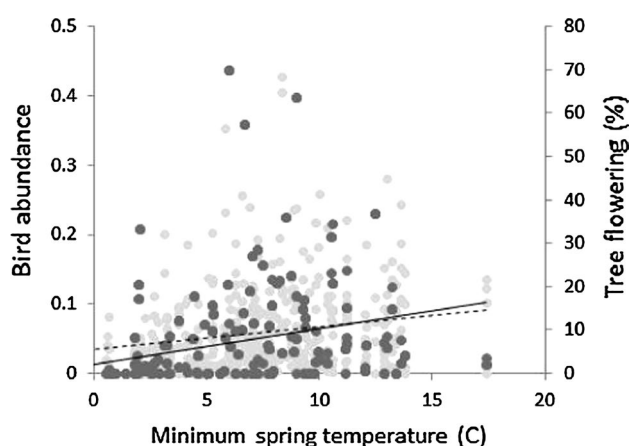
Fig. 4 Generalized Linear Models (GLMs) of relative migratory bird abundance(*dark dots*, *solid line*) and percent of tree flowering (*light dots*, *dashed line*) relative to minimum temperature during spring migration 2009-2011 across five habitat types in the Madrean Ski Islands, Arizona
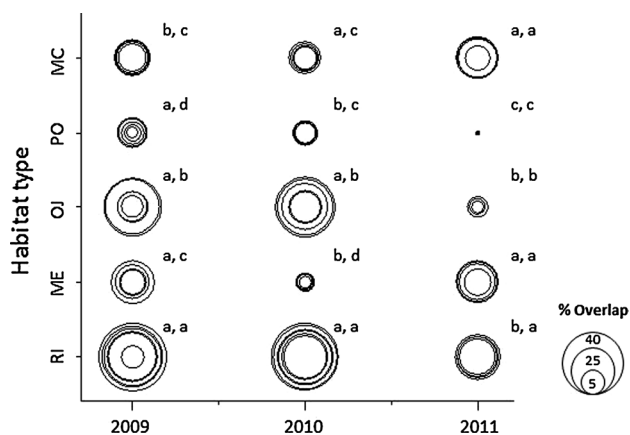

Fig. 5 Interactive effects of habitat type and year on overlap of migrant abundance and tree flowering during spring migration in montane conifer (*MC*), pine-oak (*PO*), oak-juniper (*OJ*), mesquite (*ME*), and riparian (*RI*) habitats. Each *circle* represents the overlap between each focal bird species and the focal tree species of each habitat type we assessed it in as shown in Table 1, resulting in 24 *circles*. The *size of the circle* indicates the amount of overlap. Due to overlay, not all circles are visible. The first *superscript letter* represents significant differences among habitats within years while the second indicates differences among years within habitat

Fig. 6 GLMs of percent overlap of proportional migrant abundance and percent tree flowering relative to the difference between mean date of migrant detections and peak tree flowering date for each focal bird and focal tree species combination in riparian (*thick gray line*), mesquite (*black dashed line*), oak-juniper (*black dotted line*), pine-oak (*thin black line*), and montane conifer (*gray dotted line*) habitats of the Madrean Archipelago, Arizona, USA during spring migration, 10 March to 15 May 2009–2011

We also found that phenological overlap generally declined with increased difference in mean event date, as predicted by Miller-Rushing et al. (2010). However, the strength of this trend was not consistent across habitat types. The strongest negative trend was for riparian habitat, with the other upland habitats showing more moderate declines. Riparian areas provide oases in arid regions (Skagen et al. 2005) where perennial surface waters may support mo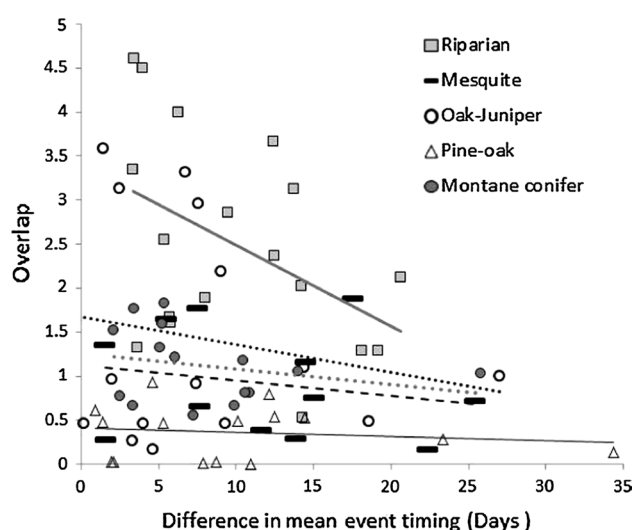re diverse vegetation communities relative to many upland habitats, and thus be more likely to have vegetation in flower that can support invertebrate prey. We only measured the phenology of Gooding's willow at our riparian sites. Migrants can shift their foraging substrate use at a site over the course of the migration season (Kellermann and van Riper 2015). Therefore, it is possible that migrants continue to use riparian areas regardless of their timing because they can shift to other, although potentially suboptimal, species. The increase of migrant abundance in riparian habitat under the dry conditions of 2011 suggests that birds may shift to riparian habitats to escape drier upland habitats (Fig. 2). Meanwhile, some migrants continue to select upland habitats in years where conditions are poor at relatively consistent times, but in lower numbers resulting in lower peaks. Therefore, overlap may change far more than mean event date. The ability of birds to shift to different substrate species or different habitat types altogether depends on their level of phenotypic plasticity (Studds and Marra 2011). Habitat specialists are of particular conservation concern (Julliard et al. 2004; Clavel et al. 2010), as are montane species (Şekercioğlu et al. 2008; La Sorte and Jetz 2010) and migratory species that do not show a response to climate change (Møller et al. 2008). Increased abundance and thus competition in riparian areas when birds shift to this habitat could decrease food abundance and individual fitness (Moore and Yong 1991; Moore et al. 1995).

We found that patterns of migration, tree flowering, and phenological overlap partially depend on interactions

of habitat and elevation with interannual climate conditions (Coblentz and Riitters 2004; Garfin et al. 2010). In low elevation riparian habitats, flowering was lowest in 2011, our driest year, yet it had the greatest abundance of migrants (Fig. 2). The resulting reduction in overlap that year is partly driven by water limitation, which can reduce willow growth and productivity (Lindroth and Bath 1999). Precipitation-driven reductions in floral resources could have significant impacts on the abundance and distribution of invertebrate prey (Fabina et al. 2010; Gonzalez-Megias and Menendez 2012). High abundance of migrants in riparian habitats in 2011 suggests that the presence of perennial surface water and greater relative humidity may create refugia in arid regions for migratory birds during dry or extreme conditions (Skagen et al. 2005), although this can have a cost of increased competition (Moore and Yong 1991; Shochat et al. 2002). Climate change projections for the American southwest and arid lands globally call for more years like we witnessed in 2011, increasing temperatures, higher frequency of extreme warm years, and severe droughts within years to decades (Seager et al. 2007). These dynamics are already driving shifts in ecological community composition and dynamics with important implications for the type, distribution, and quality of stopover habitats (Brown et al. 1997; Parmesan 2007; Garfin et al. 2013).

In contrast to riparian habitats, high elevation montane conifer habitats had the lowest phenological overlap in 2010, our wettest year with the coldest temperatures at high elevations. Despite the high pollen cone production by Douglas-fir, bird abundance was extremely reduced. A widely distributed tree species, Douglas-fir may have actually benefitted from the cold snowy El Niño conditions in 2010, as it is well adapted to montane climates (Eis 1973). However, cold snowy spring conditions may have drastically reduced the abundance of insect prey whose emergence can be strongly temperature limited (Altermatt 2012; Ellwood et al. 2012; Williams et al. 2012). Capable of tracking food availability (Rodewald and Brittingham 2007; McGrath et al. 2009; Strode 2009; Carlisle et al. 2012), and well adapted to climate conditions of high elevation and northern latitude forests (Martin 2007), montane birds such as Hermit and Townsends Warblers may have avoided these habitats and the Madrean region altogether in search of more optimal stop-over conditions (Buler et al. 2007; Kellermann and van Riper, in review). Together, these riparian and montane habitats may represent a gradient in ecological processes from water limitation on plants at low elevation to temperature limitation on insects in montane habitats, both potentially affecting prey for spring migrants (Martin 2007; Rangwala and Miller 2012). Furthermore, increased winter precipitation associated with regional climate change over the past four decades could

mean more years where high elevation sites do not provide suitable stopover habitat for montane species (Brown et al. 1997; Sekercioglu et al. 2008).

Relative to riparian and montane habitats, migrant abundance remained relatively consistent in mesquite and oak-juniper habitats although flowering intensity of oak and mesquite trees varied significantly among years. Three of the four focal migrant species that we examined in mesquite habitat also breed in the Madrean region and two of the five species in oak-juniper were local breeders. Overall, we found that these locally breeding species had greater overlap with tree flowering than through-migrant species. Most of these breeding species likely represent short-distance migratory populations which may experience more similar climate conditions between their breeding and wintering grounds than long-distance migrants (MacMynowski and Root 2007; Tottrup et al. 2010; Végvári et al. 2010). Furthermore, locally breeding species may have greater site fidelity than through-migrants that are tracking seasonal resources (Lehikoinen et al. 2004; Rodewald and Brittingham 2007; Paxton et al. 2008).

Phenological mismatch may reflect the conditions birds experienced on their wintering grounds. While photoperiod provides an initial cue that leads to the development of physiological, behavioral and morphological changes necessary for migration, these changes occur prior to the onset of migration and birds can adjust their spring departure based on local conditions they experienced during wintering. For example, low tropical precipitation and reduced food availability can delay spring departure for temperate breeding grounds (Studds and Marra 2011). However, phenology may be advanced on the breeding grounds relative to stopover or wintering sites and thus late arriving birds experience reduced productivity and fitness (Studds and Marra 2007). Some migrants are actually shortening their migration distances in response to longer breeding seasons and warming conditions on wintering grounds; however, this is not consistent across species (Smallegange et al. 2010). Several of the migrants we assessed, such as Yellow-rumped Warbler have large species ranges, can be facultative migrants, and therefore may be more responsive to interannual climate variation (Terrill and Ohmart 1984). Connectivity between wintering and breeding populations of migratory birds and the migration routes that connect them remain poorly understood.

While we found strong patterns of phenological synchrony and overlap between migratory birds and tree flowering at stopover sites in the Madrean Sky Islands, mismatch is also occurring. Mismatch, whether due to asynchronous phenology or reduced overlap from reductions in migrant abundance or percent tree flowering, was related to interannual variation in climate. Interannual variation in mismatch was also related to habitat type. High elevations

experienced increased mismatch under severe cold and snowy conditions while riparian and low elevation habitats were most impacted during periods of low precipitation. Reduced flower resources in some riparian species may be buffered by increased vegetation diversity and humidity due to greater year-round surface water availability. However, increased migrant abundance can increase competition and reduce food availability and fitness during stopover. Maintaining a diverse habitat mosaic across elevations will support the range of species plasticity and habitat specialization. Gaining greater understanding of population connectivity between breeding and wintering grounds and the stopover sites that link them in mountainous regions of the arid southwest is a priority for migratory bird conservation.

Author contribution statement JLK and CvR conceived of the research topic and developed the study design. JLK managed and performed field work and data collection. JLK performed data processing, management and analysis. JLK and CvR wrote the manuscript.

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