Carry-over effects of overwinter climate and habitat productivity on spring arrival of migratory songbirds at a northern stopover site

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Abstract

Reduced rainfall in tropical regions may impact the ability of temperate-breeding songbirds to prepare for and execute their spring migration. I used 34 years of bird banding data from Ontario to test for the presence of climate-induced carry-over effects from wintering areas on the body condition and migration timing of birds en route to breed in Canada. Using linear models, I found that overwinter habitat productivity was significantly negatively influenced by the El Niño Southern Oscillation (ENSO) in the overwintering ranges in 3 of 7 species, where conditions were drier during El Niño years as expected. However, there was no consistent effect of ENSO or overwinter habitat productivity on stopover body condition or spring arrival date in southwestern Ontario. Widespread and long-lasting carry-over effects were not observed, suggesting that songbirds may compensate en route such that negative signatures from dry winters are absent late in migration.

Acknowledgements

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Introduction

Long-distance migratory songbirds have always faced daunting challenges. On top of the physiological demands of preparing for and executing their biannual journeys of thousands of kilometers, and risks of travelling so far, they are now exposed to a myriad of anthropogenic threats and stressors across diverse geographical areas. The complexity of threats experienced throughout a bird's annual cycle complicates a full understanding of the reasons for widespread population declines in recent decades (Rushing et al., 2016). Major factors contributing to songbird declines include habitat loss, invasive predators, and migration mortality via collisions with windows and other structures (Longcore et al., 2012; Blancher, 2013; Machtans et al., 2013; Taylor & Stutchbury, 2016). However, despite extensive research by hundreds of scientists, we still do not fully understand how threats on the breeding grounds, wintering grounds, and/or during migration interact to limit populations (Latta et al., 2016) because of the logistical challenges of studying individual success across the annual cycle.

Global climate change has also emerged as a new threat that has begun to impact the breeding range, migration timing, and population dynamics of many migrants (Møller, 2013; Kirchman & Van Keuren, 2017; Zaifman et al., 2017; Cox et al., 2020). Studies have shown a general advancement of spring migration timing and arrival at breeding sites that can be attributed to the effects of climate change through warmer spring temperatures (Gordo, 2007; Usui et al., 2017). However, a bird's ability to adequately adapt their arrival at the breeding grounds to advancing spring conditions can be hampered (Mayor et al., 2017; Schmaljohann & Both, 2017) because for many long-distance migrants the onset of migration is under strong endogenous control (Both & Visser, 2001; Fraser et al., 2013). Birds across North America are experiencing an increasing mismatch between arrival at breeding areas and spring green-up (Mayor et al., 2017), and population declines have been observed in species that have not sufficiently advanced their spring migration schedules (Møller et al., 2008).

Long-distance migratory songbirds that breed in North America must also contend with changing climatic conditions during their annual 6-8 month stay in the tropics, which may have far reaching consequences for individuals. Future climate predictions for the tropics forecast an increased frequency of drought, less rainfall, and more severe climatic events (IPCC, 2014). One major influencer of worldwide patterns of temperature and precipitation is the El Niño Southern Oscillation (ENSO), an oceanic and atmospheric phenomenon. There is a clear relationship between the strength of an El Niño event and the extent of drought in tropical regions around the globe (Lyon, 2004). In the Neotropics, El Niño years generally result in drier conditions in the Caribbean, Central America, and northern South America while La Niña years generally result in wetter conditions in these regions (Holmgren et al., 2001). These patterns are consistent in northern South America, but less so in Central America and the Caribbean (Giannini et al., 2000; Chang et al., 2015; Hoyos et al., 2019; Moura et al., 2019). ENSO events are predicted to increase in frequency and intensity as climate change accelerates (Allan & Soden, 2008; Cai et al., 2014). Investigating a species' response to ENSO can be used as a proxy for understanding its broader vulnerability to the effects of climate change.

Temperature and precipitation patterns across space and time affect overwintering songbirds primarily through impacts to food resources which in turn impact body condition. In tropical overwintering habitats, habitat moisture and rainfall have been found to determine arthropod and fruit availability and, subsequently, body condition in Northern Waterthrush (*Parkesia noveboracensis*) (Smith et al., 2010), American Redstart (*Setophaga ruticilla*) (Studds & Marra, 2007), and Wood Thrush (*Hylocichla mustelina*) (McKinnon et al., 2015a). The abundance of arthropod prey for overwintering birds increases as soil moisture increases (Wilson et al., 2013; McKinnon et al., 2015a), and wetter habitats allow birds to maintain or improve their body condition over the winter (Marra & Holmes, 2001; Studds & Marra, 2007; Smith et al., 2010; Akresh et al., 2019). Rainfall in overwintering areas also influenced body condition of Prairie Warblers (*Setophaga discolor*), whereby birds retained pectoral muscle and body mass in wet winters, and lost mass and muscle in dry winters (Akresh et al., 2019). Experiments with direct or indirect food manipulation in overwintering areas have highlighted the roles of both food and moisture as key limiting factors for migratory birds during the winter. Ovenbirds (*Seiurus aurocapilla*) provided with food supplements during the winter improved body condition, while food-reduced individuals responded negatively, regardless of age or sex (Brown & Sherry, 2006). Removal experiments with American Redstarts allowed some birds to upgrade their winter territory from dry, low-quality habitat to wetter, high-quality habitat, and resulted in upgraded birds maintaining body mass over the winter compared to control birds in dry habitat which lost weight (Studds & Marra, 2005).

Climatic impacts to food resources on the wintering grounds are important not only for over-winter survival but also because birds must accumulate sufficient fat stores prior to initiating migration. Fat serves as the key fuel for migration and an insurance policy for food scarcity or adverse weather en route (Smith & Moore, 2005). In many areas of the Neotropics, this time period of fat accumulation is already a challenging time for birds because it coincides with the dry season (Studds & Marra, 2007), and arthropod and fruit abundance decrease as the dry season progresses (Wilson et al., 2013; McKinnon et al., 2015a). If food resources become increasingly scarce in some years due to ENSO’s influence on rainfall, birds may be forced to delay the initiation of spring migration. For example, American Redstarts that had their food supply experimentally reduced departed later on spring migration than control individuals (Cooper et al., 2015), whereas individuals that were experimentally upgraded to wetter habitat departed earlier on spring migration (Studds & Marra, 2005).

Poor body condition as a result of habitat drying may continue to impose a physiological or energetic handicap to a bird after migration begins. These so-called carry-over effects which arise in one point of the migratory life cycle may have long-lasting effects on survival and reproduction many months later, and even thousands of kilometers away (Harrison et al., 2011). Climatic effects associated with ENSO in tropical overwintering areas have been shown to carry-over to impact the migratory period. At the northern coast of the Gulf of Mexico, migrants were found to arrive at stopover sites in reduced energetic condition when El Niño events resulted in significantly drier conditions in their overwintering range (Paxton et al., 2014). In Central America, birds at a stopover site showed varying responses to ENSO, whereby frugivores displayed reduced body condition during El Niño years, but insectivores had inconsistent responses (Wolfe & Ralph, 2009). At a northern stopover site in south-central Canada, American Redstarts and Palm Warblers (*Setophaga palmarum*) arrived in better condition in springs preceded by a La Niña event (which was presumed to result in a wetter winter in their overwintering areas) than in springs following an El Niño event (González-Prieto & Hobson, 2013). Although these studies have found differing impacts, the general trend suggests that El Niño (drier) events in many areas of the tropics result in birds arriving to stopover sites in poorer condition.

Climatic and habitat-related conditions experienced on the wintering grounds also carry over to influence the timing of arrival at breeding sites and breeding success. Climatic variation (especially precipitation) in non-breeding habitats is an important driver of first-arrival-dates in trans-Saharan migrants, with birds arriving earlier in years with wet conditions in their non-breeding habitat and later when temperatures were high in non-breeding areas (Gordo et al., 2005). American Redstarts that overwintered in dry tropical habitats arrived to the breeding grounds later and had lower reproductive success than individuals that had occupied wet habitats (Marra, 1998; Norris et al., 2004). Kirtland's Warblers (*Setophaga kirtlandii*) were also found to arrive to their breeding grounds later, and had lower reproductive success, after winters with drier conditions in their non-breeding habitat (Rockwell et al., 2012). Furthermore, a variety of bird species overwintering in western Mexico that experienced wetter conditions during El Niño years had higher reproductive success the following summer (Nott et al., 2002). These results suggest that carry-over effects from occupying dry or wet winter habitat can persist throughout the entire spring migratory journey and even into the breeding season.

Drier and hotter environments limit the availability of insect and fruit resources, affecting the ability of overwintering migrants to prepare for, and initiate, spring migration (Strong & Sherry, 2000; Studds & Marra, 2007; McKinnon et al., 2015b). With future climate predictions for the tropics suggesting an increased frequency of dry, hot conditions, a key question is: will poor body condition as a result of habitat drying continue to impose a handicap to a bird after migration begins? Climatic effects on food availability, bird body condition, and migration departure decisions could carry-over to impact not only the migratory period, but also beyond into the subsequent reproductive season, potentially impacting the productivity of songbird populations and exacerbating population declines. Although negative carry-over effects during migration have been shown in a handful of studies, it is unclear how widespread these effects are geographically and taxonomically, and whether they persist into central-eastern Canada, a key migratory route.

Research objectives

In this study, I investigate the strength and consistency of climatic carry-over effects from wintering grounds in the Caribbean, Central America and South America on migration timing and body condition of songbirds passing into southern Ontario using a 34-year migration banding dataset. I investigated species' responses to the natural climatic fluctuations created by ENSO to understand how climate change on the wintering grounds could impact these species. Much of the research examining the impacts of climatic processes such as ENSO on migratory songbirds has focused largely on stationary stages in the breeding and overwintering periods (Sillett et al., 2000; Nott et al., 2002; Mazerolle et al., 2005; LaManna et al., 2012; García-Pérez et al., 2014). A few studies have examined the effects of ENSO on songbird migration at tropical and Gulf coast stopover sites (Wolfe & Ralph, 2009; Paxton et al., 2014) but similar studies are scarce at more northern latitudes (González-Prieto & Hobson, 2013) even though research has shown a link between tropical habitat dryness and arrival timing and body condition at northern breeding sites (Marra, 1998; Rockwell et al., 2012; González-Prieto & Hobson, 2013). To my knowledge, this is the first study in eastern Canada to relate wintering ground climate changes to the condition and migration timing of multiple bird species en route to breeding sites.

A variety of Neotropical migrants were chosen for this study to represent multiple songbird families (Parulidae, Turdidae, and Vireonidae), different wintering ranges, and multiple foraging guilds. Focal species were Yellow Warbler (*Setophaga petechia*), American Redstart, Black-throated Blue Warbler (*Setophaga caerulescens*), Ovenbird, Swainson's Thrush, Wood Thrush, and Red-eyed Vireo (*Vireo olivaceus*). I chose these species because recent migration tracking studies have identified more precise wintering ranges of the breeding populations which migrate through Ontario. For example, Red-eyed Vireo's wintering range comprises all of northern South America and Brazil, but tracking studies show that breeding populations near southern Ontario wintered only in the most northern part of this range (Callo et al., 2013). Using refined wintering ranges allows for a more accurate assessment of how climatic conditions experienced over the winter influence migratory timing and stopover body condition and is an approach that has not been used before for carry-over effect studies of multiple species.

To estimate annual differences in overwinter habitat productivity in each species' overwintering range (where higher productivity is assumed to represent wetter, food-rich conditions), I used the Normalized Difference Vegetation Index (NDVI). NDVI is derived from satellite imagery collected from Advanced Very High Resolution Radiometer (AVHRR) instruments (AVHRR/2 and AVHRR/3) (Pinzon et al., 2014). This index is a measure of vegetation productivity that is highly correlated with rainfall (Wang et al., 2003) and has been used to represent historical on-the-ground conditions experienced by birds over the winter (Saino et al., 2004; Wilson et al., 2011; McKinnon et al., 2015b; Graham et al., 2016).

I hypothesized that long-distance migrants will experience negative carry-over effects during spring migration after years that are characterized by late-season dry conditions on the wintering grounds. I predicted that:

1. ENSO (as represented by the Oceanic Niño Index) will be negatively correlated with habitat productivity (as represented by NDVI) for overwintering migrants in the tropics. El Niño events should generally be associated with drier conditions and therefore reduced NDVI, while La Niña events should be associated with wetter conditions and therefore higher NDVI.
2. The Oceanic Niño Index will be negatively correlated with bird body condition (El Niño events/drier conditions associated with poorer condition) but positively correlated with arrival date (El Niño events/drier conditions associated with later arrival).
3. Habitat productivity in overwintering areas will be positively correlated with body condition (more productive years associated with better condition) but negatively correlated with arrival date (more productive years associated with earlier arrival).

Methods

Study site and data

I used bird banding data from Long Point Bird Observatory (LPBO) in southern Ontario (Long Point Bird Observatory, 2018). Long Point is a sand spit on the north shore of Lake Erie in Norfolk County, southeast of the town of Port Rowan. LPBO provides an optimal study location as a corridor for migrants, has been in operation since 1960, and boasts over a million records. Only records from 1982-2015 were included in the analysis because the banding efforts prior to 1982 were less consistent, and the NDVI dataset to assess tropical habitat productivity is only available within this time period. April and May records were used in the analysis as this is the peak passage period of migrants, and data for the focal species included date and time of encounter, sex, age, wing chord, and weight. Other measures of body condition such as fat scores and pectoral muscle scores were not available. Records lacking either wing chord or weight measurements were excluded as these measurements were essential to calculate a size-correlated index of a bird's energy reserves (Labocha & Hayes, 2012). All recaptures were also excluded as these records are often for subsequent days from the initial encounter, and the body condition of these birds is not representative of 'arrival condition'.

A portion of records appeared to contain data entry errors, where a weight or wing chord measurement for a given bird was either far too high or too low to be feasible for that species. To avoid the inclusion of extreme outliers in the form of data entry errors, the data were filtered to standard ranges of weight and wing chord measurements. An outlier was identified as any weight or wing chord measurement for a given species (pooled from all available records in April and May that were not measurements of 0) beyond 1.5 times the interquartile range above the third quartile or below the first quartile. Between 96-99% of records fell within the standard ranges of each species. The number of available records for each focal species by year is summarized in Appendix A, including the ENSO classification for each year (i.e., El Niño event, La Niña event, or non-ENSO event).

Study species

To be considered a candidate species for this study, long-distance migratory songbird species must have been subject to migration tracking studies or stable isotope analysis to determine the primary wintering grounds of northeastern breeding populations, which pass through southern Ontario and Long Point. These migration tracking studies were completed either through fitting birds with miniature tracking devices or by examining the chemical signatures of stable hydrogen isotopes in bird feathers grown on the wintering grounds to determine the bird's general location when the feather was grown. The candidate species also had to be abundant at Long Point during migration to provide adequate statistical power. Only seven focal species were suitable for analysis. Of these, two overwinter in Central America (Wood Thrush and Ovenbird), two overwinter in the Caribbean (American Redstart and Black-throated Blue Warbler), and three overwinter in South America (Swainson's Thrush, Red-eyed Vireo, and Yellow Warbler). Range maps for the focal species' overwintering ranges were obtained from BirdLife International (BirdLife International and Handbook of the Birds of the World, 2017) and further refined based on migration tracking studies.

Wood Thrush

Wood Thrush have been experiencing significant, continent-wide declines in abundance (Evans et al., 2011) with Ontario breeding populations declining at an annual rate of -1.9%/year (95% credible interval = -2.6% to -1.1%) from 1970 to 2017 (Smith et al., 2019). In 2017, the Wood Thrush was added to Schedule 1 of Canada's Species at Risk Act as a threatened species, and it is also listed as a special concern species under Ontario's Endangered Species Act. Direct tracking of birds using archival light-level geolocators has shown that birds from breeding grounds in the northeastern part of their range (including southern Ontario) overwinter in eastern Honduras, Nicaragua, and Costa Rica (Stanley et al., 2015) (Figure 1). Wood Thrushes are ground foragers which feed largely on soil invertebrates, but they also consume fruit (Evans et al., 2011).

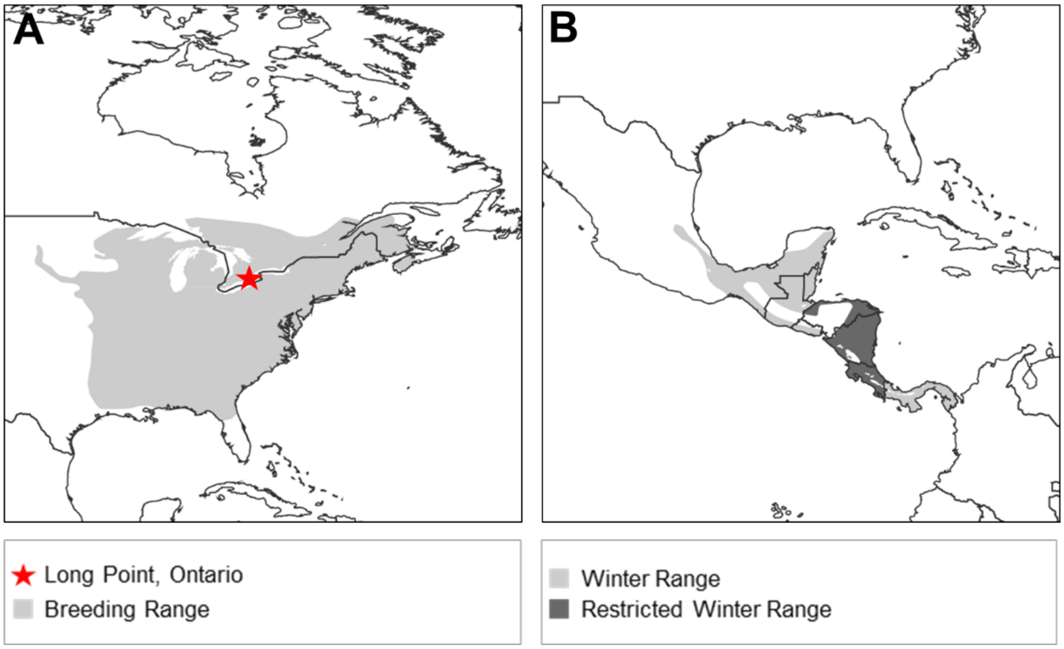

Figure 1: Wood Thrush breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by northeastern breeding populations.

Ovenbird

Ovenbirds are ground foraging birds which are omnivorous during the non-breeding season, feeding on insects and to a lesser extent on seeds (Porneluzi et al., 2011). Breeding Bird Survey data has shown an annual decrease of -0.5%/year (95% credible interval = -1.0% to -0.1%) in Ontario breeding populations from 1970 to 2017 (Smith et al., 2019). Direct tracking of Ovenbirds breeding in Saskatchewan and New Hampshire using archival light-level geolocators has shown segregation of eastern and western populations in non-breeding areas (Hallworth et al., 2015). All New Hampshire individuals overwintered in the central Greater Antilles and Saskatchewan individuals overwintered in Central America, but additional sampling locations are needed to determine exactly where the divide between eastern and western Ovenbird populations occurs (Hallworth et al., 2015). Limited band-recovery data connecting breeding and overwintering areas show that Ovenbirds south of southern Ontario spend the winter in Central America (Hallworth et al., 2015). Band-recovery data elsewhere in the Ovenbird's range also suggest that birds west of the Appalachians (including Ontario) overwinter in Central America, while birds east of the Appalachians overwinter in the Caribbean (Brewer et al., 2018).

Therefore, I assumed that birds arriving to Long Point would belong to the more western population and thus spend the winter in Central America and southern Mexico (Figure 2).

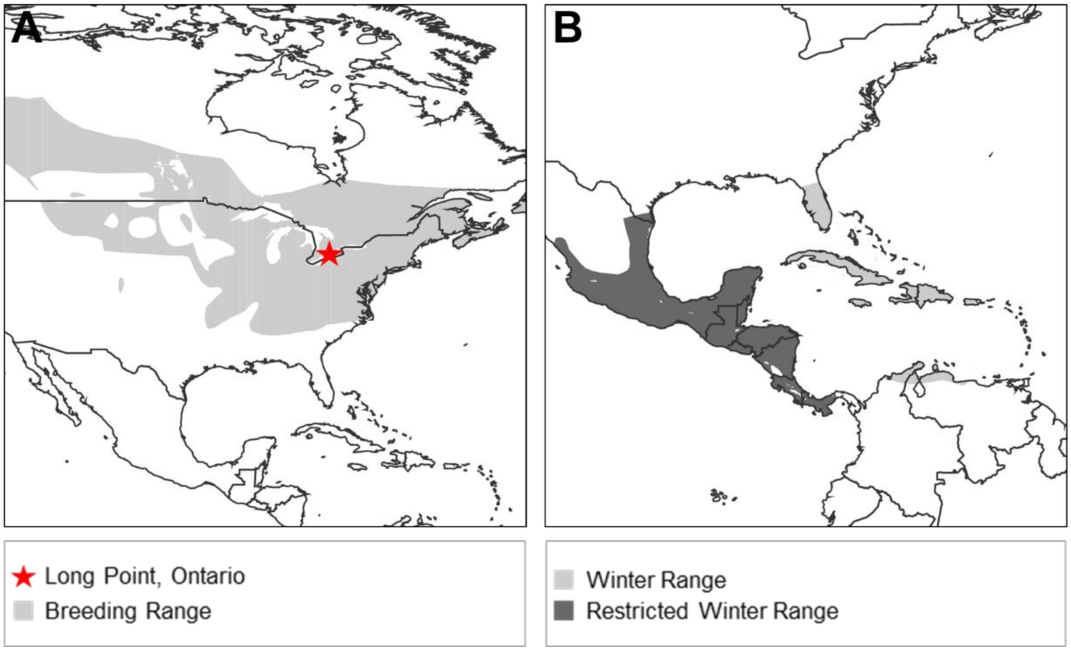

Figure 2: Ovenbird breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by central and western breeding populations.

American Redstart

American Redstarts are small insectivorous wood warblers that have been subject to many studies on seasonal interactions and carry-over effects from overwintering conditions (e.g., Norris et al., 2004; Studds & Marra, 2005; Wilson et al., 2011). Breeding Bird Survey data has shown an annual decrease of -0.4%/year (95% credible interval = -1.1% to 0.3%) in Ontario breeding populations from 1970 to 2017 (Smith et al., 2019). Through stable isotope analysis, it has been determined that northeastern populations likely overwinter in the Greater Antilles (Norris et al., 2006). Within the Greater Antilles, Cuba appears to be more strongly linked with midwestern breeding populations and consequently has been excluded from the overwintering range for this study (Figure 3).

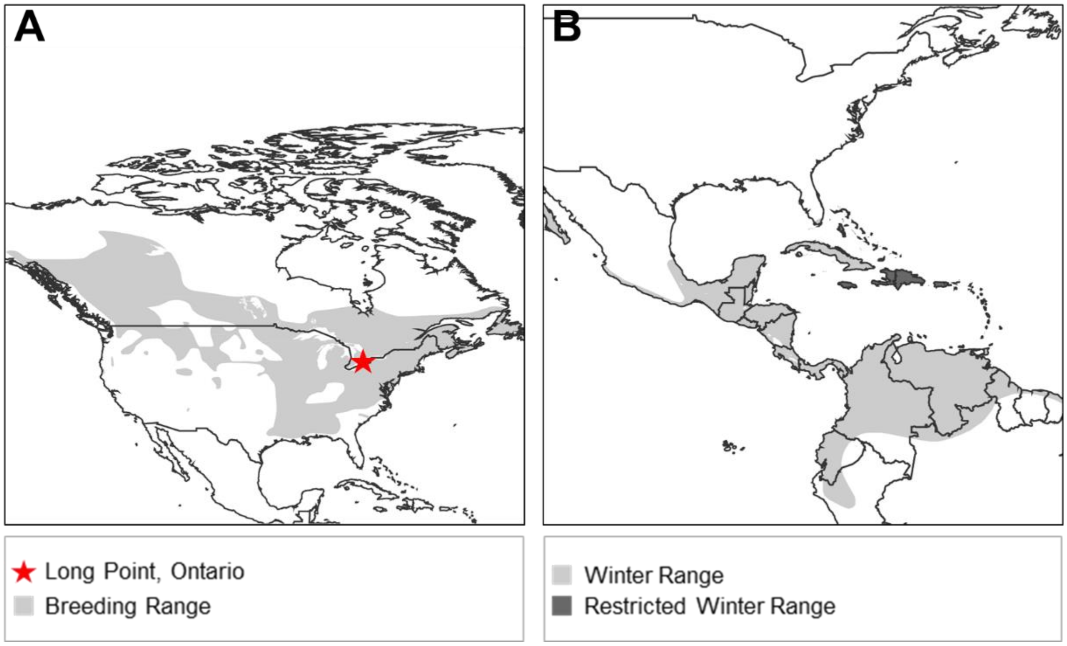

Figure 3: American Redstart breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by northeastern breeding populations.

Black-throated Blue Warbler

Black-throated Blue Warblers are omnivorous during the non-breeding season, feeding on insects, berries, fruit, and nectar (Holmes et al., 2017). Breeding Bird Survey data has shown an annual increase of 0.5%/year (95% credible interval = -0.6% to 1.6%) in Ontario breeding populations from 1970 to 2017 (Smith et al., 2019). Stable isotope studies have shown that most birds from the northern portion of the breeding range spend the winter on the western Caribbean islands of Cuba and Jamaica (Rubenstein et al., 2002) (Figure 4).

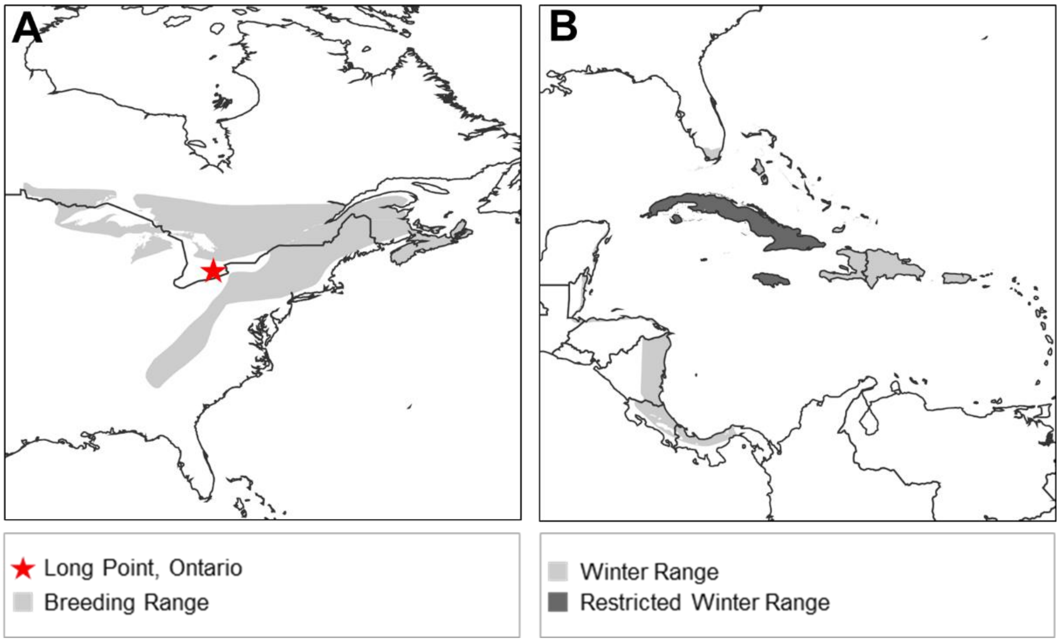

Figure 4: Black-throated Blue Warbler breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by northern breeding populations.

Swainson's Thrush

Breeding Bird Survey data has shown a small rate of annual population decline of -0.5%/year (95% credible interval = -1.4% to 0.3%) in Ontario breeding populations of Swainson's Thrush from 1970 to 2017 (Smith et al., 2019). The several subspecies of Swainson's Thrush belong to two main groups: the western, russet-backed (*ustulatus*) group and eastern, olive-backed (*swainsoni*) group. Birds in Ontario belong to the *swainsoni* group, and banding records and genetic data have determined that this group overwinters primarily in Panama and South America (mainly Ecuador, Peru, and Bolivia) (Ruegg & Smith, 2002) (Figure 5). Swainson's Thrush are generally frugivorous during the non-breeding season (Mack & Yong, 2000).

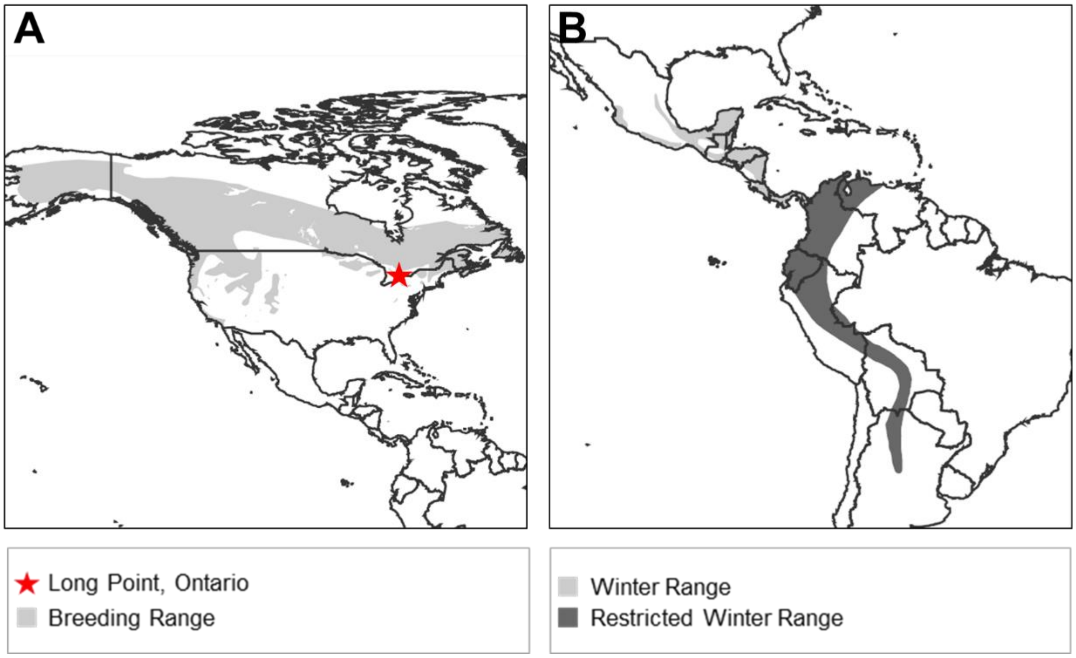

Figure 5: Swainson's Thrush breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by eastern breeding populations.

Red-eyed Vireo

Breeding Bird Survey data has shown an overall positive trend of 0.7%/year annual increase (95% credible interval = 0.3% to 1.1%) in Ontario breeding populations from 1970 to 2017 (Smith et al., 2019). Birds at a breeding site in northwestern Pennsylvania, approximately 90 km south of Long Point, were tracked using archival light-level geolocators and were found to overwinter in northwestern South America, specifically in the Orinoco River Basin (Venezuela and eastern Colombia) and the northern Amazon River Basin (Callo et al., 2013) (Figure 6). During the winter, Red-eyed Vireos are frugivorous (Cimprich et al., 2018).

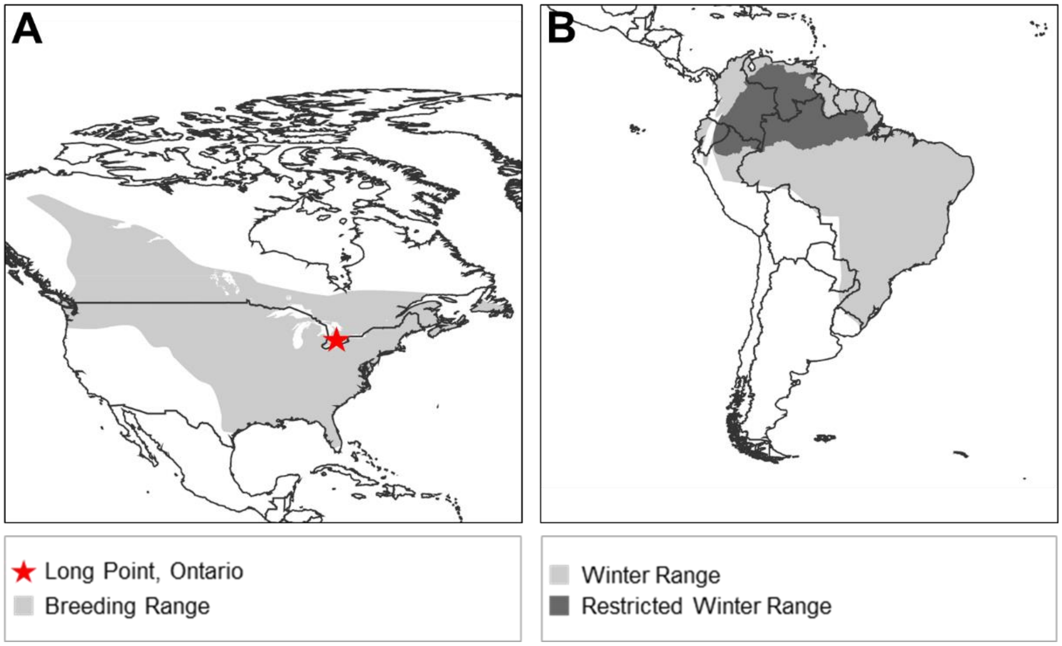

Figure 6: Red-eyed Vireo breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by a northeastern breeding population.

Yellow Warbler

Yellow Warblers are abundant and widespread, but Ontario breeding populations have shown an annual decline of -1.3%/year (95% credible interval = -1.9% to -0.8%) from 1970 to 2017 (Smith et al., 2019). Although there are no studies of diet in the non-breeding season, they eat mainly insects during the breeding season (Lowther et al., 1999). Stable isotope and mitochondrial DNA studies have determined that eastern populations of Yellow Warblers are strongly linked with wintering grounds in northern South America (Boulet et al., 2006). As such, the wintering range of Yellow Warbler for this study has been restricted to its known range in South America, excluding the Mexican and Central American overwintering range which is occupied by western breeding populations (Figure 7).

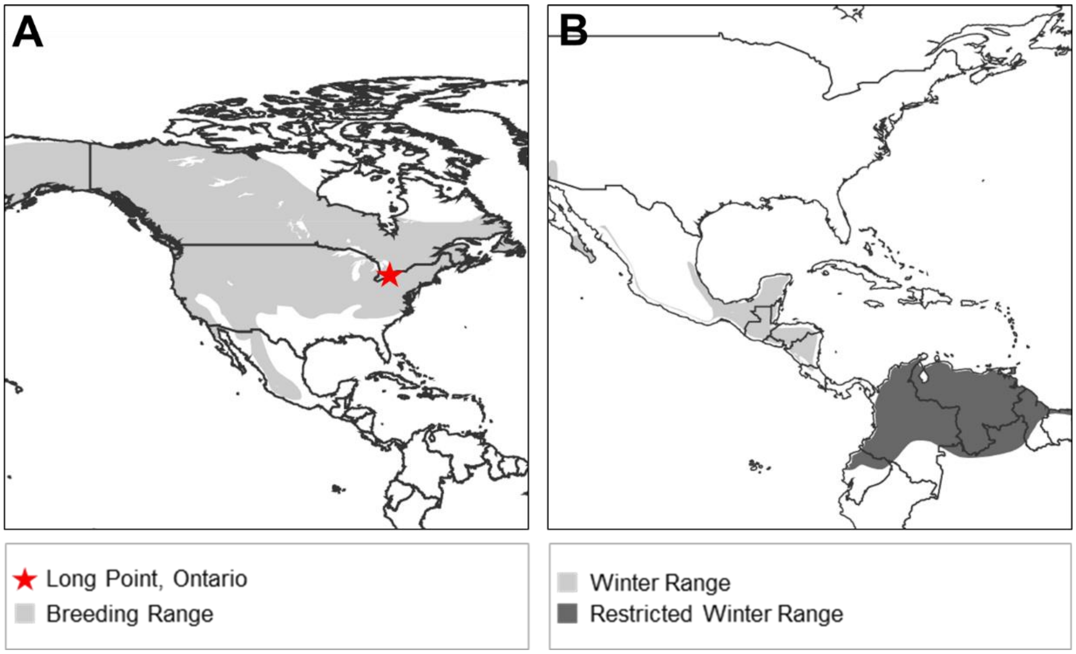

Figure 7: Yellow Warbler breeding range (A) and winter range (B). Restricted winter range indicates the parts of the winter range inhabited by eastern breeding populations.

Body Condition Index

Morphometric data including body mass and wing chord were used to calculate a size-correlated body condition index (BCI) (Labocha & Hayes, 2012). The BCI reflects the energy reserves that a bird has upon capture at the stopover site and is computed as $BCI = 100(m/w)$, where m is the bird's mass in grams and w the wing chord length in millimeters. Although body condition indices in general have been scrutinized (e.g., Green, 2009; Labocha & Hayes, 2012; Labocha et al., 2014), they are regardless a commonly used and generally accepted method of estimating the energetic condition of migratory birds. Body mass corrected for structural size indices have been used in a variety of similar studies (e.g., Latta & Faaborg, 2002; Wolfe & Ralph, 2009; González-Prieto & Hobson, 2013), and Seewagen (2008) found that body mass/wing chord measurements were highly correlated with chemically extracted lipid mass in Common Yellowthroat (*Geothlypis trichas*), Ovenbird, and Swainson's Thrush.

Oceanic Niño Index

The Oceanic Niño Index (ONI) was used as a measure of ENSO in this study and is available from the National Oceanic and Atmospheric Administration (NOAA) as a 3-month running mean of sea surface temperature anomalies in the east-central Pacific Ocean from 1950 to present (available: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). Values within this dataset range from -2.0 to 2.6, where positive values over 0.5 are associated with an El Niño event, and negative values below -0.5 are associated with a La Niña event. I used ONI as a continuous variable for statistical analysis, using the 3-month running mean for December, January, and February (as per Paxton et al., 2014).

Normalized Difference Vegetation Index

NDVI is a widely used index in ecological studies as a proxy for environmental conditions and habitat quality (Pettorelli et al., 2005) and to represent on-the-ground-conditions experienced by birds (Saino et al., 2004; Wilson et al., 2011; Paxton et al., 2014; Graham et al., 2016). NDVI is highly correlated with rainfall (Wang et al., 2003) and ground-truthed measures of vegetation such as annual cover of ephemeral plants (De La Maza et al., 2009), reflects broad scale differences in habitat types (Martinuzzi et al., 2008), and has been shown to reflect changes in precipitation due to El Niño conditions (Batista et al., 1997). NDVI values range can range from -1 to 1, where a value of zero or less indicates no green vegetation and high values indicate a high density of productive vegetation and it is assumed wetter and more food-rich areas for birds. Within the overwintering ranges of each species, NDVI within the period of 15 February through 31 March, the period prior to onset of spring migration, was used as a proxy for habitat productivity.

NDVI mapping originates from the Global Inventory Modelling and Mapping Studies (GIMMS) NOAA AVHRR dataset, which is available from July 1981-2015 as a bimonthly index (available: https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v1/) and is packaged in NetCDF data files. This dataset has been thoroughly examined for accuracy and corrected for errors such as navigation errors or bad scans (Tucker et al., 2005). The NDVI data has a spatial resolution of 0.0833 decimal degrees and was processed in ArcMap using the ModelBuilder application. For each set of bimonthly values, the NetCDF data file was converted to a raster layer and clipped to the known wintering range of each species using range maps from BirdLife International that had been modified as per recent migration tracking studies. Original NDVI values and qualifying 'flags' associated with the quality and origin of the measurement were calculated. NDVI values were subsequently filtered so that only values with flags 1 and 2, which indicated a 'good value', were used. This resulted in a dataset of reliable NDVI values for each bimonthly period (3 periods total) between 1982 and 2015 in each species' overwintering range. After the NDVI data were processed in ArcMap, they were exported as TIFF files to R (Version 3.5.2), where the mean NDVI values in each bimonthly period were calculated for each species using the package *raster* (Hijmans, 2019). Then, a yearly mean NDVI value for each species' overwintering range during the pre-migratory period of 15 February through 31 March was calculated by averaging the means of the 3 bimonthly periods.

Statistical analysis

Using R 3.5.3 (R Core Team, 2019) for statistical analysis, linear regression models were constructed to explore the relationships among overwinter habitat productivity, ENSO, bird body condition and migration timing. Visual inspection of the data suggested that strong non-linear patterns were not present. Models explored the influence of factors in the non-breeding season on bird response variables upon arrival, namely body condition and arrival timing. In each year, a mean BCI was calculated for each species by averaging the body condition of all individuals. Median capture dates (as day of year), herein referred to as median arrival dates, were used to represent a peak passage and so that extremely early or late individuals would not bias the results in a given year. Furthermore, in order to account for variation in arrival timing and condition that may be attributed to local weather conditions in Ontario (González-Prieto & Hobson, 2013) and not overwinter conditions, mean May temperature (ºC) and total May precipitation (millimeters) were included in multiple linear regression models as independent variables. Historic monthly summaries of weather data were obtained from weather stations within the same ecoregion (7E) and within 60 km of Long Point, primarily in Brantford, Ontario (available: https://climate-change.canada.ca/climate-data/#/monthly-climate-summaries). Unfortunately, monthly summaries for May temperature and precipitation were not consistently available at a single weather station for the entire study period. As such, data from nearby alternate weather stations in Tillsonburg and Delhi were used where historic summaries for Brantford were unavailable.

Linear regression models were run separately for each species, due to diverse wintering ranges and habitats. The first part of the analysis determined the effect of ENSO (as represented by ONI) on overwinter habitat productivity (as represented by NDVI) in the overwintering range of each species, as habitat productivity is the proposed causal mechanism by which ENSO affects food supply and bird body condition in the tropics. Simple linear regression models were run for each species, with NDVI as the dependent variable and ONI as the independent variable. The second part of the analysis determined how ONI affected bird response variables. Multiple linear regression models were run for each species, with median arrival date or mean BCI as the dependent variable and ONI, local mean May temperature, and local total May precipitation as independent variables. The third part of the analysis examined the direct relationship between bird response variables and overwinter NDVI. Multiple linear regression models were again run for each species, with median arrival date or mean BCI as the dependent variable and NDVI, local mean May temperature, and local total May precipitation as independent variables.

Sex and age-related differences in effects were explored for American Redstart and Yellow Warbler which have been reliably aged and sexed from plumage characteristics and for which sample sizes were large. For both species, potential interactions were broken down for male and female birds, as well as older birds (after second year [ASY]: ≥ 2 years old) and younger birds (second year [SY]: 1 year old). Responses for each group were explored using multiple linear regression, separate for each species, focusing on the direct influence of overwinter NDVI on body condition and migration timing, while accounting for local weather conditions (mean May temperature and total May precipitation) upon arrival.

Model and coefficient significance and parameter estimates were determined using functions in base R. The summary function provided summary statistics for each linear regression model including a determination of the significance of fixed effects. A result was considered statistically significant at an alpha value of 0.05. For all models, model diagnostic plots were visually examined to ensure that model assumptions were not violated. Q-Q plots were examined to ensure normality of residuals. Plots of residuals against fitted values were examined to confirm homoscedasticity of residuals and that no clear patterns were evident. The presence of influential data points was determined by examining plots of Cook's distance and running models both with and without influential data points to determine how resulting conclusions may change.

Results of the models were displayed using the *ggplot2* (Wickham, 2016) and *visreg* (Breheny & Burchett, 2017) packages. The visreg function in the *visreg* package was used to display the results of the multiple linear regression models. This function creates partial residual plots, holding parameters besides the variable of interest at their median value. The resulting plots help to isolate and visualize the relationship between variables of interest while taking into account the variability in the data that can be attributed to the other components of the model (Breheny & Burchett, 2017).

Results

Impact of ENSO on overwinter habitat productivity (NDVI)

Habitat productivity in each species' overwintering range was expected to vary predictably with ENSO due to year-to-year differences in rainfall patterns. Within the 34 years of the study, 11 years were classified as El Niño years, 14 as La Niña years, and 9 as non-ENSO years. ENSO, as represented by ONI, was significantly negatively correlated with habitat productivity in the wintering ranges of 3 of 7 species, with a fourth near-significant (Figure 8). As expected, El Niño events resulted in drier, less productive overwintering conditions for these species than wet, La Niña years, or non-ENSO years. In Central America, Wood Thrush experienced a significant negative relationship between overwinter NDVI and ENSO (Figure 8; F = 8.2, df = 1 and 32, adjusted R^2 = 0.18, P = 0.007), but the relationship was not significant for Ovenbird (Figure 8; F = 1.7, df = 1 and 32, P = 0.20) or the Caribbean overwintering species (Figure 8; American Redstart: F = 0.3, df = 1 and 32, P = 0.62; Black-throated Blue Warbler: F = 0.7, df = 1 and 32, P = 0.42). The wintering ranges of the South American focal species were mainly concentrated in northern South America (Figure 5, 6, and 7), generally within the areas thought to be strongly impacted by ENSO (Holmgren et al., 2001; Hoyos et al., 2019; Moura et al., 2019). Swainson's Thrush and Yellow Warbler experienced a significant negative relationship between NDVI and ENSO (Figure 8; Swainson's Thrush: F = 5.2, df = 1 and 32, adjusted R^2 = 0.11, P = 0.03; Yellow Warbler: F = 7.6, df = 1 and 32, adjusted R^2 = 0.17, P = 0.009) and Red-eyed Vireo approached significance (F = 3.2, df = 1 and 32, P = 0.08).

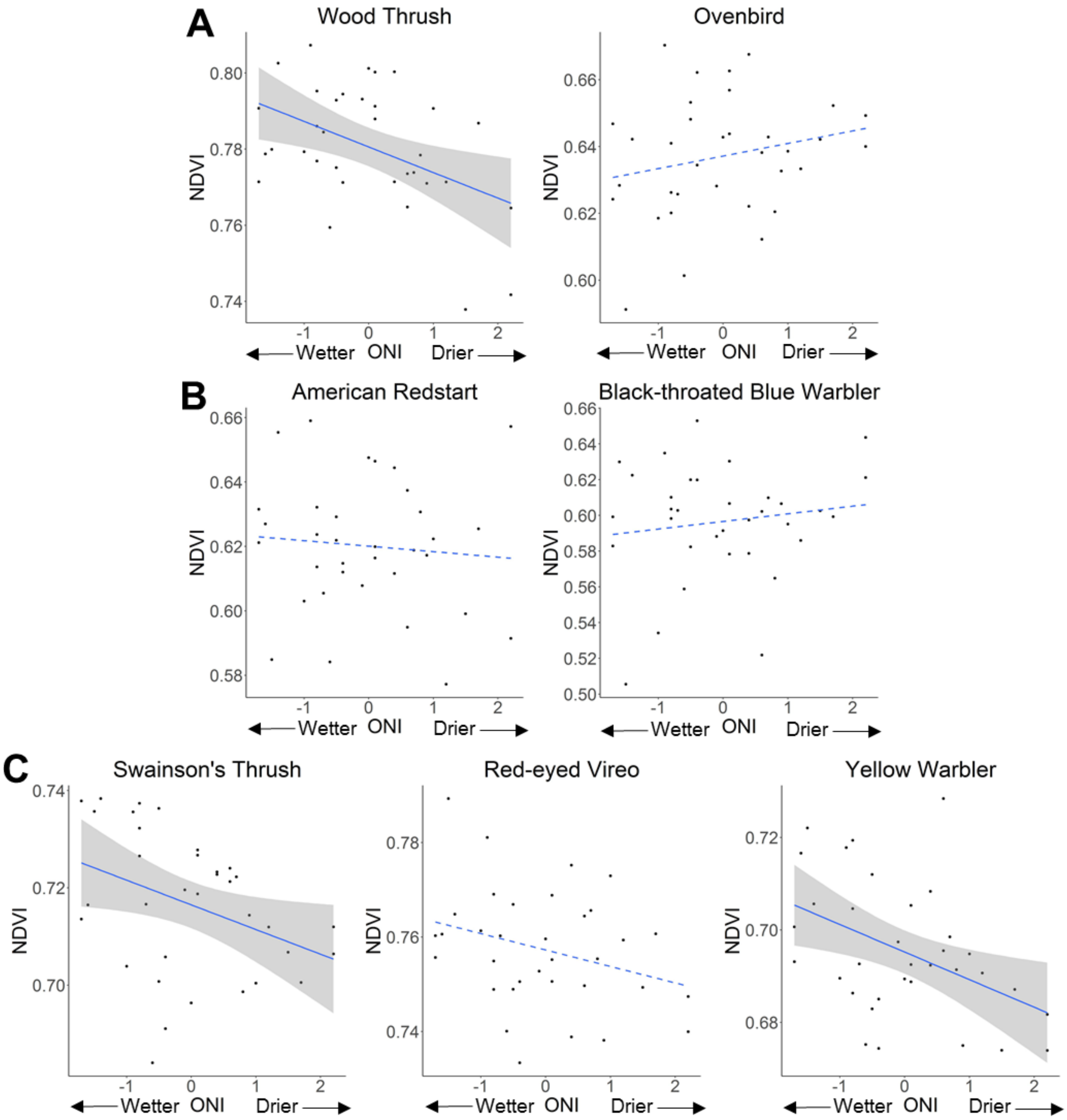

Figure 8: Relationship between mean overwinter habitat productivity (NDVI) and ENSO as represented by ONI for species overwintering in Central America (A), the Caribbean (B), and South America (C). Conditions in the tropics are anticipated to be drier when ONI > 0.5 (an El Niño event) and wetter when ONI < -0.5 (a La Niña event). Statistically significant relationships are shown with a solid line and a shaded area indicating 95% confidence intervals. Dashed lines indicate the relationship between variables was not statistically significant. The results for Red-eyed Vireo approached the significance level (P = 0.08).

Impact of ENSO on migratory body condition and arrival date

Contrary to the prediction that birds would arrive to Ontario in poorer condition after dry, El Niño years, ENSO was not a significant predictor of stopover body condition in Wood Thrush, Swainson’s Thrush, Yellow Warbler, and Red-eyed Vireo (Figure 9; Table 1) even though their wintering areas generally showed the expected relationship between ENSO and habitat productivity (Figure 8). For the remaining focal species, ENSO was also not a significant predictor of body condition upon arrival (Figure 9; Table 1). Furthermore, contrary to the prediction that birds would arrive to Ontario later after dry, El Niño years, ENSO was not a significant predictor of median arrival dates at Long Point for the majority of focal species (Figure 10; Table 1). The results for Red-eyed Vireo approached the significance level ($P = 0.06$) but in the opposite direction to what was predicted. When an outlier for 1983 was removed, the results became statistically significant ($P = 0.004$) but with arrival dates earlier in drier El Niño years and not later as predicted.

Mean May temperature and total May precipitation in southern Ontario were included in the models to control for fluctuations in response variables that may be attributed to local and not overwintering conditions. For all three species overwintering in South America, mean May temperature in Ontario was a significant predictor of median arrival dates, with birds arriving earlier in warmer springs (Table 1). The influence of temperature on arrival date was near significant for Black-throated Blue Warbler (Table 1; $P = 0.07$), as was the influence of temperature on body condition for Wood Thrush, with a negative relationship (Table 1; $P = 0.09$).

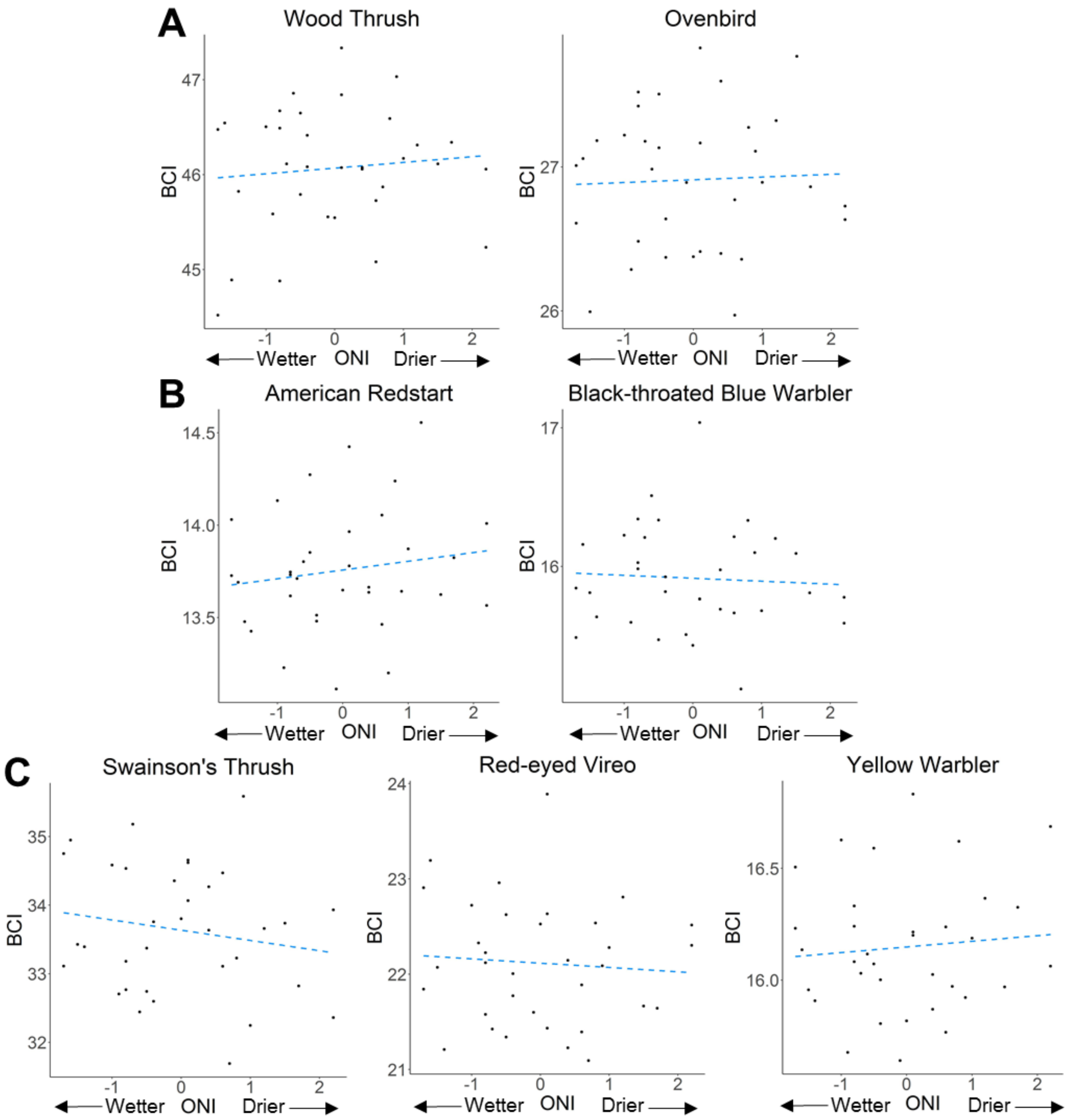

Figure 9: Relationship between mean BCI and ENSO as represented by ONI for species overwintering in Central America (A), the Caribbean (B), and South America (C). Conditions in the tropics are anticipated to be drier when ONI > 0.5 (an El Niño event) and wetter when ONI < -0.5 (a La Niña event). Dashed lines indicate the relationship between variables was not statistically significant.

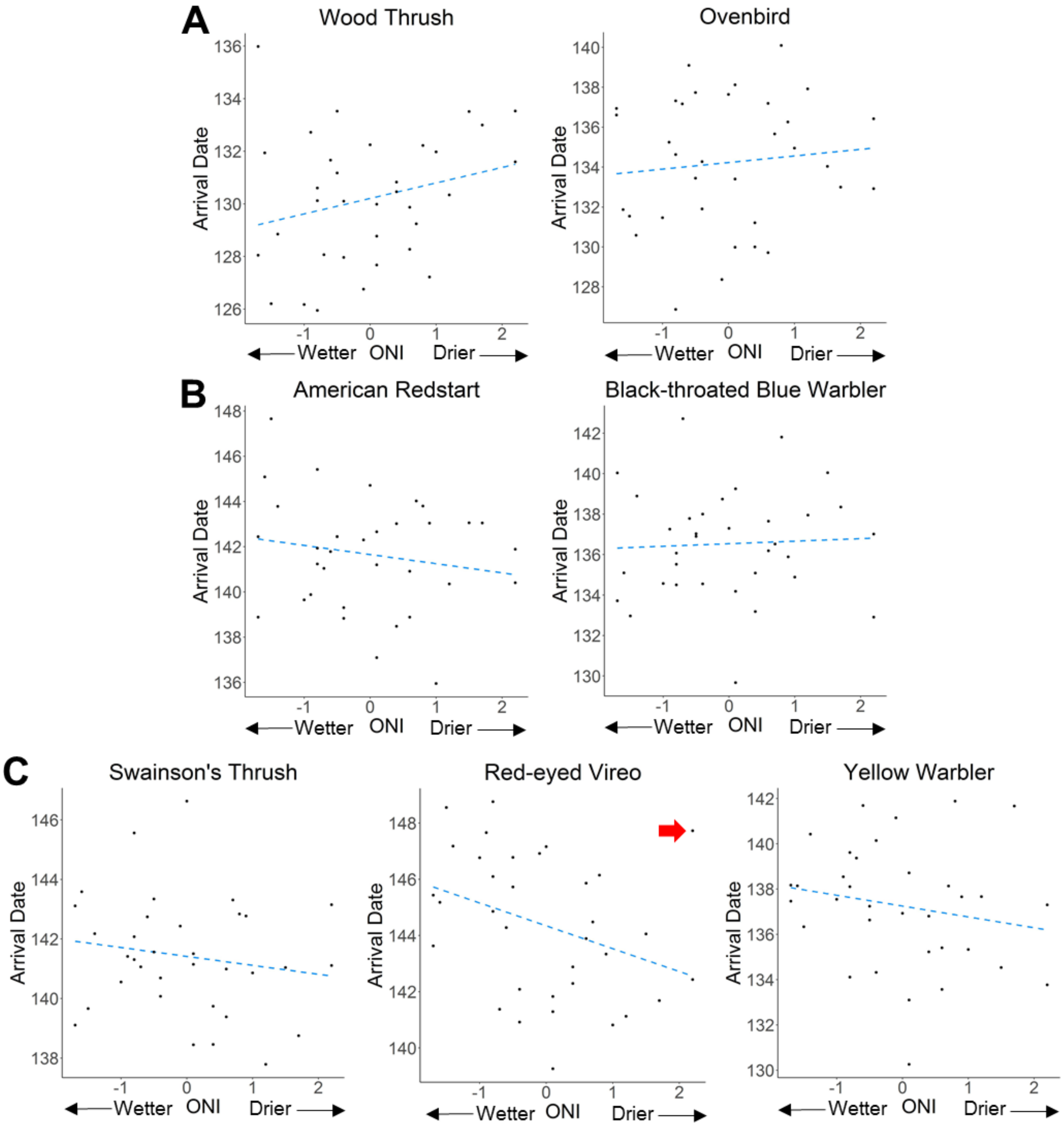

Figure 10: Relationship between yearly median arrival dates (as day of year) and ENSO as represented by ONI for species overwintering in Central America (A), the Caribbean (B), and South America (C). Conditions in the tropics are anticipated to be drier when ONI > 0.5 (an El Niño event) and wetter when ONI < -0.5 (a La Niña event). Dashed lines indicate the relationship between variables was not statistically significant. Results for Red-eyed Vireo approached significance (P = 0.06), with the results for 1983 identified as an outlier (indicated by red arrow). When this data point was removed, results were statistically significant (P = 0.004) but in the opposite direction to what was predicted.

Table 1: Coefficient significance, estimates, and standard errors from multiple linear regression models of body condition and median arrival dates in relation to wintering ground conditions (ONI), as well as locally near the area of capture on spring migration (precipitation and May temperature). Coefficients that were statistically significant are bolded; those approaching statistical significance are italicized.

Species	**Response**	**Local Precipitation**	**Local May Temperature**	**Oceanic Niño Index**
Wood Thrush	Body Condition	P = 0.38 -0.004 ± 0.004	*P = 0.09* *-0.133 ± 0.075*	P = 0.59 0.060 ± 0.110
	Median Arrival Date	P = 0.87 0.003 ± 0.016	P = 0.69 -0.112 ± 0.278	P = 0.16 0.589 ± 0.408
Ovenbird	Body Condition	P = 0.88 -0.000 ± 0.003	P = 0.22 -0.070 ± 0.056	P = 0.82 0.019 ± 0.083
	Median Arrival Date	P = 0.74 0.008 ± 0.022	P = 0.45 -0.292 ± 0.383	P = 0.56 0.331 ± 0.562
American Redstart	Body Condition	P = 0.30 0.002 ± 0.002	P = 0.52 -0.024 ± 0.038	P = 0.40 0.047 ± 0.056
	Median Arrival Date	P = 0.37 0.015 ± 0.016	P = 0.26 -0.326 ± 0.283	P = 0.34 -0.404 ± 0.415
Black-throated Blue Warbler	Body Condition	P = 0.49 0.002 ± 0.003	P = 0.47 0.032 ± 0.043	P = 0.74 -0.021 ± 0.064
	Median Arrival Date	P = 0.88 -0.003 ± 0.018	*P = 0.07* *-0.586 ± 0.313*	P = 0.79 0.126 ± 0.459
Swainson's Thrush	Body Condition	P = 0.24 0.007 ± 0.006	P = 0.72 0.039 ± 0.107	P = 0.35 -0.150 ± 0.157
	Median Arrival Date	P = 0.38 -0.011 ± 0.013	**P = 0.003** **-0.734 ± 0.225**	P = 0.37 -0.299 ± 0.331
Red-eyed Vireo	Body Condition	P = 0.51 0.003 ± 0.004	P = 0.59 0.040 ± 0.074	P = 0.68 -0.045 ± 0.109
	Median Arrival Date	P = 0.40 -0.014 ± 0.016	**P = 0.002** **-0.975 ± 0.279**	*P = 0.06* *-0.813 ± 0.410*
Yellow Warbler	Body Condition	P = 0.73 0.001 ± 0.002	P = 0.75 -0.011 ± 0.034	P = 0.62 0.025 ± 0.050
	Median Arrival Date	P = 0.30 -0.019 ± 0.018	**P = 0.009** **-0.869 ± 0.309**	P = 0.30 -0.479 ± 0.455

Impact of overwinter habitat productivity (NDVI) on migratory body condition and arrival date

Reduced habitat productivity as a result of climatic effects (such as decreased rainfall during El Niño events) is expected to reflect a reduction in food resources for birds and negatively impact migratory performance. The relationship between overwinter habitat productivity and bird response variables was directly tested, but contrary to prediction, overwinter NDVI was not a significant predictor of stopover body condition or arrival date in Ontario for any of the focal species (Figure 11, 12; Table 2). Results approached the significance level for body condition of Black-throated Blue Warbler and American Redstart ($P = 0.07$ and $P = 0.06$ respectively), but the relationship was negative and opposite to what was predicted. Age class and sex effects were explored for American Redstart and Yellow Warbler because smaller individuals (who are less competitive) could be more strongly impacted by negative carry-over effects. Results of the models did not indicate significant differences in effects of overwinter habitat productivity on body condition or arrival date between age and sex classes of either species (Appendix B: Figures S1-S4).

Table 2: Coefficient significance, estimates, and standard errors from multiple linear regression models of body condition and median arrival dates in relation to wintering ground conditions (overwinter NDVI), as well as locally near the area of capture on spring migration (precipitation and May temperature). Coefficients that were statistically significant are bolded; those approaching statistical significance are italicized.

Species	**Response**	**Local Precipitation**	**Local May Temperature**	**Overwinter NDVI**
Wood Thrush	Body Condition	P = 0.33 -0.004 ± 0.004	*P = 0.08* *-0.136 ± 0.075*	P = 0.65 3.341 ± 7.357
	Median Arrival Date	P = 0.96 0.001 ± 0.016	P = 0.72 -0.103 ± 0.286	P = 0.51 -18.89 ± 28.07
Ovenbird	Body Condition	P = 0.80 -0.001 ± 0.003	P = 0.20 -0.074 ± 0.056	P = 0.56 2.932 ± 4.973
	Median Arrival Date	P = 0.74 0.007 ± 0.022	P = 0.48 -0.278 ± 0.385	P = 0.65 -15.552 ± 34.042
American Redstart	Body Condition	P = 0.24 0.003 ± 0.002	P = 0.82 -0.009 ± 0.037	*P = 0.06* *-5.379 ± 2.803*
	Median Arrival Date	P = 0.28 0.018 ± 0.016	P = 0.37 -0.267 ± 0.292	P = 0.43 -17.748 ± 22.070
Black-throated Blue Warbler	Body Condition	P = 0.35 0.002 ± 0.002	P = 0.42 0.033 ± 0.041	*P = 0.07* *-3.810 ± 2.033*
	Median Arrival Date	P = 0.87 -0.003 ± 0.018	*P = 0.07* *-0.586 ± 0.312*	P = 0.77 -4.480 ± 15.423
Swainson's Thrush	Body Condition	P = 0.19 0.008 ± 0.006	P = 0.67 0.047 ± 0.108	P = 0.42 9.572 ± 11.614
	Median Arrival Date	P = 0.42 -0.011 ± 0.013	**P = 0.003** **-0.743 ± 0.227**	P = 0.48 -17.566 ± 24.453
Red-eyed Vireo	Body Condition	P = 0.48 0.003 ± 0.004	P = 0.58 0.041 ± 0.075	P = 0.91 1.084 ± 9.520
	Median Arrival Date	P = 0.70 -0.007 ± 0.017	**P = 0.002** **-0.951 ± 0.287**	P = 0.16 53.331 ± 36.597
Yellow Warbler	Body Condition	P = 0.92 0.000 ± 0.002	P = 0.61 -0.018 ± 0.036	P = 0.49 -2.676 ± 3.861
	Median Arrival Date	P = 0.311 -0.019 ± 0.019	**P = 0.009** **-0.909 ± 0.328**	P = 0.63 -17.145 ± 35.472

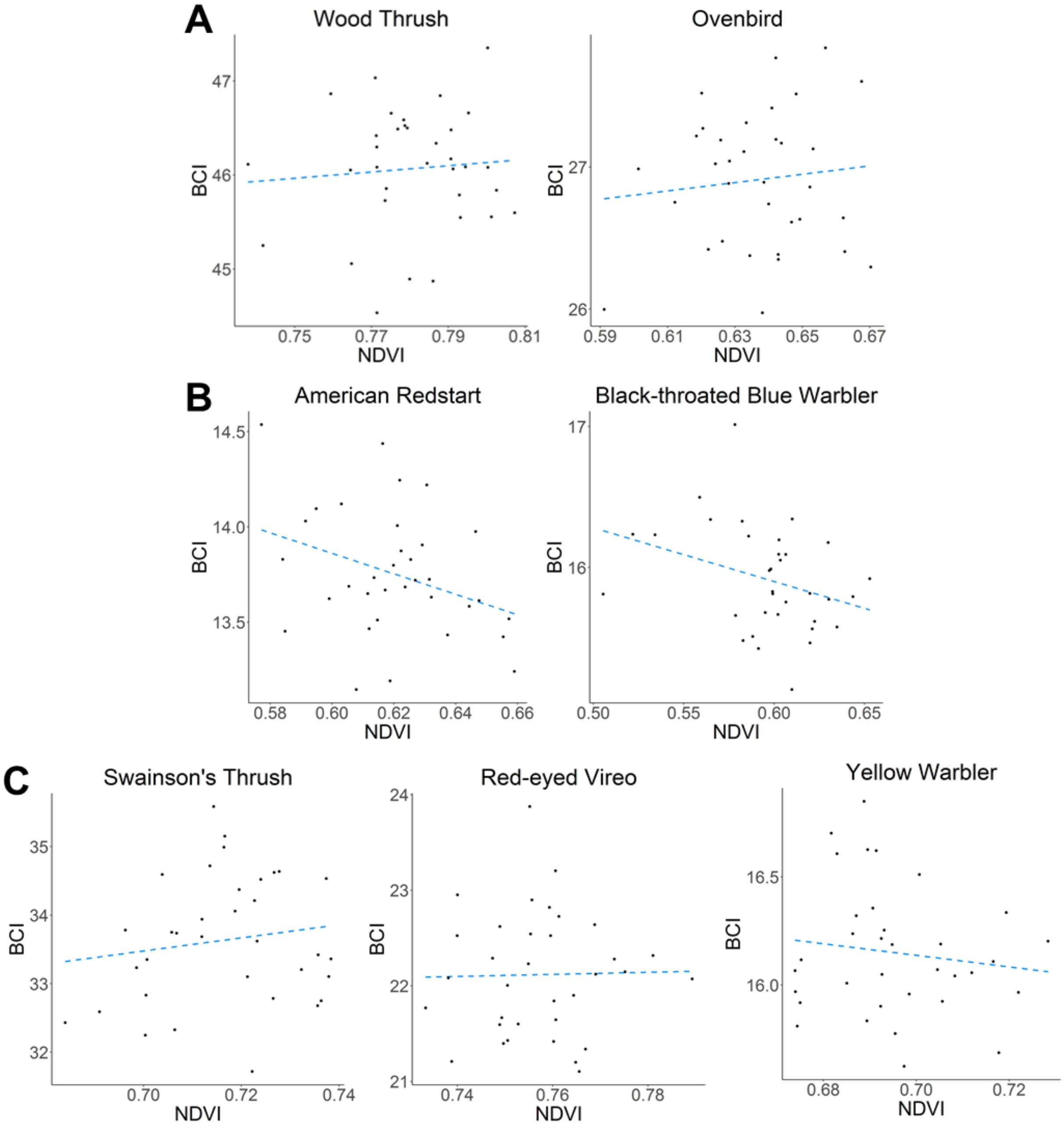

Figure 11: Relationship between mean BCI and mean overwinter habitat productivity (NDVI) for species overwintering in Central America (A), the Caribbean (B), and South America (C). Dashed lines indicate the relationship between variables was not statistically significant.

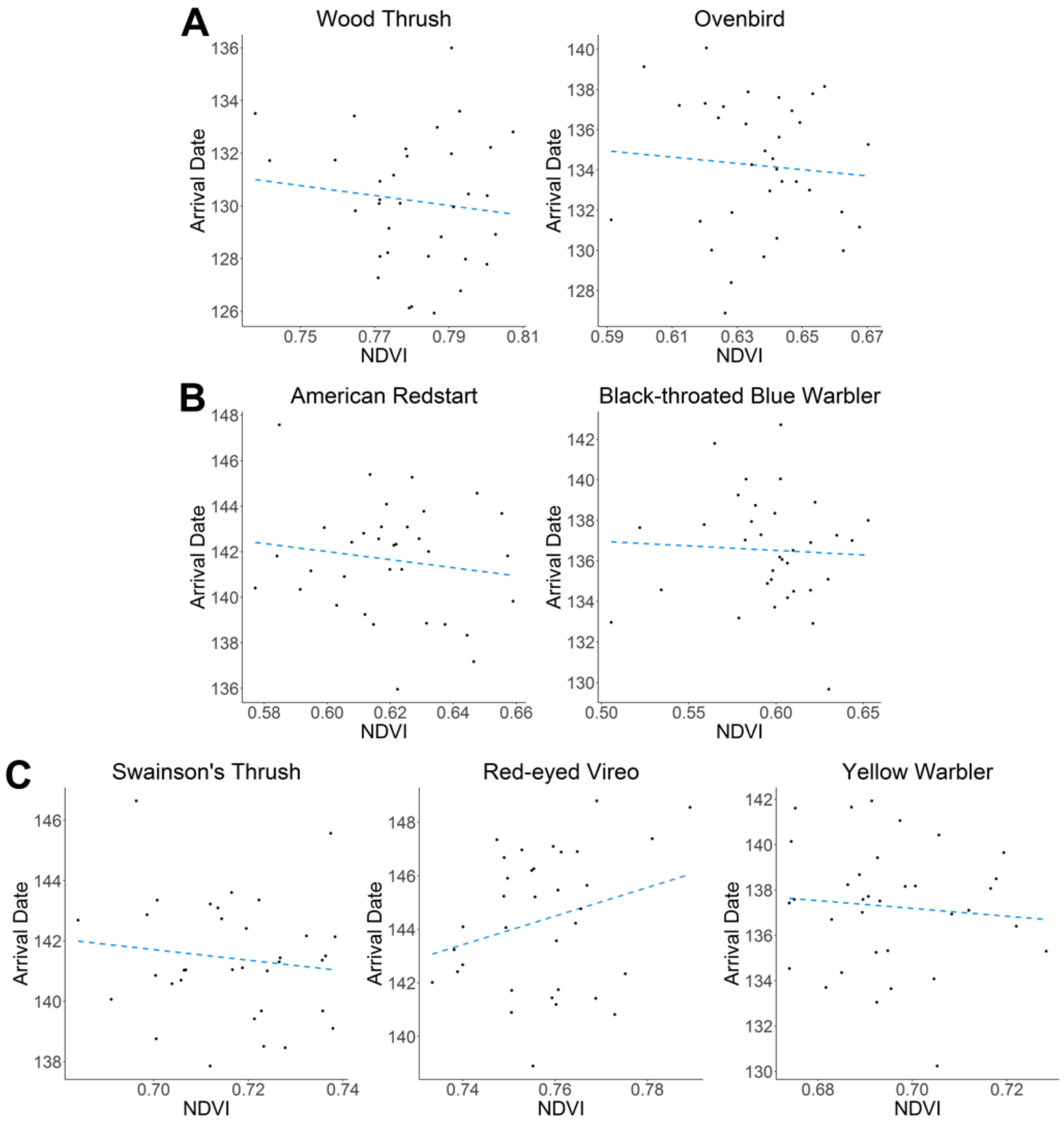

Figure 12: Relationship between yearly median arrival dates (as day of year) and mean overwinter habitat productivity (NDVI) for species overwintering in Central America (A), the Caribbean (B), and South America (C). Dashed lines indicate the relationship between variables was not statistically significant.

Discussion

ENSO effects on habitat productivity (NDVI)

While many studies have linked ENSO to changes in body condition, spring migration timing, survival, and productivity in migratory songbirds (Sillett et al., 2000; Nott et al., 2002; Wolfe & Ralph, 2009; LaManna et al., 2012; González-Prieto & Hobson, 2013; García-Pérez et al., 2014; Paxton et al., 2014) most of these studies have assumed that ENSO is linked to habitat productivity on the relevant wintering grounds (with the exception of Paxton et al., 2014). Here, I tested that assumption and found that year-to-year variation in ENSO had the predicted effect on annual variation in overwinter habitat productivity (NDVI) for only 3 of 7 species overwintering in the tropics (Wood Thrush, Yellow Warbler, and Swainson's Thrush), with another near significant (Red-eyed Vireo). For these species, El Niño years were associated with lower habitat productivity in their wintering areas. These results corroborate the findings of Paxton et al., (2014) showing that species overwintering in South America generally experience drier conditions during El Niño years, while this may not always be the case for Caribbean or Central American overwintering species. Although there is variability in the spatial extent and amplitude of ENSO impacts in northern South America and parts of the Amazon Basin (Marengo & Espinoza, 2016; Rifai et al., 2019), in general, recent regional analyses support the presumption of drier than normal conditions during El Niño events and wetter than normal states during La Niña events (Hoyos et al., 2019; Moura et al., 2019). Furthermore, analysis of precipitation anomalies show that the same pattern is strong in the winter months over Costa Rica and Nicaragua, which comprise the majority of the Wood Thrush's overwintering range (Hoyos et al., 2019).

Other focal species did not experience a consistent effect of ENSO on NDVI in their overwintering ranges. Ovenbirds share a portion of their overwintering range with Wood Thrush, but the range for Ontario-breeding Ovenbirds is much larger with nearly two-thirds of the wintering range in Mexico. Most of Mexico experiences increased rainfall during El Niño winters, a pattern more similar to the United States than the rest of the Neotropics (Caso et al., 2007; Seager et al., 2009). Throughout the Caribbean, there are also subregional differences in precipitation patterns, and ENSO has an influence in some areas but not others (Jury et al., 2007;

Torres-Valcárcel, 2018). Even Cuba, the largest island in the Caribbean which comprises a large portion of the Black-throated Blue Warbler's overwintering area, consists of different zones which are unique from each other both in terms of precipitation patterns and the influence of ENSO on precipitation (Jury et al., 2007). These subregional differences throughout the Ovenbird's, American Redstart's, and Black-throated Blue Warbler's overwintering ranges may explain why there are no consistent range-wide patterns for these species.

In large geographical areas with diverse habitat types, the interpretation of NDVI values is impeded because different habitats respond differently to climatic events (Oliveira et al., 2010). Differences in vegetation structure and functional types of vegetation play an important role in how habitats respond to changes in precipitation and integrate it into primary productivity that forms the basis of NDVI datasets (Golluscio et al., 1998; Jobbágy & Sala, 2000; Yahdjian & Sala, 2006). In Hawaii for example, rainforests and dry forests exhibit differing responses to El Niño droughts, whereby the response of NDVI in dry forests is more strongly linked to precipitation than in rainforest (Pau et al., 2010). Responses of dry forests may indicate that these systems are more water-limited, while rainforests are more light-limited (Pau et al., 2010). High species diversity in some forest types can also make them more resistant to drought (Lloret et al., 2007). Furthermore, water-use efficiency varies between habitats, with forest ecosystems and areas with high amounts of vegetation cover having a higher water-use efficiency than non-forested areas (Yang et al., 2016). Lastly, ecosystems have been found to have a 'memory' of the previous year's drought, in which the water-use efficiency in the current year is impacted by drought in the previous year (Yang et al., 2016). Although NDVI anomalies caused by ENSO reflect changes in precipitation patterns, the response of vegetation may also experience a time-lag effect which may not show until several months later (Rishma & Katpatal, 2016).

Each pixel in the NDVI dataset encompasses an area of approximately 86 km^2 (0.0833 decimal degrees) and there are likely fine scale differences in habitat productivity that are biologically important to individual birds but are impossible to detect with this dataset. In complex habitats, the calculation of NDVI is heavily influenced by conditions in the canopy and cannot take into account conditions in the lower vegetation levels, which may be relevant to birds and their arthropod prey (Lassau & Hochuli, 2008). Furthermore, natural habitats are often embedded within agricultural landscapes which also contribute to the calculation of overwinter habitat productivity for each pixel across the wintering range. Within each of the focal species' wintering ranges, the overall variability in NDVI in a given year was high (Appendix C: Figure S5), and a mean NDVI value for the entire overwintering range may not be representative of conditions experienced by individuals at the small spatial scales that impact carry-over effects. In previous studies, large scale NDVI in Mexico and Central America did not influence how long Purple Martins (*Progne subis*) stayed on their prolonged stopovers during fall migration (Van Loon et al., 2017), nor did it explain differences in refueling rates in migratory songbirds in Europe (Ktitorov et al., 2008). Despite the unavoidable limitations of NDVI data, it nevertheless is used widely in conservation biology to assess spatial and temporal changes in habitat quality over broad scales. The availability of the NDVI dataset used in the present study provides an otherwise impossible opportunity to assess the response of multiple species to over three decades of historical changes in their overwintering areas.

Carry-over effects on body condition

There is strong evidence that habitat drying in overwintering areas negatively affects songbird body condition through impacts to food availability (Studds & Marra, 2007; Smith et al., 2010; McKinnon et al., 2015a; Akresh et al., 2019) and that conditions experienced over the winter in the tropics can carry-over to affect birds even many months later in breeding areas (e.g., Norris et al., 2004; Rockwell et al., 2012; Drake et al., 2013). However, in the present study, long-term negative carry-over effects on body condition from ENSO or overwinter habitat productivity are not evident when birds arrive at Long Point, even for species where the link between ENSO and NDVI was strong. Although there was a high amount of yearly variation in mean body condition of each of the focal species at Long Point (representing fluctuations of approximately 6-14% body weight), neither ENSO nor overwinter NDVI explained this variability.

Previous studies showed clear negative carry-over effects of ENSO or overwinter habitat productivity on body condition during the early part of the migratory journey (Bearhop et al., 2004; Wolfe & Ralph, 2009; Paxton et al., 2014), while studies at more northern latitudes showed mixed results (Norris et al., 2004; González-Prieto & Hobson, 2013). Negative carry-over effects may be strongest, and most evident, during the earlier stages of migration. Prolonged stopovers early in migration allow birds to refuel for subsequent migratory flights and may let them compensate for poor departure condition during dry years. For instance, Red-eyed Vireo, Swainson's Thrush, and Blackpoll Warbler (*Setophaga striata*) are known to have spring stopovers in northern South America, Central America, the Caribbean, Mexico, and even the United States, ranging from a week to a month (Delmore et al., 2012; Callo et al., 2013; DeLuca et al., 2015). If conditions are more productive in these stopover habitats, birds may be able to refuel at high rates and make up for poor departure condition (Ktitorov et al., 2008; Gómez et al., 2017; Bayly et al., 2019). Although birds may depart their overwintering areas in comparatively poor condition during dry, food-poor years, the effects may wear off over the time and the thousands of kilometers it takes to reach Ontario (Clausen et al., 2015).

Weather conditions in passage areas have been shown to impact body condition of songbirds captured during spring migration (Robson & Barriocanal, 2008; González-Prieto & Hobson, 2013; Krause et al., 2016) which may mask carry-over effects from the wintering grounds. However, in the present study, mean May temperature in southern Ontario and total May precipitation were not significant predictors of body condition for any of the focal species. Fluctuations in weather variables on a shorter time scale (e.g., daily) may better explain variation in individual body condition. For example, in migrating Barn Swallows (*Hirundo rustica*), warm days with low wind speed and high humidity were associated with higher body mass, while rain and cloudy conditions were associated with lower body mass (Robson & Barriocanal, 2008). Studies of Black-and-white Warblers (*Mniotilta varia*) found that body condition during spring migration was influenced by distance to a bird's final breeding destination (either southeastern United States or boreal forest of Canada), timing of migration, and sex (Paxton & Moore, 2015). Males arriving mid-migration had better body condition than both early and late males, but the body condition of females remained consistent (Paxton & Moore, 2015). Black-and-white Warblers near their final breeding destination also accumulate additional fat stores, presumably to prepare for breeding (Paxton & Moore, 2017). Thus, within-year variation in local weather and individual migration strategies could mask the coarser year-to-year differences in body condition that may be attributed to ENSO or NDVI variation.

Although knowledge of migratory connectivity, or how tightly populations stay linked throughout the annual cycle, has been considerably refined in recent years, overwintering ranges of many of the focal species still encompass a large geographical area. For example, through a direct-tracking study of Ovenbirds (Hallworth et al., 2015), the potential overwintering range of birds passing through Long Point was restricted from the entire tropical winter range to Central America and Mexico (Figure 2). Although this analysis was able to exclude the Caribbean, southern United States, and northern South America, the remaining wintering range is still a massive area, with inconsistent ENSO effects between Mexico and Central America (Cavazos & Hastenrath, 1990; Caso et al., 2007; Seager et al., 2009). On the other hand, Wood Thrushes from the northeastern portion of their breeding range (which includes southern Ontario) overwinter almost exclusively in a relatively small wintering area comprising eastern Honduras, eastern Nicaragua, and Costa Rica (Stanley et al., 2015). Across this region, year-to-year differences in how ENSO impacts winter habitat quality are expected to be fairly uniform (Hoyos et al., 2019) and so carry-over effects (if present) may be more detectable at the population level. Finer-scaled tracking of bird populations across the breeding range may further restrict potential wintering areas to allow for a more precise determination of how ENSO impacts habitat productivity and thus carry-over effects. However, if migratory connectivity in a species is naturally low and individuals mix extensively with other populations over a large winter range (e.g., Fraser et al., 2012; Renfrew et al., 2013), then ENSO-related carry-over effects may be difficult to detect at a population level.

Carry-over effects on arrival date

There is good reason to expect that arrival at northern latitudes would be delayed due to dry overwintering conditions (Marra, 1998; Norris et al., 2004; Rockwell et al., 2012; González-Prieto & Hobson, 2013), thus it is surprising that effects during the migratory period are not evident in this study. In the aforementioned studies, arrival to northern areas was delayed for American Redstart, Kirtland’s Warbler, Palm Warbler, and Northern Waterthrush when conditions were dry on the wintering grounds. Reduced body condition at the beginning of the migratory period is the proposed mechanism that causes later departure and therefore later arrival of birds. These small-bodied warblers may be more sensitive than large-bodied species, though in the present study, no carry-over effects of winter habitat productivity were noted for the three warbler species (American Redstart, Black-throated Blue Warbler, and Yellow Warbler). Although median arrival dates for each species were quite variable from year to year, neither ENSO nor NDVI were significant predictors of arrival dates for any of the focal species, even for those where overwintering habitat productivity was significantly impacted by ENSO. In contrast to studies which showed negative carry-over effects from dry conditions, other studies found that migration timing in Afro-Palearctic birds is actually delayed when habitat productivity is high in wintering and passage areas, potentially because birds are taking advantage of positive refuelling opportunities (Tøttrup et al., 2008; Robson & Barriocanal, 2011). It is possible that the effects of NDVI on migration timing are mixed between species and regions and thus a consistent relationship may be difficult to detect.

There is much evidence from direct tracking studies that departure date from overwintering areas strongly predicts arrival date at breeding sites (Stanley et al., 2012; Callo et al., 2013; Jahn et al., 2013; Ouwehand & Both, 2017) and that some birds have limited flexibility to change their departure timing from their overwintering areas, suggesting strong innate constraints to the onset of migration (Conklin et al., 2010; Stanley et al., 2012; Fraser et al., 2013). In Purple Martins for example, temperature and rainfall in overwintering areas did not explain spring migration timing, and departure timing was instead a result of breeding latitude and sex (Fraser et al., 2013). However, even if birds are forced to delay the onset of migration due to low habitat productivity in wintering areas, it is possible that late birds can compensate for lost time by migrating faster and stopping less frequently (McKinnon et al., 2015b; Gómez et al., 2017; Paxton & Moore, 2017). In a study of individually tracked Wood Thrushes, reduced habitat productivity in the late winter caused a delay in departure for spring migration. However, despite leaving later, birds from dry habitats migrated more quickly, so that the effect disappeared by the time they arrived at the breeding grounds (McKinnon et al., 2015b). Gray-cheeked Thrushes (*Catharus minimus*) minimize the time spent migrating by taking the shortest and most direct routes during spring migration, and birds departing late from stopover habitats have higher fat loads which allows them to migrate faster and reach North America before birds that departed earlier but in poorer condition (Gómez et al., 2017). The amount of time spent on stopover can also significantly impact the pace of migration and arrival at breeding sites (Schmaljohann et al., 2017), and Black-and White Warblers arriving late to stopover sites close to their breeding destination may try to catch up by staying a shorter time (Paxton & Moore, 2017).

Arrival dates are also known to be influenced by a variety of factors unrelated to overwintering conditions, such as temperatures in passage areas (Mazerolle et al., 2011; Kelly et al., 2016) and wind speed and direction (Drake et al., 2014). Despite leaving wintering habitats earlier or later based on conditions there, environmental constraints en route such as temperature and resource availability can impact a bird's arrival time at breeding locations (Tøttrup et al., 2008; Both, 2010). During the spring, a bird's rate of migration is much more rapid than during fall migration (Stutchbury et al., 2009) as birds are under strong selection to arrive early to the breeding grounds since arrival date influences reproductive success (Norris et al., 2004). Birds may have less opportunity to speed up during spring migration because their migration rate is already rapid, but far more opportunity to slow down in response to weather conditions (such as cold spells or droughts) during the last phase of migration (Tøttrup et al., 2012; Briedis et al., 2017). Local temperature near breeding areas has been found to explain arrival dates for a variety of short and long-distance migrants (Marra et al., 2005; Tøttrup et al., 2010). In the present study, for all three species overwintering in South America, mean May temperature in southern Ontario was a significant predictor of median arrival dates, with birds arriving earlier in warmer springs but delaying their arrival in colder springs, which is consistent with other studies (Mazerolle et al., 2011; González-Prieto & Hobson, 2013; Krause et al., 2016). Climatic conditions experienced in passage areas and late in migration may explain the high amount of yearly variation in arrival dates of the focal species.

Conclusions

A growing body of literature has documented convincing evidence of carry-over effects from conditions on the wintering grounds that persist into subsequent migration and breeding seasons. In contrast to these studies, even when narrowing the wintering range using isotope and tracking studies, I did not observe negative carry-over effects from climate and habitat productivity in overwintering areas on birds at a northern stopover site. A strong link between ENSO and habitat productivity (and subsequently resource availability) is the proposed mechanism for the observed carry-over effects in many studies (Sillett et al., 2000; Nott et al., 2002; Wolfe & Ralph, 2009; LaManna et al., 2012; González-Prieto & Hobson, 2013; García-Pérez et al., 2014; Paxton et al., 2014), yet I showed that this causal link was not consistently found in the overwintering ranges of all focal species. Despite using a 34-year dataset for a set of species with diverse life histories, large sample sizes, and strong year-to-year differences in ENSO and overwinter habitat productivity, carry-over effects were still not visible at the population-level. There is good reason to conclude that severe, population-level carry-over effects of ENSO and overwinter habitat productivity on arrival timing or body condition are not widespread or consistent in the focal species so late in migration.

Although the only other study of multiple species (including American Redstart, Yellow Warbler, and Swainson's Thrush) at a northern stopover site in Canada did detect carry-over effects for some species (González-Prieto & Hobson, 2013), the present study suggests that long-lasting effects are not consistent. To test if these carry-over effects are indeed mainly isolated to earlier stages of migration (Bearhop et al., 2004; Wolfe & Ralph, 2009; Paxton et al., 2014) it would be useful to recreate this exercise along migration routes at a gradient of southern to northern bird banding stations within the same time period to understand at which point effects begin to wear off. A future exercise could also use geospatial processing programs to exclude non-suitable ecosystem types from the overwintering range (e.g., developed areas or agricultural habitat) and use finer-scale NDVI products to determine the historic habitat productivity of only potentially suitable habitat within the overwintering range. This could reduce the 'noise' of highly variable NDVI values that include non-wintering habitat of a given species. It is also worth noting that there were few species for which this investigation was possible as there are relatively few studies that have identified the estimated wintering grounds of Ontario-breeding songbird populations. Continued and continent-wide tracking studies of species common enough to be monitored at stopover banding sites would be informative in the study of carry-over effects throughout the annual cycle, especially in populations where migratory connectivity is high and wintering ranges are relatively small. Furthermore, as more and more bird banding stations across North America collect data during this time of extreme anthropogenic change, these data continue to provide a largely untapped opportunity to examine the response of bird populations to environmental change.

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Appendix A: Number of records for each focal species by year and ENSO event

Year	Yellow Warbler	American Redstart	Black-throated Blue Warbler	Ovenbird	Swainson's Thrush	Wood Thrush	Red-eyed Vireo	Oceanic Niño Index	ENSO Event
1982	94	94	21	59	180	41	111	0.0	Non-ENSO
1983	100	41	22	91	92	24	25	2.2	El Niño
1984	68	45	21	144	85	55	48	-0.6	La Niña
1985	145	70	43	175	162	75	75	-1.0	La Niña
1986	51	60	51	121	139	49	54	-0.5	La Niña
1987	51	31	22	52	14	37	29	1.2	El Niño
1988	78	80	40	52	91	31	99	0.8	El Niño
1989	96	67	25	47	44	23	14	-1.7	La Niña
1990	89	47	21	59	52	25	44	0.1	Non-ENSO
1991	191	103	38	58	77	28	78	0.4	Non-ENSO
1992	206	86	46	45	76	63	117	1.7	El Niño
1993	190	118	50	108	86	63	70	0.1	Non-ENSO
1994	163	70	31	89	58	35	69	0.1	Non-ENSO
1995	146	59	67	65	62	39	38	1.0	El Niño
1996	129	62	55	85	97	45	50	-0.9	La Niña
1997	162	114	87	138	103	38	29	-0.5	La Niña
1998	376	123	46	58	107	51	72	2.2	El Niño
1999	297	120	91	94	72	45	71	-1.5	La Niña
2000	133	96	71	70	71	39	47	-1.7	La Niña
2001	278	84	59	80	103	47	48	-0.7	La Niña
2002	172	87	36	68	68	32	63	-0.1	Non-ENSO
2003	178	65	61	44	69	26	40	0.9	El Niño
2004	397	128	61	96	113	50	111	0.4	Non-ENSO
2005	361	113	67	84	95	52	50	0.6	El Niño
2006	520	113	56	102	118	75	93	-0.8	La Niña
2007	270	152	84	112	152	75	166	0.7	El Niño
2008	390	75	61	102	57	33	66	-1.6	La Niña
2009	584	155	90	117	178	58	117	-0.8	La Niña
2010	408	110	55	67	169	42	93	1.5	El Niño
2011	438	198	106	134	140	48	150	-1.4	La Niña
2012	627	135	85	98	181	49	76	-0.8	La Niña
2013	474	96	53	85	158	62	165	-0.4	Non-ENSO
2014	595	294	119	140	204	66	132	-0.4	Non-ENSO
2015	516	139	40	75	118	55	111	0.6	El Niño
Grand Total	**8973**	**3430**	**1881**	**3014**	**3591**	**1576**	**2621**		

Appendix B: Analysis of age and sex effects in American Redstart and Yellow Warbler

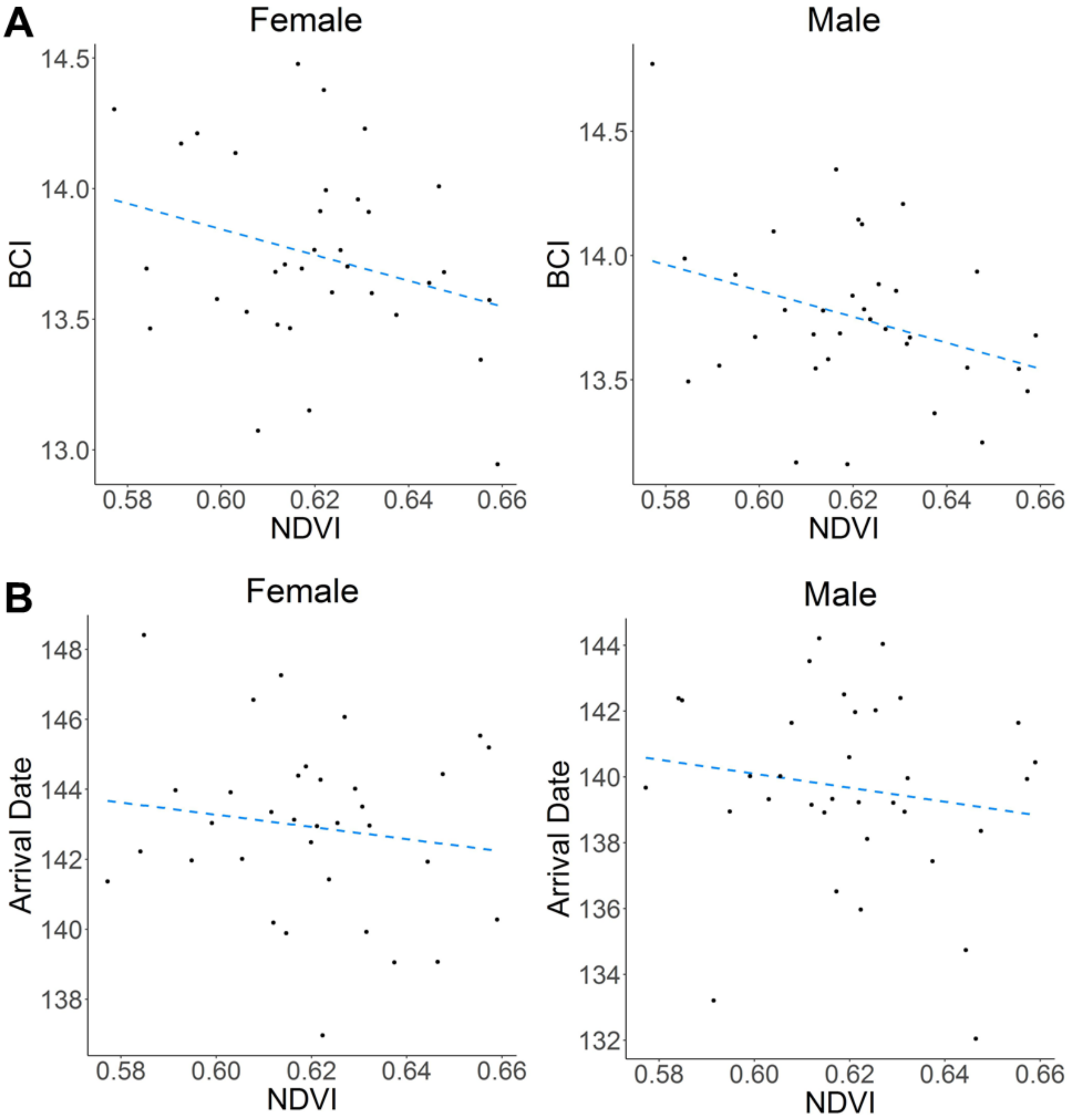

Figure S1: Relationship for female and male American Redstarts between mean BCI and overwinter NDVI (A), and median arrival date and overwinter NDVI (B). Dashed lines indicate the relationship between variables was not statistically significant.

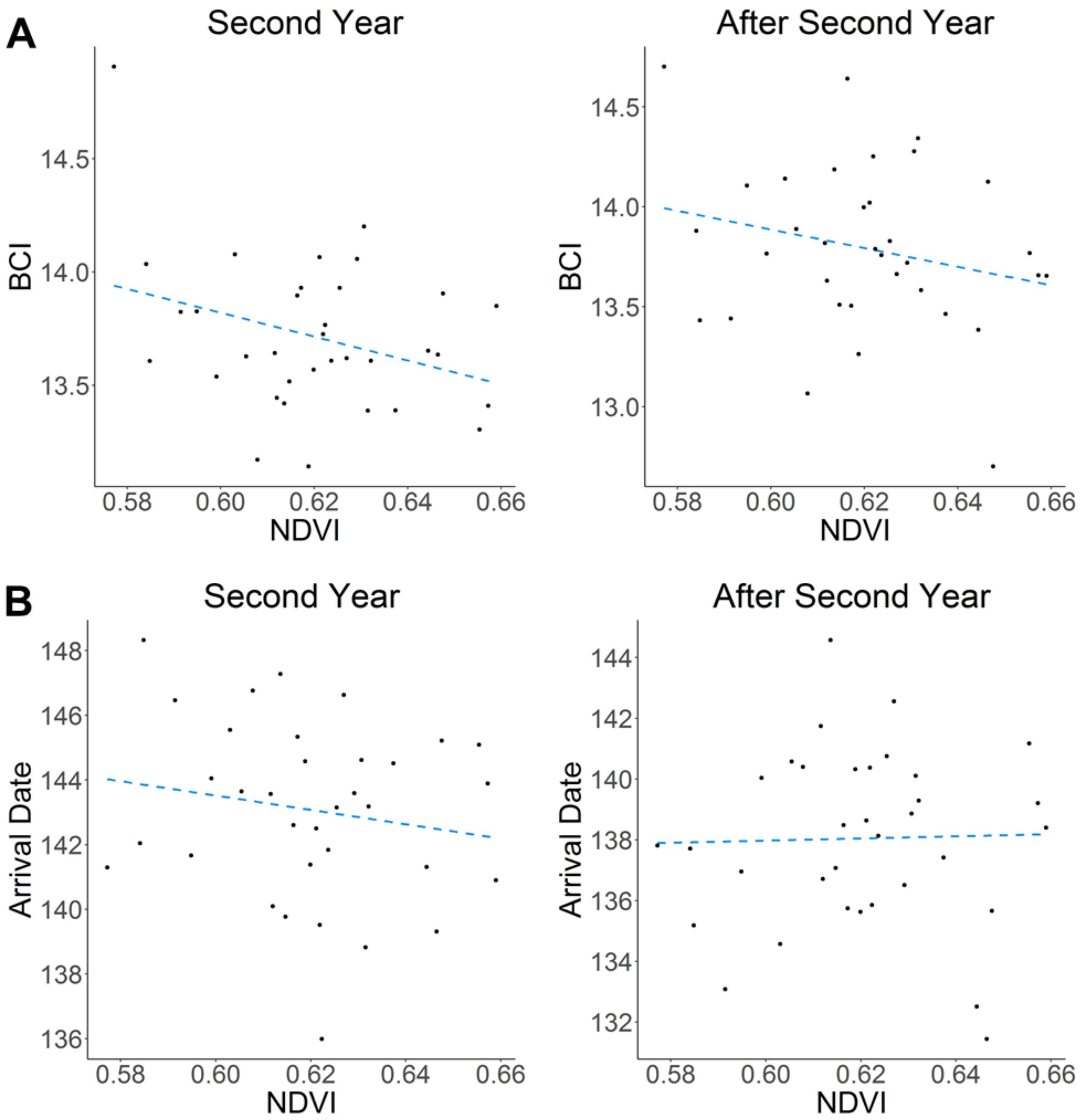

Figure S2: Relationship for second year and after second year American Redstarts between mean BCI and overwinter NDVI (A), and median arrival date and overwinter NDVI (B). Dashed lines indicate the relationship between variables was not statistically significant.

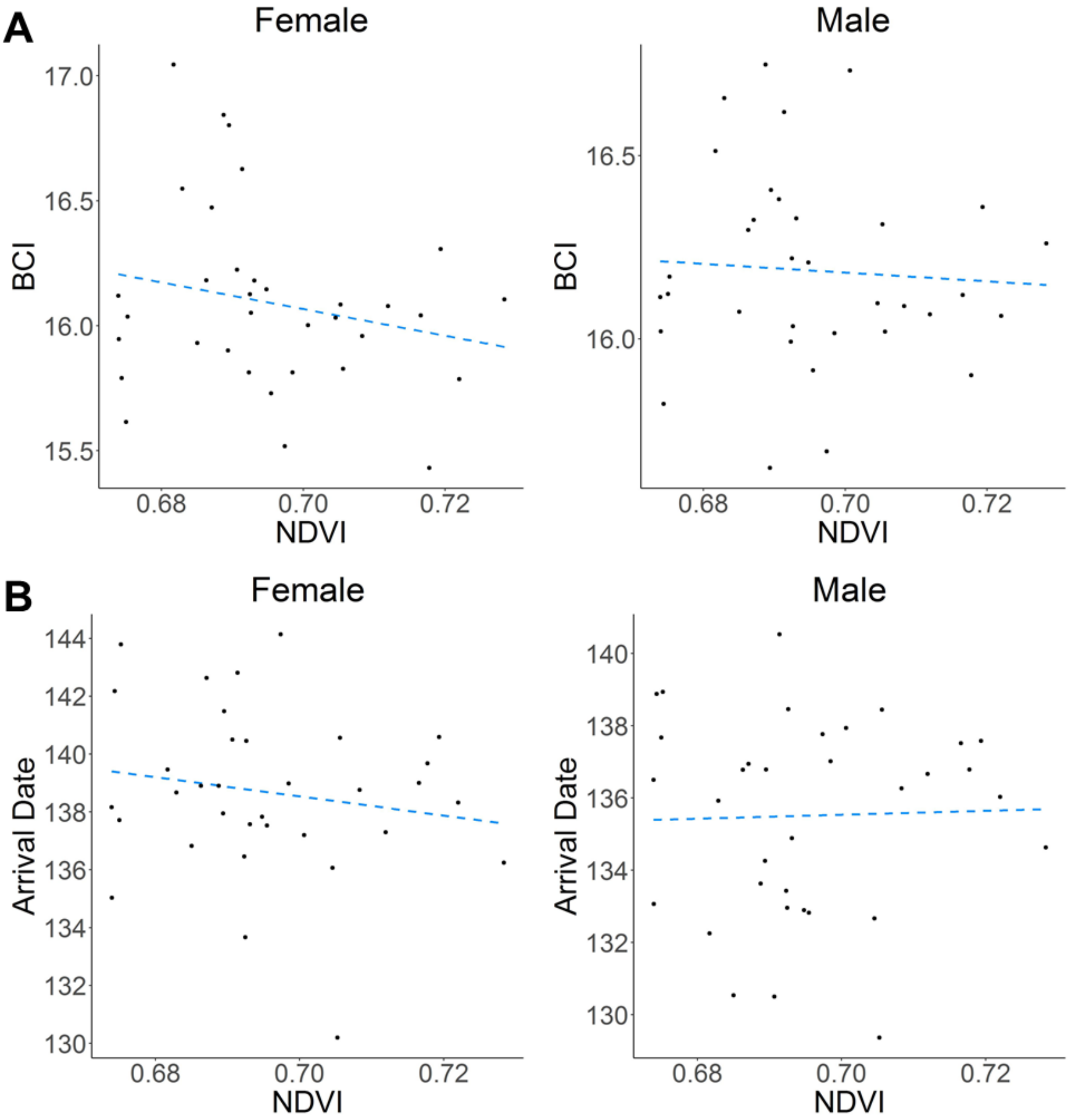

Figure S3: Relationship for female and male Yellow Warblers between mean BCI and overwinter NDVI (A), and median arrival date and overwinter NDVI (B). Dashed lines indicate the relationship between variables was not statistically significant.

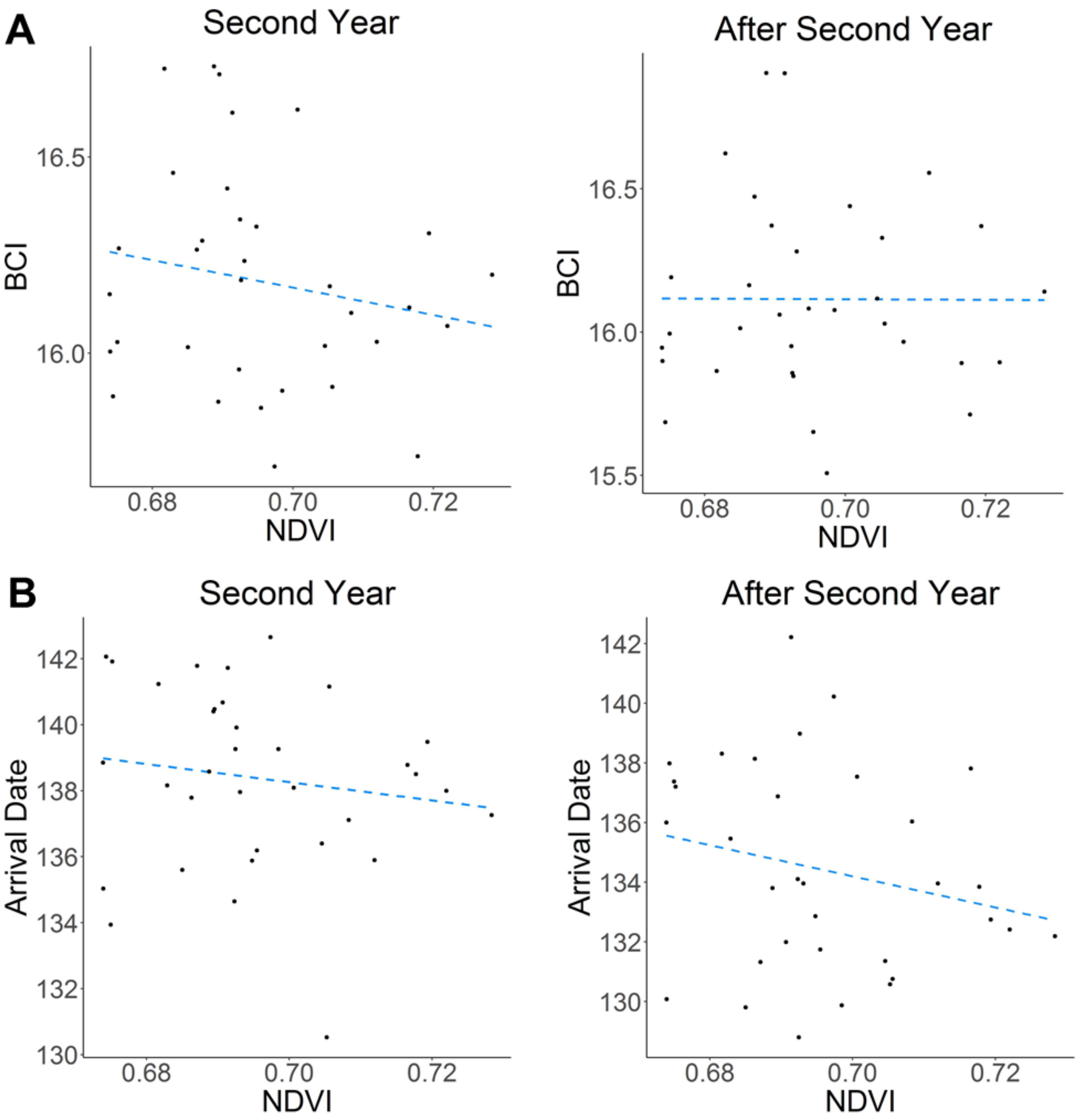

Figure S4: Relationship for second year and after second year Yellow Warblers between mean BCI and overwinter NDVI (A), and median arrival date and overwinter NDVI (B). Dashed lines indicate the relationship between variables was not statistically significant.

Appendix C: NDVI variability

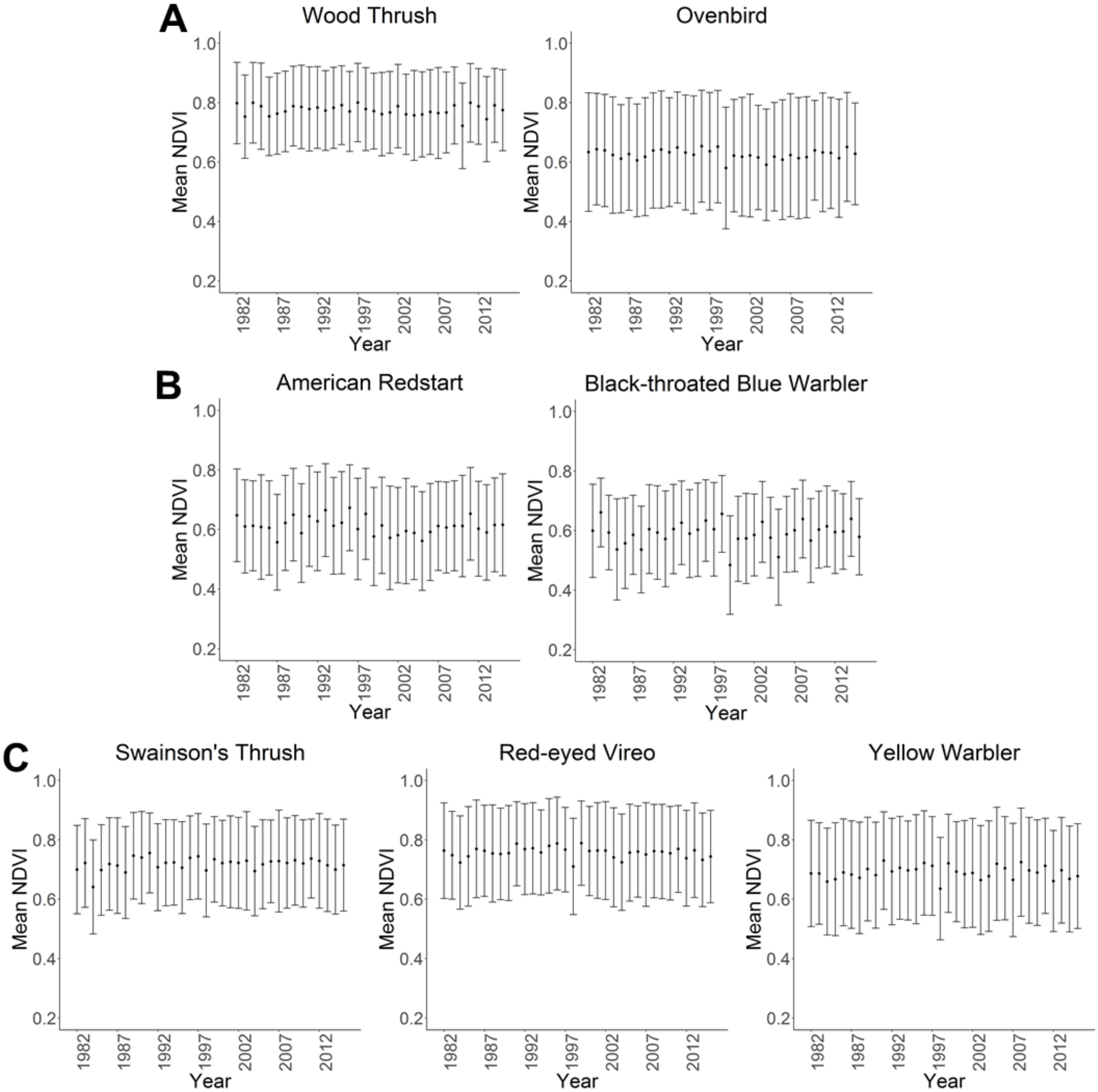

Figure S5: Variation in NDVI shown by the mean and standard deviation for the second half of March for species overwintering in Central America (A), the Caribbean (B), and South America (C). The average number of 8 km by 8 km pixels used in the calculation of mean NDVI in each species' range are as follows: Wood Thrush (504); Ovenbird (3300); American Redstart (277); Black-throated Blue Warbler (309); Swainson's Thrush (136725); Red-eyed Vireo (6490); Yellow Warbler (5115).