Identification and Management of Priority Winter Bird Habitats for Migratory Landbirds

Research Results and Implications for Conserving and Managing Winter Habitat

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Report submitted to the US Fish and Wildlife Service in partial fulfillment of NMBCA grant agreement CA-N801, 6 November 2012

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Executive Summary

In an effort to provide spatially extensive data on habitat needs of Neotropical migratory landbirds during the overwintering period, The Institute for Bird Populations (IBP) and partners across the northern Neotropics established the Monitoreo de Sobrevivencia Invernal (MoSI) program in 2002. MoSI consists of a cooperative network of bird-banding stations that follow standardized mist-netting protocols. For a suite of migratory landbirds on their wintering grounds, MoSI goals are to (1) provide broad-scale data on winter site persistence, annual survival, and body condition; (2) relate site persistence, survival, and body condition to environmental covariates; and (3) use monitoring and research results to inform conservation.

Support from the Neotropical Migratory Bird Conservation Act (NMBCA) has facilitated growth of the MoSI program from the original 33 stations during winter 2002-03 to an average of 70 stations operated per year between winter 2003-04 and winter 2010-11. In total, > 170 stations have operated during at least one winter between 2002-03 and 2010-11. Early results from the MoSI program suggested the importance of overwintering survival on population trends and links between remote-sensed vegetation indices and winter body condition and survival rates. Here we summarize research results and management implications for 26 migratory landbird species from analyses supported through our most recent NMBCA grant. We focus specifically on the distribution of species in relation to remote-sensed variables based on the Enhanced Vegetation Index derived from data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite (http://terra.nasa.gov/) and on relationships between these variables and monthly winter site persistence and annual (between-winter) survival rates.

Nineteen species (73%) had either early- (mean Oct-Dec) or late- (mean Feb-Apr) season EVI values that significantly differed between sites with captures and those without captures. Of these, 11 species had EVI values higher at capture sites than at non-capture sites, and eight species had EVI values lower at capture than at non-capture sites. Five species had EVI difference values that significantly differed between capture and non-capture sites. Four of these had EVI differences that were lower (i.e., more negative change) at capture sites than at sites without captures, while only one species, Hermit Thrush that had differences that were more positive at capture sites.

We found strong support for monthly variation in site persistence for 14 (53% of species) and EVI-related variation in persistence for 17 (65%) of species. Ten species had support for persistence-mean EVI (EVI.MN) relationships, while seven species showed support for relationships between persistence and change in EVI (EVI.DIFF) over the winter. Among species with positive persistence-EVI.MN relationships included Bell's Vireo (*Vireo bellii*) and Northern Waterthrush (*Parkesia noveboracensis*). The positive response highlights the importance of forest cover for this species typical of riparian areas within arid regions of western Mexico. The positive (albeit relatively weak) relationship for Northern Waterthrush, a species commonly associated with standing water, may reflect higher persistence in high-EVI in areas with relatively high moisture levels. In some cases, positive persistence-EVI.MN relationships became weak or negative by the end of the winter season. This could be due to birds in high-quality habitat departing early in spring or movement between habitats. Several species showed

negative relationships between site persistence and EVI.MN, including Hermit Thrush and Ovenbird. We found mixed relationships between site persistence and EVI.DIFF. As for persistence-EVI.MN relationships, persistence-EVI.DIFF relationships were not always consistent through the entire winter and could also represent movement in habitats in response to resource variation as the winter progresses.

We found statistical support for effects of remote-sensed covariates on annual apparent survival for six of 13 species with sufficient multi-year data to be analyzed. We found support for a time-varying negative effect of mean EVI (MEAN), and marginally less support for a negative effect of mean late-season EVI (M.LATE) on annual survival of Ovenbird. We also found support for negative effects of MEAN for Worm-eating Warbler and Yellow Warbler. We found a positive time-specific effect of the mean difference between early and late season EVI (M.DIFF) on annual apparent survival for Prothonotary Warbler, and both positive and negative year-specific effects for Wilson's Warbler. We also found support for a positive effect of mean monthly EVI during the late (mean Feb-Apr) season (M.LATE) for Hooded Warbler.

Remote-sensed covariates that we considered here, although coarse in nature, appear to be useful predictors of within-winter site persistence and annual survival for many of the species that we considered. One imminent threat that will change the distributions of these variables in space and time, and will complicate the ability to manage habitat for these species in the coming years is climate change. Temperature increases, sharp declines in mean precipitation, and increased precipitation variability are all expected across the region. Declines in wet-season precipitation are expected region-wide and could limit early winter increases in EVI, particularly in drier habitats. Declines in dry-season precipitation are also expected in many parts of the region and could increase leaf loss in drier habitats. These declines in precipitation could have strong negative effects on species that overwinter in relatively arid regions and that are dependent on areas that are resilient to drying. In wet forests, increases in seasonal drought could lead to greater synchronization of flowering and fruiting and more annual variability in the abundance of these resources. An additional important threat for forest-inhabiting species, particularly when combined with deleterious effects of climate change, is deforestation, particularly in cloud forests and remaining intact lowland forests.

We suggest that effective conservation efforts will need to consider maintaining a diversity of winter habitats and overwintering strategies to preserve the ability of populations to respond to climate variability and trends that will likely drive changes in these population in the coming years. Better understanding of how various regions and habitats will change under climate scenarios will be needed to most effectively target conservation and management actions within general recommendations about the relative value of specific areas or habitats based on current EVI values. Furthermore, temporal variation in habitat relationships through the winter, high levels of transient birds in our data set, as well as data on small- and large-scale movements of individual birds in the literature suggest that movements during the winter are common and adaptive. We suggest that effective conservation of many of Neotropical migratory songbird species on their wintering grounds will require maintaining networks or mosaics of habitats that span areas that contain from tens to tens of thousands of square kilometers.

Introduction

In an effort to provide spatially extensive data on habitat needs of Neotropical migratory landbirds during the overwintering period, The Institute for Bird Populations (IBP) and partners across the northern Neotropics established the Monitoreo de Sobrevivencia Invernal (MoSI) program in 2002. MoSI consists of a cooperative network of bird-banding stations that follow standardized mist-netting protocols (DeSante et al. 2005). Although such networks have been successfully implemented to study demographic characteristics of breeding bird populations in North America and Europe (Saracco et al. 2008a, DeSante and Kaschube 2009, Robinson et al. 2009), the MoSI program represents the first effort that aims to provide complementary data on overwintering migratory bird populations. For a suite of migratory landbirds on their wintering grounds, MoSI goals are to (1) provide broad-scale data on overwintering survival, annual survival, and body condition; (2) relate survival and body condition to environmental covariates; and (3) use monitoring and research results to inform conservation.

Support from the Neotropical Migratory Bird Conservation Act (NMBCA) has facilitated growth of the MoSI program from the original 33 stations during winter 2002-03 to an average of 70 stations operated per year between winter 2003-04 and winter 2010-11. In total, > 170 stations have operated during at least one winter between 2002-03 and 2010-11 (Fig. 1). Stations operated in the southern United States have also operated under the MoSI protocol (from 2003-04 through 2007-08), and in cases where Neotropical-wintering species have winter ranges that extend into the United States, we have also included data from these stations in analyses. Early results from the MoSI program suggested the likely importance of overwintering survival on population trends (Saracco et al. 2004) and links between remote-sensed vegetation indices and winter body condition and survival rates (Saracco et al. 2008b). Here we summarize research results and habitat management implications derived from our most recent NMBCA-supported work. In particular, we focus on the distribution of species in relation to remote-sensed variables based on the Enhanced Vegetation Index derived from data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite (http://terra.nasa.gov/) and on relationships between these variables and monthly winter site persistence and annual (between-winter) survival rates.

Methods

Field methods

Capture-recapture data were collected at mist-netting stations operated by collaborators of the Monitoreo de Sobrevivencia Invernal (MoSI) program in 14 countries stretching from Mexico to Colombia and in the Caribbean (DeSante et al. 2005) and at mist-netting stations operated by The Institute for Bird Populations on military installations in the southeastern United States (Fig. 1). A typical station consisted of a sampling area of ca. 20 ha. In some cases where multiple stations were immediately adjacent to one another, they were grouped (i.e., treated as a single station) for analyses. A variety of habitats were sampled including temperate forests and edges (US stations), tropical dry forests, scrub, pine-oak forest, cloud forest, lowland rain forest, and agricultural habitats.

Birds were captured at 10-16 mist nets arrayed over the central 12 ha area of stations. Mist nets were operated during 3-5 monthly pulses of field work between November and March of nine winter seasons (2002-03 through 2010-11). Each pulse consisted of 1-3 days of mist-net operation. Migratory birds captured were identified to species, age, and (if possible) sex (Pyle 1997); and, if unbanded, were marked with uniquely numbered, USGS-Bird Banding Laboratory (BBL) metal leg bands. Band numbers of recaptured birds were carefully recorded.

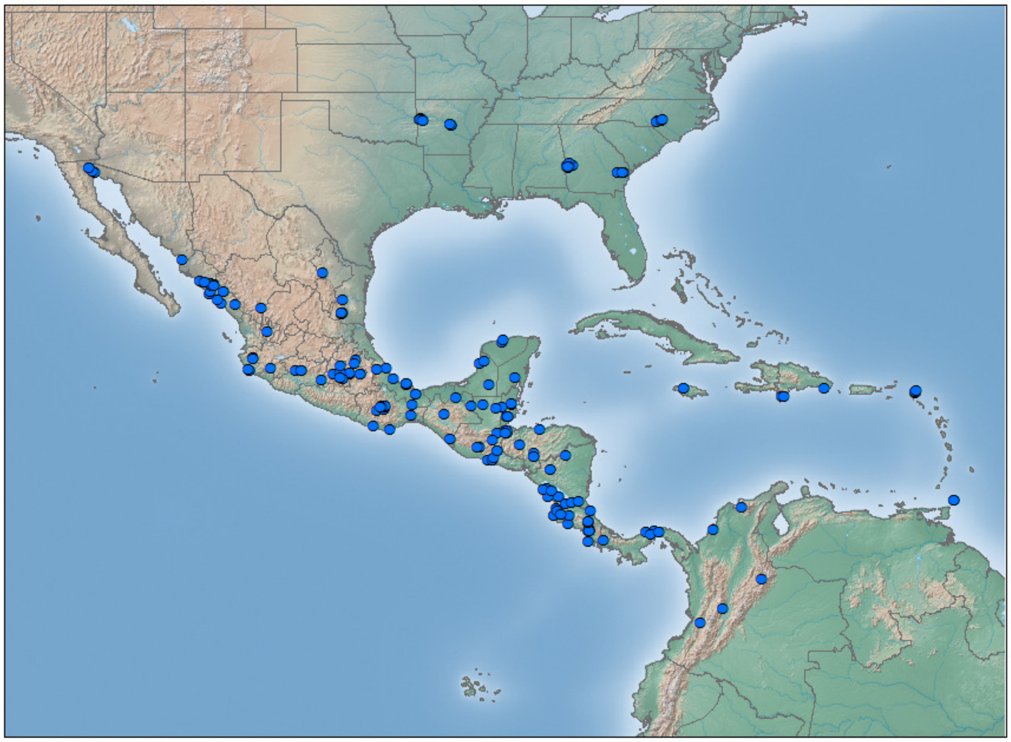

Fig. 1. Distribution of 172 bird-banding stations operated during at least one season as part of the Monitoreo de Sobrevivencia Invernal (MoSI) program in 14 Neotropical countries and 24 Monitoring Avian Winter Survival (MAWS) stations in the southeastern US.

Remote-sensed Habitat Data

We summarized Enhanced Vegetation Index (EVI) data (Glenn et al. 2008) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite (http://terra.nasa.gov/) to calculate covariates for capture-recapture analyses. We based summaries on monthly EVI values at 1-km2 resolution (MODIS product MOD13A2). Prior to summarizing EVI data and extracting station-scale covariates, we removed cloud and aerosol contaminated pixels based on the quality assurance (QA) layer provided with the monthly EVI files (Saleska et al. 2007).

EVI is a composite metric of vegetation greenness that reflects primary productivity (leaf chlorophyll content), leaf area, canopy cover, and vegetation complexity. As such, it effectively captures both structural and seasonal components of habitat quality. EVI outperforms other vegetation indices such as the Normalized Difference Vegetation Index (NDVI) in complex and humid habitats (e.g., tropical rainforest) because it exhibits less saturation at high values (Huete et al. 2006, Xiao et al. 2004) and is less sensitive to clouds and smoke (Miura et al. 1998; Xiao et al. 2003). Relationships between MODIS-derived EVI and local vegetation conditions have not been extensively studied, but case studies have shown strong relationships between EVI and vegetation features measured on the ground, such as leaf area index (Glenn et al. 2008, Park 2009, Potithepa et al. 2010).

For each of seven months (Oct-Apr) extending from one month prior to one month after the typical MoSI season, we extracted station-scale values of EVI that represented interpolated monthly EVI values over the four 1-km2 pixels closest to station coordinates (using the 'bilinear' option of the 'extract' function in the 'raster' R package; Hijmans and van Etten 2012).

We created two covariates for capture-recapture analyses examining within-season dynamics (ORD-MSU model below): EVI.MN and EVI.DIFF. We used EVI.MN to characterize overall habitat complexity and primary productivity for each station and season (e.g., 2003-04); it was derived by averaging the station- and year-specific EVI values across all months (Oct-Apr). We used EVI.DIFF to characterize changes in vegetation greenness over the winter period for each winter and station; it was calculated as the difference between the mean EVI in late months (Feb-Apr) and the mean EVI in early months (Oct-Dec). Positive values of EVI.DIFF represented station-season combinations where vegetation became greener (i.e., increased in productivity) over the winter period, while negative values represented station-season combinations with declining plant productivity over the winter period. EVI change values for the entire study region and study period tended to be negative (mean = -0.040; intraquartile range = -0.071–0.002), as the overwintering period for migrant birds spans the end of the wet season to the end of the dry season across much of the region. Leaf loss during this time can be especially pronounced in tropical deciduous habitats, while increases in vegetation greenness are seen in some regions and habitats that are not water-limited and that tend to have persistent cloud cover during the wet season (e.g., cloud forests, riparian rain forests).

For capture-recapture analyses examining relationships between annual survival and habitat, we calculated three additional station-specific covariates that were averaged across years. EVI.EARLY (mean Oct-Dec EVI), EVI.LATE, (mean Feb-Apr EVI), MEAN (mean Oct-Apr EVI), and M.DIFF (mean[Feb-Apr EVI] - mean [Oct-Dec EVI]; i.e., year-averaged EVI.DIFF values). To provide a picture of the distribution of values of these covariates for the various target species considered, we compared distributions of these variables between MoSI stations with captures of a species to distributions at nearby stations (< 100 km from stations with captures) without captures, based on data from stations with ≥ 5 pulses of data. To provide an idea of how representative MoSI stations were of their surrounding region, we also compared the distribution of EVI variable values at MoSI stations for each species (i.e., capture sites and nearby non-capture sites) to nearby (again < 100 km from stations) randomly selected points.

In addition to EVI, we also used International Geosphere-Biosphere Programme (IGBP) land cover type (MODIS product MOD12Q1; Friedl et al. 2002) as a covariate of detection probability in capture-recapture analyses. The IGBP categorization is a coarse approximation of land-use that does not change across years, and is not an especially sensitive indicator of habitat quality. We only use this broad classification system to help correct for differences in capture probabilities between contrasting habitat types (see below).

Capture-recapture Analyses

Modeling within-winter site persistence and between-winter survival in an open robust design multi-state framework.—We employed two approaches to modeling the capture-recapture data. Both were based on an open robust design multi-state framework (Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Kendall and Nichols 2002). These models are well-suited to exploiting the hierarchical nature of our sampling scheme and provide a novel platform for incorporating permanent and temporary emigration into capture-recapture analyses. Here we provide a brief description of modeled parameters, and the implementation of models in Program MARK (White and Burnham 1999). We provide additional model detail and a thorough comparison of methods for treating resident and non-resident individuals in capture-recapture models in Ruiz-Gutierrez et al. (in review).

For both of our modeling approaches, we constructed models for each species independently. We considered each winter season from 2003-04 to 2010-11 to be a primary sampling occasion and the five monthly pulses (1-5 d) of mist-netting within each winter to be secondary sampling occasions. Multiple sampling days within secondary sampling occasions were collapsed to provide a single capture event per month. Populations were assumed to be open across primary and secondary sampling occasions allowing individuals to enter or leave sampling sites at any time. Such movement can be an important aspect of migratory bird populations during both breeding and non-breeding seasons.

Within-season analyses: open robust design multi-state models with state uncertainty.— To estimate monthly winter site persistence, we applied an open robust design multi-state model with state uncertainty (ORD-MSU) to capture-recapture data using Program MARK (White and Burnham 1999). The ORD-MSU model is based on an open robust design multi-state framework (Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Kendall and Nichols 2002). In this class of models, the population is assumed to be open across secondary samples (months) within each primary season (overwintering period). The addition of an uncertain state allows us to model demographic characteristics independently for resident and non-resident individuals, without defining *a priori* the state of each individual. Therefore, this model provides a novel platform for estimating overwintering persistence of resident and non-resident, or transient migratory birds in their overwintering grounds. We provide additional model detail for the use of the uncertain state in the open robust design framework for treating resident and non-resident individuals in Ruiz-Gutiérrez et al. (in review).

The ORD-MSU model has eight estimable parameters in Program MARK: S_s is the apparent survival rate between primary occasions for state *s;* ψ^{rs} is the transition probability from state *r* to state *s* between primary occasions; $pent_t^s$ is the probability of entry onto the study area for state *s* between secondary occasions *t* and *t* + 1; ϕ_t^s is the probability of remaining on the study area for state *s* between secondary occasions *t* and *t* + 1, given that the individual had previously entered the study area; p_t^s is the capture probability of the individual on the study area for state *s* at time *t*, given that the individual is present on the study area at time *t*; π^s is the proportion of the population released in state *s* for each primary period; Ω^s is the proportion of the population in state *s* for each primary period; and Δ^s is the probability of correctly classifying the state of a captured individual for state *s*.

We used the ORD-MSU model to examine within-winter demographic characteristics for 26 overwintering migrant bird species. We considered each winter season from 2003-04 to 2010-11 to be a primary sampling occasion and the five monthly pulses (Nov-Mar) of mist-netting within each winter to be secondary sampling occasions. Multiple sampling days for each monthly secondary sampling occasion were collapsed to provide a single capture event per month. Populations were assumed to be open across secondary sampling occasions for each winter season, allowing individuals to enter or leave sampling sites between these occasions. Such movement can be an important aspect of migratory bird populations during both breeding and non-breeding seasons.

For our application, we 'stacked' primary samples for all seasons to create single-season capture histories consisting of $t = 1, ..., 5$ secondary sampling occasions, across all stations. For each station-primary sampling combination, we considered individuals to be in one of two possible states: overwintering resident (*r*) or non-resident (*n*). Because we collapsed our data into a single season, annual survival (*S*) and transition probabilities between states (ψ^{rs}) across years were fixed to zero. This also means that we are assuming that the status of resident or non-resident for a given year does not depend on the previous year. We did not assign any individuals to a state (*r* or *n*), and all captures were indexed as a "u" instead of a "1" in our capture histories. As a result, we also fixed the Δ^s parameter to zero. We further set persistence of non-residents (ϕ^n) to zero and set capture probabilities of non-residents and residents as equal ($p_t^r = p_t^n$). Therefore, we were left with five estimable parameters in our model: ϕ^r, Ω^r, Ω^r, p^r, $pent^n$, and $pent^r$.

We constructed a set of models representing hypotheses about temporal and spatial variation in demographic parameters and capture probability, and relationships of these parameters to environmental covariates (Table 1). We considered three parameterizations for the proportion of resident individuals (Ω^r): one that constrained the proportion of residents to be constant over space and time (i.e. intercept only or 'dot' [·] models); one that allowed the proportion of residents to vary by EVI.MN; and one that allowed the proportion to vary as a continuous effect of winter season, SEAS (i.e., a trend model). For detection probability (p^r), we considered seven models: a constant model; one that allowed detection probability to vary by month (t); as a function of EVI.MN; as a function of SEAS; one as a function of land cover category, IGBP; and two additive models, SEAS + EVI.MN and SEAS + IGBP. We considered three parameterizations for the probability of entry of non-resident ($pent^n$) and resident ($pent^r$)

individuals: constant (·); varying by month (t); and a model for trend across secondary sampling occasions (T). We tested a total of 13 models for persistence of resident individuals (ϕ^r): both constant (·) and monthly time-varying (t) models; a model with a SEAS effect; additive (t + SEAS) and interaction (t × SEAS) models; a model with a constant EVI.MN effect; additive (t + EVI.MN) and full interaction (t × EVI.MN) models; a model with an EVI.DIFF effect; additive (t + EVI.DIFF) and interaction (t × EVI.DIFF) models; and additive SEAS + EVI.MN and SEAS+ EVI.DIFF models.

We ran models for each species independently. To determine goodness of fit, we ran Cormack-Jolly-Seber (CJS) models to estimate survival and recapture probability on our stacked, single-season data, replacing the "u" in each capture history with a "1", and estimating the variation inflation factor ($\hat{c}$) using the median c-hat routine in Program MARK. We present all model averaged parameter estimates. Relationships with habitat covariates were based on the model with the most support from the data.

Annual survival analyses: open robust design multi-state models.— The ORD-MSU model detailed above is well-suited to modeling both within- and between-year aspects of the demography of resident and non-resident birds because it makes no presupposition about the state of individuals in any primary sampling period. However (as noted above), limitations of our data set (small sample sizes, inconsistencies in sampling among stations), only allowed modeling within-year aspects of the demography of target species. For a subset of 13 species with sufficient between-year captures, we modeled within- and between-year demography of birds using open robust design multi-state (ORD-MS) models. In their simplest form, these models assume that all captured individuals in a given year were winter residents in that year (i.e., state = r). However, to relax this assumption and to minimize negative bias on estimates of winter site persistence due to permanent emigration, we also considered TSM models (Pradel et al. 1997) within the ORD-MS framework (see detail below).

For the multi-season ORD-MS models, we modeled the following parameters: S_{ij}, the apparent survival probability of birds at station i between winter seasons j and j + 1; $\psi^{r\rightarrow n}$ and $\psi^{n\rightarrow r}$, the state transition probabilities from resident to non-resident and non-resident to resident between winter seasons; site persistence, ϕ_{ij} the probability of a bird remaining alive and on study area i during winter j, given that it had entered the study area during that winter; $pent_k$, the probability of entry onto study areas during secondary sampling occasion k given availability on study areas (i.e., winter residents only); and p_{ij}, the probability of capturing a bird at station i during season j given that it was present on the study area during season j. Given our assumption that captured individuals in a given year were winter residents in that year, we set parameters for site persistence, entry probability, and capture probability for birds in the unobservable state (i.e., those individuals not on study areas and so not available for sampling in a given year) as constant and equal to zero. Note that we also constrained survival probabilities for unobservable and observable individuals to be equal based on suggestions previously determined as necessary for multi-state mark-recapture models with a single unobservable state (Kendall and Nichols 2002).

We considered 15 parameterizations for between-winter annual survival, S_{ij}. These included a space-time constant model; a model with continuous season effects, SEAS; a model with MEAN effects (as defined in Remote-sensed Habitat Data above); a model allowing survival to vary as a function of mean monthly late-season EVI (Feb-Apr) averaged across years, EVI.LATE; the mean difference between mean monthly late-season EVI (Feb-Apr) and mean monthly early-season EVI (Oct-Dec), M.DIFF; and all additive and interaction models for each averaged spatially varying EVI covariate and SEAS effects. For between-season state transition probabilities, $\psi^{r \to n}$ and $\psi^{n \to r}$, we only considered space-time constant models. For site persistence, ϕ_{ij}, we considered 12 parameterizations, including a space-time constant model; models with SEAS , MEAN, and M.DIFF effects; a model with early-season EVI (Feb-Apr) averaged across years, EVI.EARLY; models with additive spatially varying EVI covariates and annual SEAS effects. To test for the importance of permanent emigrants in samples and to reduce negative bias in site-persistence estimates due to these emigrants, we repeated each of the ϕ_{ij} parameterizations described above for a TSM model, such that survival estimates were based on only the second and subsequent intervals after capture, and covariates in were only included as effects for these later intervals. We differentiate these TSM models from base models by denoting site-persistence as ϕ_{ij}^{2+}. We considered space-time constant, t, and T models for pent_k. For capture probability, p_{ijk}, we considered space-time constant models; single variable models with IGBP effects, MEAN effects, and SEAS effects; and additive two-variable models.

To test for goodness of fit, we were not able to use the median c-hat procedure found in Program MARK, for it is not yet available for these classes of models. Therefore, we first conducted a sensitivity analysis for each species, and examined changes in model weight and support as defined by ΔAIC_c, with incrementing values of the median c-hat coefficient for each species within Program MARK. We present model-averaged estimates (Burnham and Anderson 2002). We present model-averaged estimates (Burnham and Anderson 2002).

Results and Discussion

Distribution of EVI values

Nineteen species (73%) had either early- (mean Oct-Dec) or late- (mean Feb-Apr) season EVI values that significantly differed (t-test) between sites with captures and those without captures. Of these, 11 species had EVI values higher at capture sites than at non-capture sites, and eight species had EVI values lower at capture than at non-capture sites (Figs. 2-3). Five species had EVI difference values that significantly differed between capture and non-capture sites (Fig. 4). Four of these had EVI differences that were lower (i.e., more negative change) at capture sites than at sites without captures, while only one species, Hermit Thrush that had differences that were more positive at capture sites (partly due to its common occurrence at deciduous US sites that begin greening up in early spring).

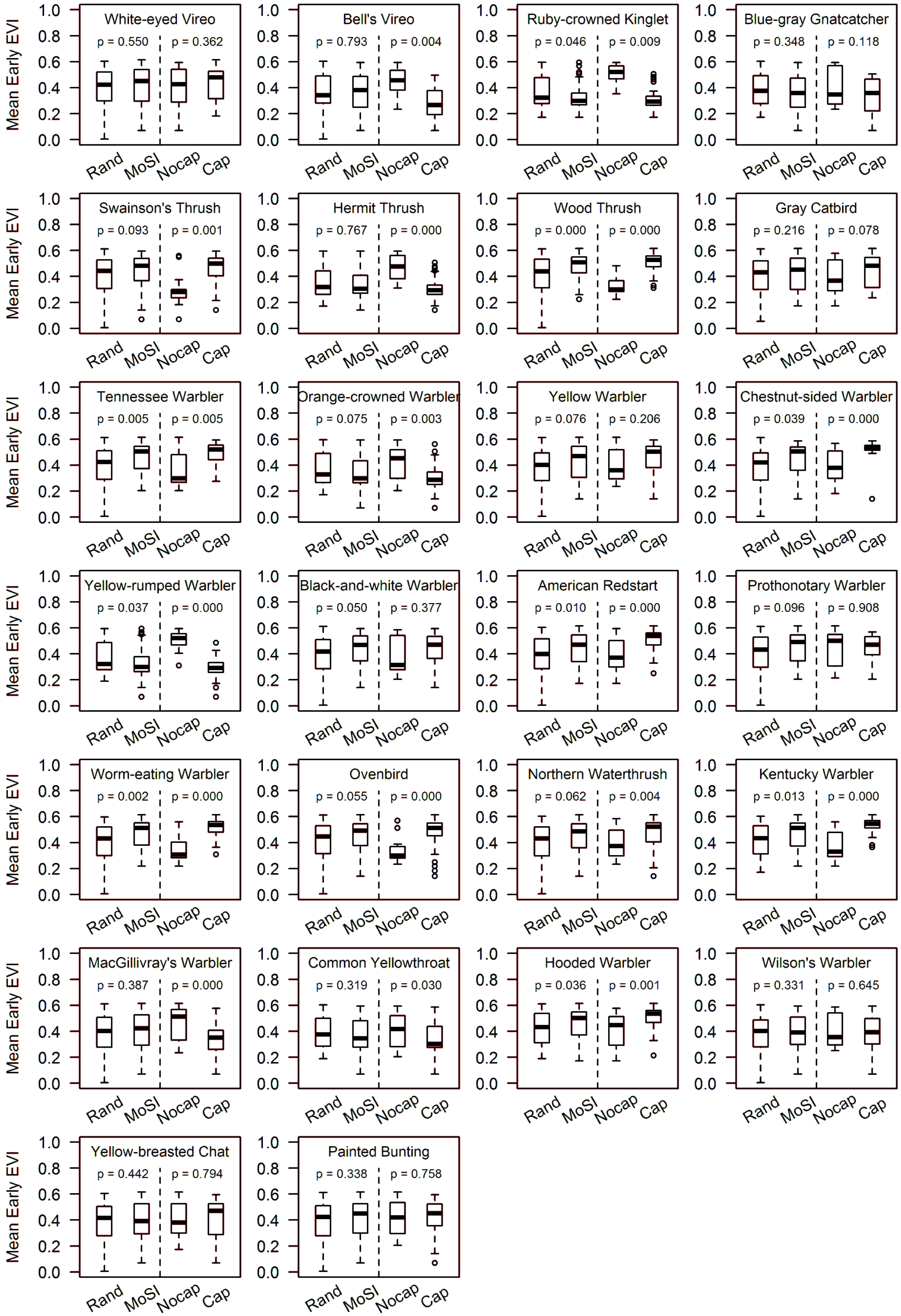

Fig. 2. Distribution of mean early-season (Oct-Dec) values of the Enhanced Vegetation Index (EVI) at MoSI stations compared to nearby random stations (left) and between MoSI sites with captures and sites without captures (but with ≥ 5 pulses of data). P-values show significance level from t-test.

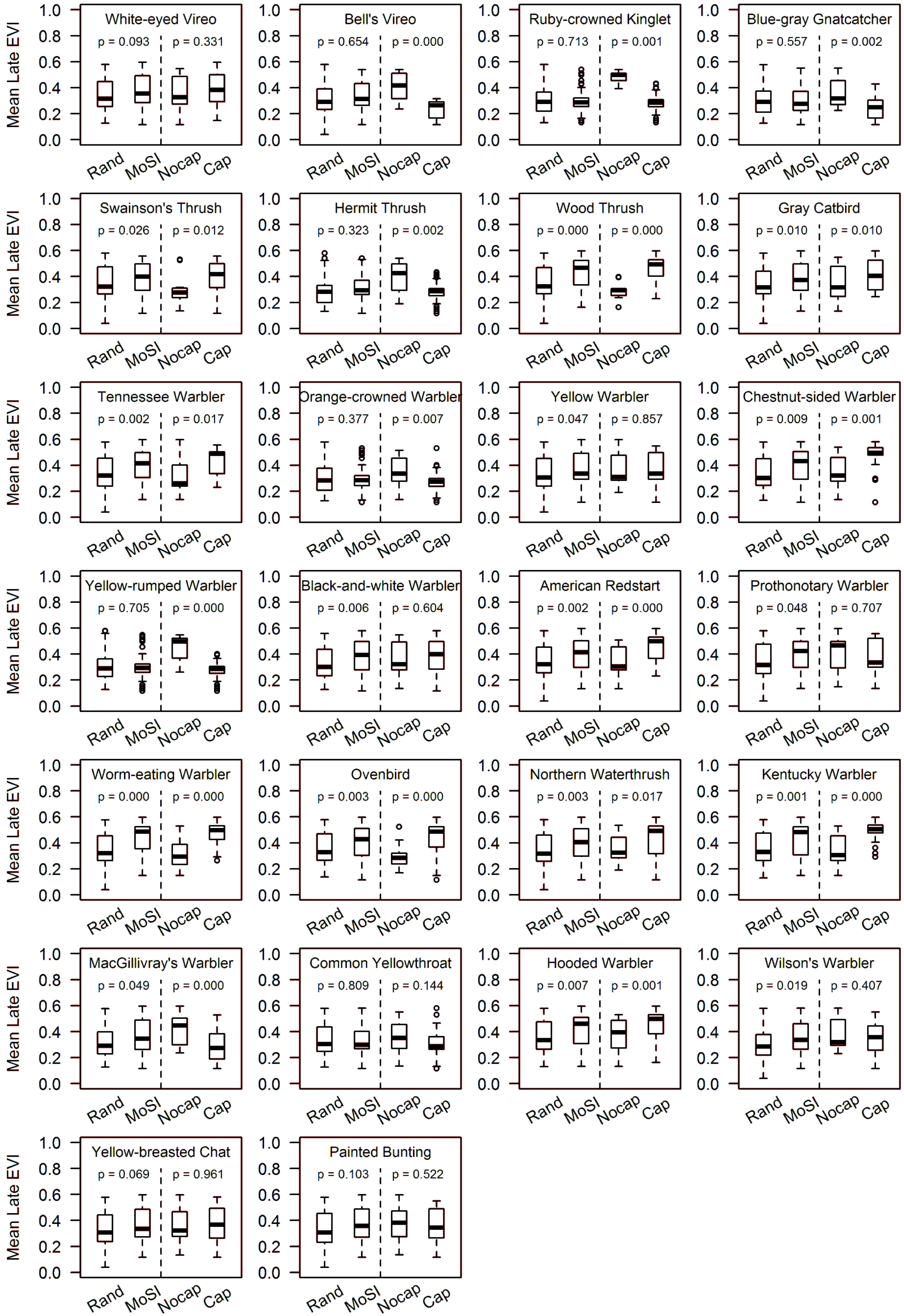

Fig. 3. Distribution of mean late-season (Feb-Apr) values of the Enhanced Vegetation Index (EVI) at MoSI stations compared to nearby random stations (left) and between MoSI sites with captures and sites without captures (but with ≥ 5 pulses of data). P-values show significance level from t-test.

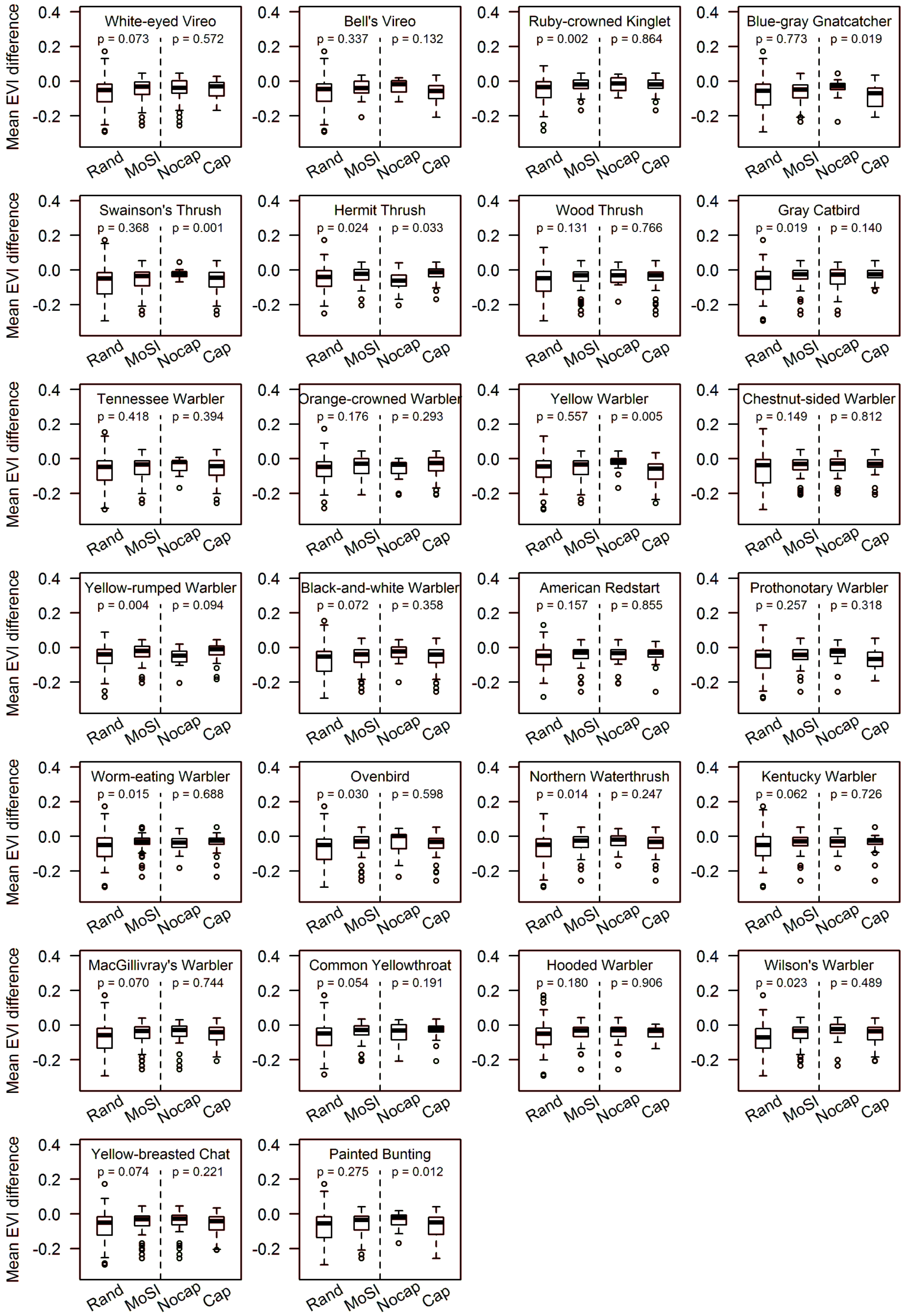

Fig. 4. Distribution of differences in the Enhanced Vegetation Index (EVI) between early and late winter at MoSI stations compared to nearby random stations (left) and between MoSI sites with captures and sites without captures (but with ≥ 5 pulses of data). P-values show significance level from t-test.

EVI variables tended to be more positive at MoSI sites compared to nearby random sites (Figs. 3-5). For early-season EVI, eight species had significantly higher values at MoSI sites compared to random sites, while only two species had significantly lower values at MoSI sites. For late-season EVI, differences were greater: 16 (61%) species had significantly higher values at MoSI sites compared to random sites, and there were no significantly lower differences. For the early-to-late season difference in EVI, nine species had significantly more positive values at MoSI sites than at random sites.

Within-season Site Persistence

Detailed results of within-winter dynamics for 26 species are presented in Saracco et al. (in review). Here we provide a brief summary of results for the resident site persistence parameter and how it related to EVI covariates for several of the 26 species for which we were able to obtain estimates.

We found strong support for monthly variation in site persistence for 14 (53% of species) and EVI-related variation in persistence for 17 (65%) of species. Ten species had support for persistence-EVI.MN relationships, while 7 species showed support for persistence-EVI.DIFF relationships. Among species with positive persistence-EVI.MN relationships included Bell's Vireo (*Vireo bellii*) and Northern Waterthrush (*Parkesia noveboracensis*) (Fig. 5). The positive response of Bell's Vireo persistence to EVI.MN highlights the importance of forest cover for this species typical of riparian areas within arid regions of western Mexico. The positive (albeit relatively weak) relationship for Northern Waterthrush, a species commonly associated with standing water, may reflect higher persistence in high-EVI in areas with relatively high moisture levels.

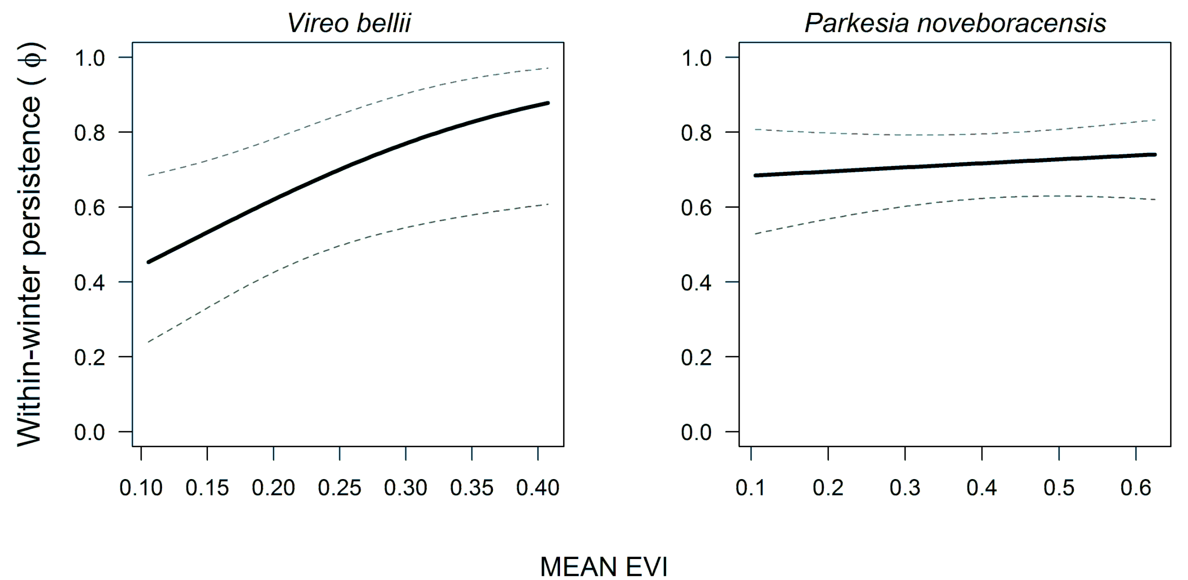

Fig. 5. Predicted site persistence for two species with positive relationships between persistence and mean EVI (EVI.MN).

In some cases, persistence-EVI.MN relationships were generally positive but changed over the winter period. For example, Prothonotary Warbler persistence was positively related to EVI.MN for all but the last (Feb-Mar) time interval (Fig. 6). Reversal of the positive EVI.MN-persistence relationship late in the season could be due to birds in high-quality habitat departing early in spring, which may incur benefits for obtaining high quality breeding territories (Marra et al. 1998). This would seem to be reflected in large numbers of transient birds entering populations between January and February (Saracco et al. in review). However, this result may also reflect movement between habitats. For example, in mangrove (*Avecinnia* spp.) habitat in Costa Rica, mangrove leaves become coated with salt crystals by mid-winter, at which point birds appear to move to adjacent dry forest to feed in flowers of dry forest trees and lianas (J. Woodcock, pers. comm.).

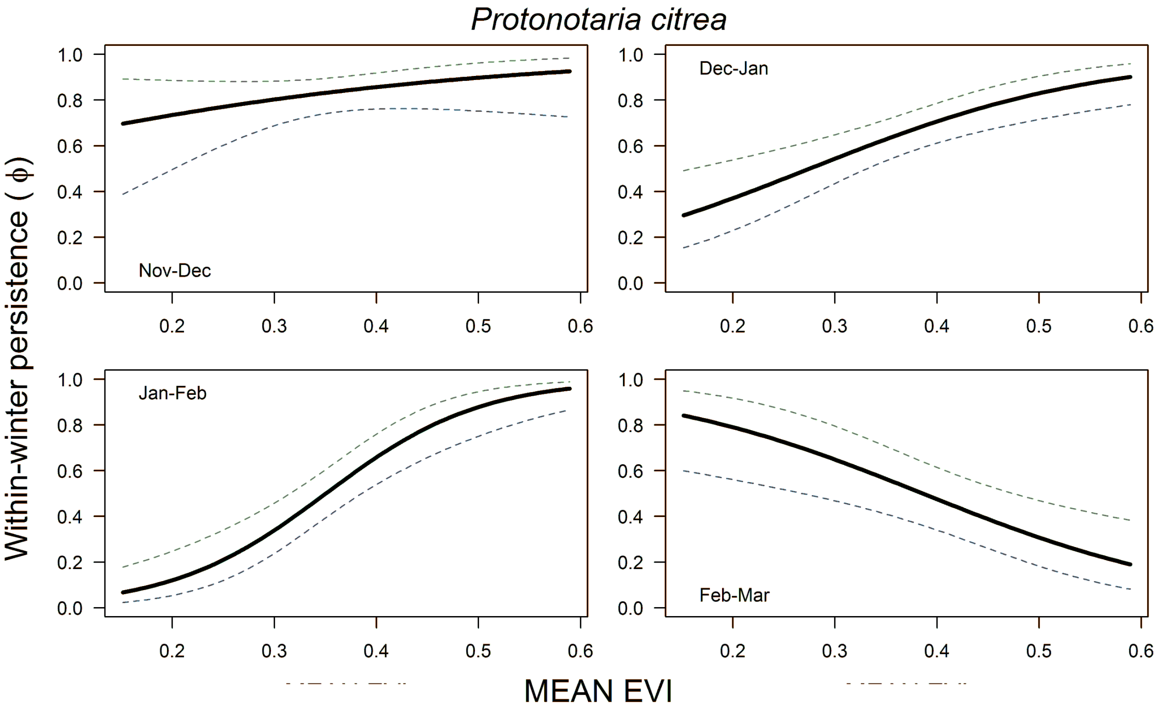

Fig. 6. Predicted site persistence for Prothonotary Warbler in relation to mean EVI (EVI.MN) for each of four monthly time intervals.

Several species showed evidence of negative relationships between site persistence and EVI.MN, including Hermit Thrush and Ovenbird (Fig. 7). For Hermit Thrush, this likely reflects a tendency to occur in relatively dense shrubby habitats that may have relatively low EVI values compared to more heavily forested sites. In addition, many Hermit Thrush captures were from southeast US stations with deciduous trees that lose leaves earlier and more completely than dry tropical habitats farther south. For Ovenbird, site persistence was high overall and the negative persistence-EVI relationship was relatively weak.

We found mixed relationships between winter site persistence and changes in EVI over the winter season (EVI.DIFF). For example, two species commonly found in relatively mesic forested habitats of Southeastern Mexico, Central America and the Greater Antilles, Worm-eating Warbler and Chestnut-sided Warbler showed opposite responses to EVI.DIFF (Fig. 8). Worm-eating Warbler is generally a species of the understory, where vegetation may be light-limited and for which EVI may increase as a result of plant productivity increases as irradiance peaks during the dry season. Insect herbivores of the understory might likewise increase during that time (Coley and Barone 1996). In contrast, Chestnut-sided Warbler tends to forage in the mid- and upper-stories of forests where light may not be limited, and it may also be responding to flowers and fruit resources that may increase as EVI declines (Richardson and Brauning 1995).

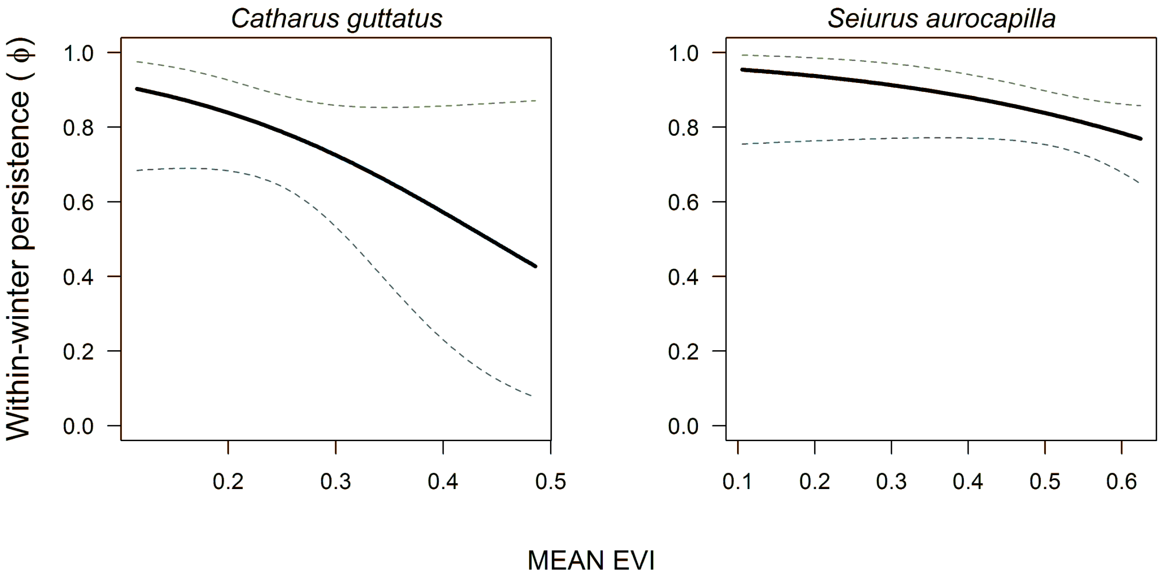

Fig. 7. Predicted site persistence for two species with negative relationships between persistence and mean EVI (EVI.MN).

As for persistence-EVI.MN relationships, persistence-EVI.DIFF relationships were also not always consistent through the entire winter period. For example, Orange-crowned Warbler persistence was strongly negatively related to EVI.DIFF early in the season, but later this relationship reversed (Fig. 9). Although at least on subspecies (*Oreothlypis celata lutescens*) is an early spring migrant (Gilbert et al. 2010), changes in habitat-persistence relationships in latewinter were not accompanied by large influxes of transient birds (as for Prothonotary Warbler; Saracco et al. in review). Capture rates of this species at MoSI stations suggested movements to high-elevation habitats in western Mexico that track temporal changes in leaf area (Saracco et al. 2008). At large scales, model predictions suggest that persistence is high throughout much of the winter range in Mexico in early winter but as conditions get drier late in winter persistence is highest in the northern temperate part of the winter range and low in western and northeastern Mexico (Fig. 10).

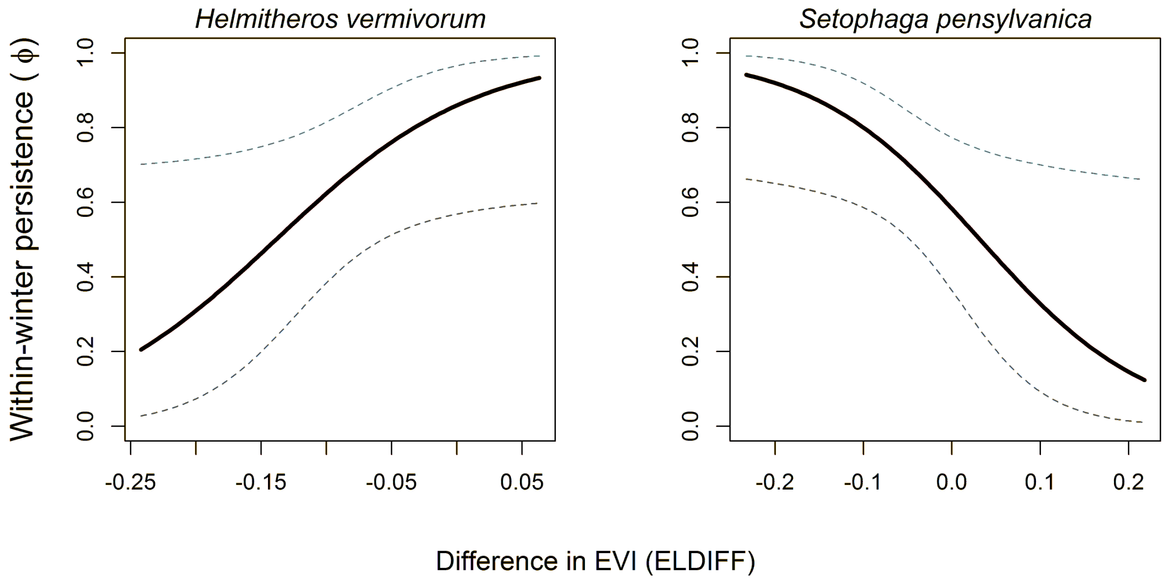

Fig. 8. Predicted site persistence for two species of mesic forest habitats in relation to changes in EVI over the winter period (EVI.DIFF)

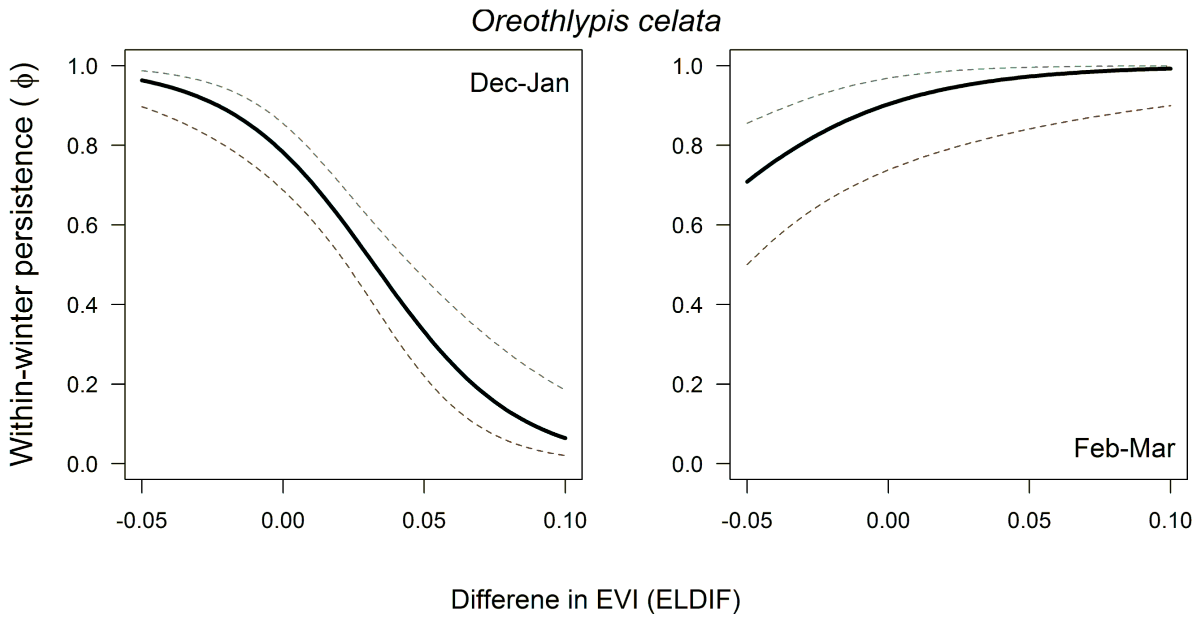

Fig. 9. Predicted site persistence for Orange-crowned Warbler during two winter time intervals in relation to changes in EVI from early to late winter (EVI.DIFF).

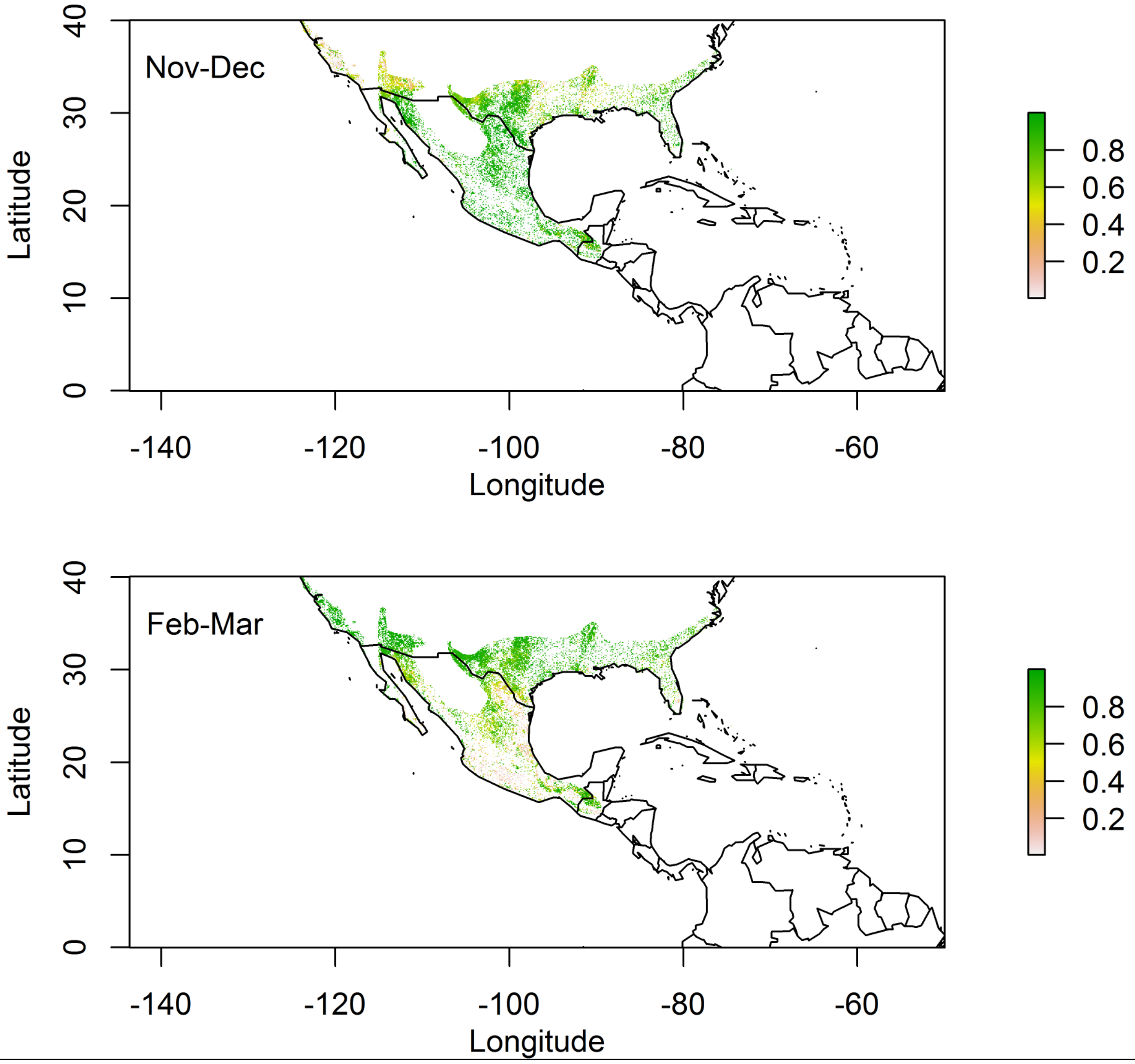

Fig. 10. Predicted site persistence for Orange-crowned Warbler across its winter range based on relationships shown in Fig. 9. Predictions were clipped to winter ranges (Ridgeway et al. 2007) and only include predictions for International Geosphere-Biosphere Programme (IGBP) land cover types for which the species was recorded in the MoSI data set (Friedl et al. 2002).

Annual Survival Probability

We estimated annual apparent survival probabilities (*S*) for 13 species of migratory landbirds (Table 1). We found statistical support for effects of remote-sensed covariates on annual apparent survival for six of these species (Figs. 11-12). We found support for a time-varying negative effect of mean EVI (MEAN), and marginally less support for a weak negative effect of mean late-season EVI (M.LATE) for Ovenbird. We found support for negative effects of MEAN for Worm-eating Warbler and a slight effect for Yellow Warbler (Figure 11).We found a positive time-specific effect of the mean difference between early and late season EVI (M.DIFF) on annual apparent survival for Prothonotary Warblerand both positive and negative time-specific effects for Wilson's Warbler (Figure 12). We also found support for a positive effect of mean monthly EVI during the late (mean Feb-Apr) season (M.LATE) for Hooded Warbler (Figure 12).

Table 1. Model-averaged annual survival rate estimates (S), standard errors (SE) and 95% confidence bounds (LCL, UCL) for 13 species based on data from the Monitoreo de Sobrevivencia Invernal (MoSI) program 2002-03 through 2010-11.

Species		*S*	SE	LCI	UCI
Blue-gray Gnatcatcher	(*Polioptila caerulea*)	0.238	0.116	0.082	0.521
Swainson's Thrush	(*Catharus ustulatus*)	0.427	0.041	0.349	0.509
Wood Thrush	(*Hylocichla mustelina*)	0.393	0.092	0.234	0.579
Ovenbird	(*Seiurus aurocapilla*)	0.140-0.99	0.008-0.222	0.035	0.999
Worm-eating Warbler	(*Helmitheros vermivorum*)	0.467	0.072	0.332	0.606
Northern Waterthrush	(*Parkesia noveboracensis*)	0.457	0.209	0.139	0.814
Black-and-white Warbler	(*Mniotilta varia*)	0.444	0.656	0.004	0.993
Prothonotary Warbler	(*Protonotaria citrea*)	0.438-0.699	0.162-0.385	0.061	0.988
Tennessee Warbler	(*Oreothlypis peregrina*)	0.541	0.551	0.015	0.989
Kentucky Warbler	(*Geothlypis formosa*)	0.918	0.33	0.002	1.000
Hooded Warbler	(*Setophaga citrina*)	0.334	0.171	0.100	0.694
Yellow Warbler	(*Setophaga petechia*)	0.446	0.119	0.239	0.675
Wilson's Warbler	(*Cardellina pusilla*)	0.345-0.972	0.133-0.306	0.128	0.656

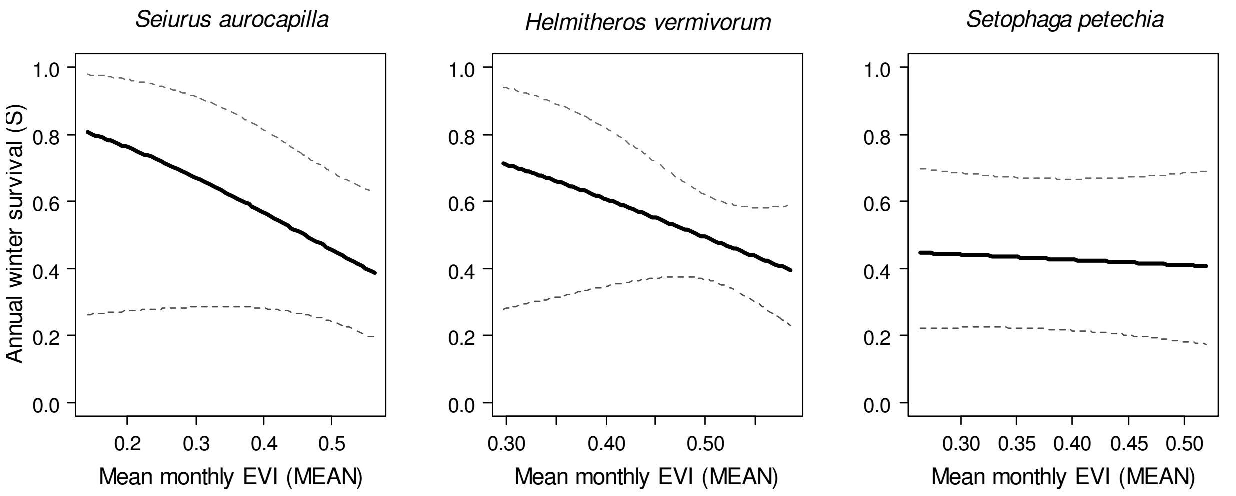

Fig. 11. Predicted annual survival as a function of mean monthly EVI (MEAN).

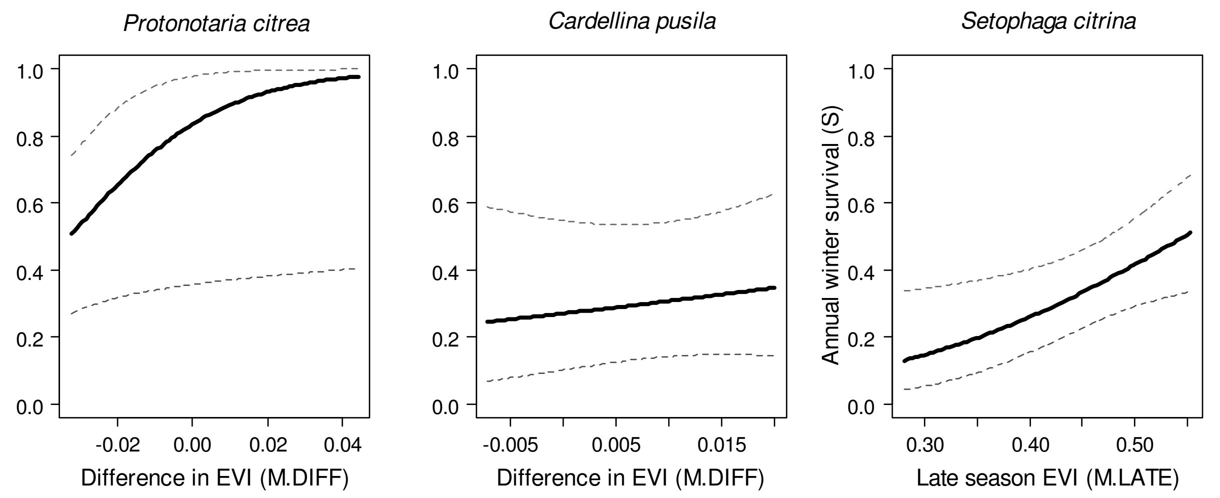

Fig. 12. Predicted annual survival as a function of the difference in monthly EVI between the early (Oct-Dec) and late season (Jan-Mar) (M.DIFF).

Implications for Management of Winter Habitat

Research on habitat needs of Neotropical migratory birds on their wintering grounds has lagged far behind research on breeding habitat needs of these species (Faaborg et al. 2010). However, there is an increasing appreciation for the role that the non-breeding season may play in driving annual survival rates (Mazerolle et al. 2005, LaManna et al. 2012), breeding productivity (Nott et al. 2002, Norris et al. 2004), and population trends (DeSante et al. 2001, Saracco et al. 2008b, Wilson et al. 2011) in these species. The need for more and better data on the wintering grounds is pressing because many of of these species are experiencing long-term population declines (Sauer et al. 2011, Sauer and Link 2011).

Remote-sensed covariates that we considered here, although coarse in nature, appear to be useful predictors of within-winter site persistence and annual survival for many of the species that we considered. One imminent threat that will change the distributions of these variables in space and time, and will complicate the ability to manage habitat for these species in the coming years is climate change. Temperature increases, sharp declines in mean precipitation, and increased precipitation variability are all expected across the region (Giorgi 2006, Neelin et al. 2006, Parry et al. 2007, Karmalkar et al. 2011). Declines in wet-season precipitation are expected region-wide (Neelin et al. 2006, Karmalkar et al. 2011) and could limit early winter increases in EVI, particularly in drier habitats. Declines in dry-season precipitation are also expected in many parts of the region and could increase leaf loss in drier habitats (Bradley et al. 2011). These declines in precipitation could have particularly strong negative effects on species that overwinter in relatively arid regions and that are dependent on areas that are resilient to drying (e.g., importance of riparian areas for Bell's Vireo). In wet forests, increases in seasonal drought could lead to greater synchronization of flowering and fruiting and more annual variability in the abundance of these resources (Wright et al. 1999). An additional important threat for forest-inhabiting species, particularly when combined with deleterious effects of climate change, is deforestation, particularly in cloud forests and remaining intact lowland forests (e.g., the southern Yucatán, the Petén of Guatemala, Mosquitia in Honduras and Nicaragua; Vester et al. 2007, Bray 2010, Ponce-Reyes 2012).

We suggest that effective conservation efforts will need to consider maintaining a diversity of winter habitats and overwintering strategies to preserve the ability of populations to respond to high climate variability and climate trends that will likely drive changes in these population in the coming years. In some cases, such as Prothonotary Warbler and Worm-eating Warbler, prioritizing conservation of relatively high EVI valued habitats within their wintering ranges seems a relatively straight-forward general recommendation. However, better understanding of how various regions and habitats will change under various climate scenarios will be needed to most effectively target conservation and management actions within that general recommendation. In addition, we found that in general transient birds are a common feature of migratory landbirds throughout the winter period, and for at least some species movements appear to represent movements among regions or habitats and may reflect tracking of resources throughout the winter period (see Saracco et al. in review for detail). These findings are consistent with data from individual thrushes tracked with geolocators, which show that at least some individuals show relatively slow migration movements in autumn and can show large mid-season movements (Stuchbury et al. 2009, Heckscher et al. 2011, Delmore et al. 2012). Documentation of small-scale movements of individuals between habitats that are consistent between years also suggest that such movements may be common and adaptive. Thus, we suggest that effective conservation of many of Neotropical migratory songbird species on their wintering grounds will require maintaining networks or mosaics of habitats that span areas that contain from tens to tens of thousands of square kilometers.

Acknowledgements

Funding for data collection and analyses presented here was provided by the U.S. Fish and Wildlife Service's Neotropical Migratory Bird Conservation Act. Additional funding for the MoSI (and US MAWS) program has been provided by the U. S. Department of Defense's Natural Resource Legacy Program, The University of California at Los Angeles through grants with the NIH-NSF and UC-Mexus, The Fledgling Fund, the DuPont Corporation, private donations to The Institute for Bird Populations (IBP) and by individual MoSI program cooperators and their funders. P. Pyle coordinated the MoSI program at IBP. C. Romo de Vivar Alvarez (Mexico), M. Guierrez, and S. Morales (Central America) served as regional coordinators in past years. Field methods were developed in consultation with T. S. Sillett, R. Siegel, A. Cerezo, and B. Milá. N. Michel and D. Kaschube developed database structures, verification programs and data sheets; and R. Taylor managed all data bases.

We are indebted to the many collaborators that operated MoSI stations and contributed data. These include F. Aceituno, J. L. Alcántara, D. Anderson, L. Andino, I. Angarita Martinez, K. Aparicio, R. Aragon, S. Arenas, O. Arróliga, A. de Avila, C. Batista, A. Brown, E. Castañeda, A. Cerezo, J. P. Ceyla, N. Chavez, Y. Cifuentes. R. Coates, N. Collier, D. Collister, D. Curiel, L. and G. Duriaux-Chavarría, H. Dougherty, C. Elton, N. Ferriz, H. M. Espinosa Flores, V. Galán,

H. A. Garza Torres, C. Gonzales, M. Gonzales, M. Grosselet, R. Guerrero, M. Guevara, M. Gurrola, M. Gutiérrez, R. Guzman, D. Hamilton, A. Hannuksela, A. Hernández Jaramillo, S. Hernandez, H. Herrera, O. Hinojosa, H. Iturribarria, B. Jiménez, E. J. Jiménez, J. C. Juarez, S. Koenig, O. Komar, A. Langle, A. Leal, P. López, S. López, L. Lozano, M. Maglianesi, J. E. Martinez Leyva, A. Martínez Salinas, J. McNicoll, M. Mena, A. Miranda, J. Medina, M. D. Mendez, O. Efraín Montes, J. Nocedal, A. Oliveras, V. Piaskowski, P. Pilego, E. Pineda Diez de Bonilla, J. L. Pena Ramírez, C. J. Ralph, D. Ramirez, F. Ramírez, M. Ramírez, P. Ramírez, R. Rodriguez, L. Rubio, A. Ruiz, C. J. Ruiz, E. Selvin, B. Smith, J. Smith, A. Solano, A. de Sucre, P. Thorn, M. Tórrez, S. Ugalde, F. Urbina, J. Vargas, J. H. Vega, D. Valencia Vilchas, S. Vilchez, K. Wilcox, J. and M. Woodcock, R. Zambrano, and J. M. Zolotoff. This is Contribution No. 450 of The Institute for Bird Populations.

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