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Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle

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Worldwide, migratory species are undergoing rapid declines but understanding the factors driving these declines is hindered by missing information about migratory connectivity and the lack of data to quantify environmental processes across the annual cycle. Here, we combined range-wide information about migratory connectivity with global remote-sensing data to quantify the relative importance of breeding and non-breeding environmental processes to persistent long-term population declines of a migratory songbird, the wood thrush (*Hylocichla mustelina*). Consistent with theoretical predictions about population limitation of migratory birds, our results suggest that habitat loss and climate have contributed to the observed declines in wood thrush breeding abundance, yet the relative importance of breeding versus non-breeding factors is population-specific. For example, high-abundance core breeding populations appear to be more limited by habitat loss, whereas low-abundance, peripheral populations appear to be limited by climate-driven seasonal interactions. Further, our analysis indicates that the relative impact of breeding habitat loss is at least three to six times greater than the impact of equivalent non-breeding habitat loss and therefore the steepest regional declines have likely been driven by the loss of breeding habitat. These results underscore the need for population-specific conservation strategies implemented throughout the annual cycle to reverse long-term declines.

1. Introduction

Identifying the mechanisms that govern population dynamics has long been a central goal of population ecology [1,2], but the factors that limit population growth remain poorly understood because demographic processes are typically determined by multiple biotic and abiotic processes operating simultaneously over large spatial scales [2]. Quantifying the causes of population fluctuations is particularly challenging for migratory species because the breeding abundance of these species can be influenced by events experienced across the annual cycle [3,4]. Worldwide, migratory species, including over half of migratory bird species [5], are undergoing rapid, enigmatic declines, and implementing effective conservation measures is hindered by both the lack of information about limiting factors and the political, social and economic complexities of international conservation [6].

Unfortunately, the large spatial scales associated with the annual movements of migratory birds and the inability to accurately track individuals across their annual cycle have hindered our understanding of when and where migratory birds experience limiting factors. To date, most empirical research on this subject has focused on documenting whether local populations experience limiting factors during the breeding season and to a lesser degree during the non-breeding season [7,8]. However, because limiting factors often vary across a species range [9] and through time, it is generally not possible to extrapolate from these local studies to understand range-wide population dynamics [10]. Furthermore, hypotheses about breeding versus non-breeding limitation are oversimplified. Theoretical and empirical studies have demonstrated that the breeding abundance of migratory birds is limited by both breeding and non-breeding habitat [3,11] and that processes operating across the annual cycle can interact in complex ways at both the individual and population levels (i.e. seasonal interactions) [4]. Unfortunately, because few studies have simultaneously quantified the contribution of breeding versus non-breeding processes on range-wide population dynamics [12], there is little empirical information to test theoretical predictions about the relative importance of seasonal limitation or how seasonal interactions manifest at the population level.

Given the complexity of these challenges, advancing our understanding of population dynamics of migratory birds requires at least three conditions to be met. First, information about migratory connectivity should be used to link breeding populations to specific wintering locations and migration routes. Second, because demographic rates and limiting factors often vary across a species range, inferences should be made at range-wide spatial scales rather than extrapolated from local studies. Third, because populations may experience limiting factors during both the breeding and non-breeding periods, researchers should simultaneously quantify the influence of environmental covariates acting on demography across the annual cycle. Until recently, meeting these three conditions was not feasible due to missing information about migratory connectivity, the absence of methods for identifying spatial variation in demographic rates and the lack of data for quantifying environmental processes across the annual cycle.

Fortunately, several recent advances provide unprecedented opportunities for overcoming these three challenges to study the processes influencing population dynamics and identify the causes of population declines in migratory birds. First, advances in the use of extrinsic (e.g. light-level and GPS geolocators) and intrinsic (e.g. stable isotopes, genetic) markers now allow researchers to quantify patterns of migratory connectivity for even the smallest migratory songbirds [13–15]. Second, statistical methods now allow researchers to combine local population surveys into composite estimates of regional population abundance, while accounting for known sources of sampling error [16]. When sampling sites are grouped based on geography and local demographic rates rather than geopolitical boundaries, researchers can now estimate temporal variation in abundance among demographically defined populations [17]. Third, advances in remote sensing have produced high-resolution maps of global forest cover and climate, providing range-wide estimates of environmental processes hypothesized to influence demographic rates.

In this paper, we quantify how climate and habitat loss across the entire range and over the entire annual cycle have contributed to recent population declines in a migratory songbird, the wood thrush (*Hylocichla mustelina*). Using 17 demographically distinct breeding populations [17], we combined information on migratory connectivity and remote-sensing data to: (i) model annual abundance as a function of habitat availability and large-scale climatic conditions on both the breeding and non-breeding grounds; and (ii) determine the factors driving regional variation in the magnitude of population declines.

2. Material and methods

(a) Study species, monitoring data and basic model

Wood thrush are a long-distance migratory songbird that breeds throughout eastern North America and winters from southern Mexico to Colombia. Wood thrush breed exclusively in mature deciduous woodlands and winter in tropical forests below 1000 m in elevation [18]. Although widespread, wood thrush have undergone an overall population decline greater than 60% since 1966 [19]. Recent research suggests that this decline has been primarily driven by the loss of non-breeding habitat [20], although the modelling framework used in that study did not examine how key factors, such as climate and seasonal interactions, may have contributed to population declines. Additionally, the magnitude of decline has not been uniform across the breeding range and previous analysis of wood thrush demographics identified 17 demographically distinct populations that differ with regard to both trend and abundance [17]. These populations form the basis for our analysis (figure 1).

We used data from the North American Breeding Bird Survey (BBS) to quantify annual variation of wood thrush breeding abundance within each of the 17 populations. The BBS is a roadside survey conducted annually in May and June since 1966 across most of North America [19]. The survey consists of 50 three-minute point counts conducted along a 40.2 km route. For our analysis, we summed the number of wood thrush across all 50 counts to provide a single measure of annual abundance at each route. We restricted our analysis to BBS counts conducted from 2001 to 2013 because this is the time period covered by our forest cover dataset. To model annual changes in wood thrush numbers within each population, we adapted a hierarchical model that has been developed to estimate regional trends and abundances from BBS data while accounting for variation introduced by observers and route and is fit using Markov chain Monte Carlo (MCMC) algorithms [16,21].

(b) Environmental covariates

One of the primary benefits of the basic model introduced by Link & Sauer [16] is that it can be adapted to include environmental processes believed to influence abundance [10,12]. For our analysis, we used two large-scale remote-sensing datasets to model wood thrush abundance within each population as a function of annual forest loss and climate on both the breeding and non-breeding grounds.

To quantify forest loss and climate on the non-breeding grounds, we divided the wood thrush winter range into five regions based on a combination of geography and information about the migratory connectivity of breeding populations (figure 1). We quantified the extent of annual forest loss within breeding populations and non-breeding regions using a 30-m-resolution Landsat-derived map of global forest change from 2000 to 2012 [22]. This dataset provides high-resolution information about the per cent forest cover in the year 2000, annual forest loss and total forest gain between 2001 and 2012 for the entire wood thrush breeding and non-breeding ranges. Within each breeding population and non-breeding region, we used this dataset to estimate the cumulative annual forest loss between 2001 and 2012 (electronic supplementary material, appendix A). To ensure that rates of habitat loss were comparable across regions and populations, forest loss estimates were converted to proportions by dividing annual forest loss estimates by the amount of forest cover in the previous year.

All breeding and non-breeding regions experienced a net loss of forested habitat over the time period included in our analysis (figure 1). Some regions, particularly in the southeastern United States, did undergo some reforestation over this time, but because the Hansen *et al.* [22] dataset does not contain annual estimates of forest gain, we were unable to account for reforestation in our estimates of annual forest change. Although much of this gain is likely driven by commercial timber operations [23] and does not, therefore, represent gain of wood thrush habitat, we tested whether total forest change over the entire time period influenced population trends by regressing the overall rate of decline against the

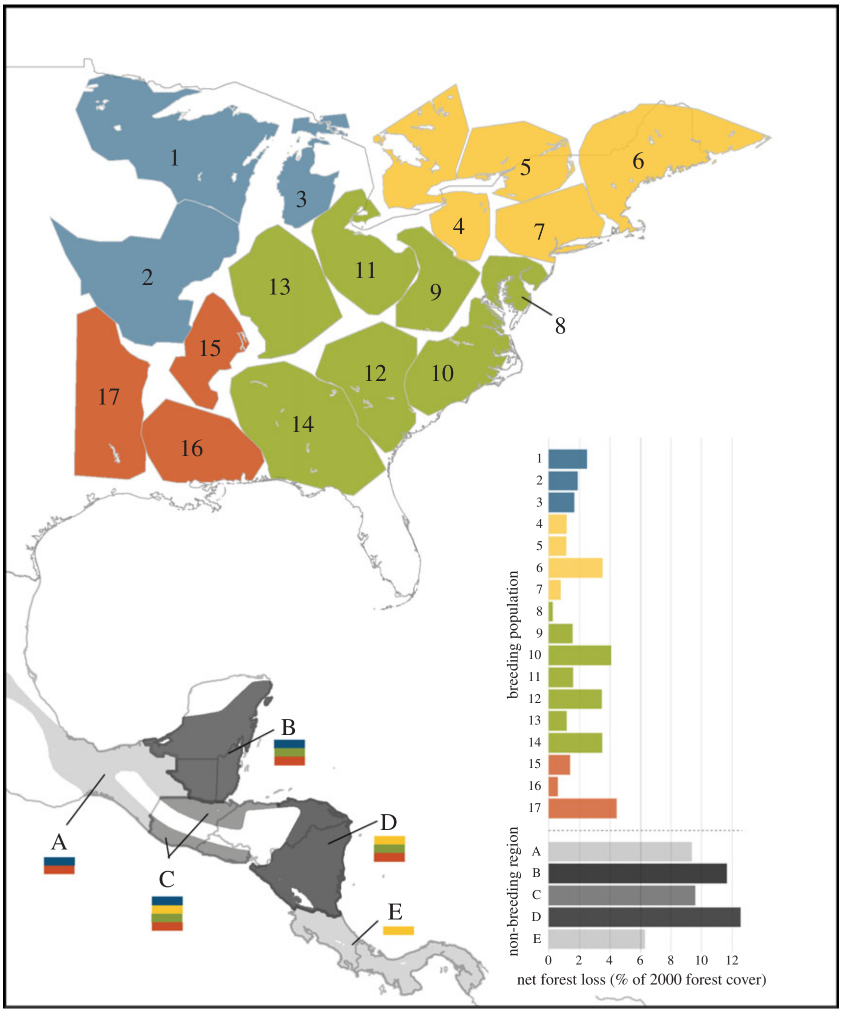

Figure 1. Boundaries of and net forest loss within the 17 wood thrush breeding populations and the five non-breeding regions. Known patterns of migratory connectivity are indicated by the colour of the rectangles below each non-breeding region label.

net forest change (i.e. the number of forested cells in the year 2000, minus the total number of deforested cells, plus the total number of reforested cells) for each population.

To quantify the effects of breeding and non-breeding climate on wood thrush abundance, we used MODIS-derived estimates of monthly Enhanced Vegetation Index (EVI) at the 1000 km^2 scale (https://lpdaac.usgs.gov/products/modis_products_table/mod13a3). EVI is a composite metric of vegetation greenness that reflects primary productivity and vegetation complexity, which are positively correlated with habitat suitability for wood thrush [24]. Given that June is the peak of wood thrush reproduction [18], we computed as the mean June EVI value for all pixels within each breeding population as an annual index of breeding climate. Likewise, March is the period when non-breeding regions are at their driest point in the year and when wood thrush are preparing for spring migration (C. Stanley 2015, unpublished data). As such, we computed the mean March EVI values for each non-breeding region as the most likely period to impact wood thrush demography.

Non-breeding climate may influence breeding abundance over different timescales depending on whether EVI has a direct effect on survival or an indirect effect on reproduction (i.e. a seasonal interaction). Because few data exist for wood thrush to decide *a priori* how non-breeding EVI influences breeding abundance, our models included several biologically plausible scenarios. If the non-breeding climate primarily influences over-winter survival or survival during spring migration, then the impact of EVI in March of year$_t$ should manifest on the breeding grounds in year$_t$. Conversely, non-breeding climate may also influence body condition on spring migration, which in turn could influence reproductive success when individuals return to the breeding grounds. In this case, the effect of March EVI in year$_t$ would not manifest until year$_{t+1}$, when more or fewer recruits enter the population. Given that these mechanisms are not mutually exclusive and could vary among populations, we include both in our analysis and use a model selection approach to determine which mechanism has the strongest effect on wood thrush abundance in each population.

An important consideration for understanding long-term population declines is that these declines can only be driven by covariates that also display a linear trend over the same time period [25]. However, the widespread decline in forest cover and habitat quality across all regions makes it difficult to conclusively demonstrate that wood thrush declines were driven by habitat degradation within any specific region. Therefore, we followed Grosbois *et al.* [25] and removed temporal trends from all covariates and used the detrended estimates as the annual covariates in our analysis. Thus, important covariates must account for a significant fraction of the variation in annual abundance after accounting for the linear decline of the covariate. Because our primary objective was to determine which factors have caused observed wood thrush declines, we also tested whether each covariate displayed a significant decline over the period of this study (electronic supplementary material, tables S1 and S2).

(c) Model fitting and selection

The two breeding ground predictors ($forest\ loss_{t-1}$ and EVI_{t-1}) and 15 non-breeding predictors ($forest\ loss_{t-1}$, EVI_{t-1}, and EVI_t × 5 regions) resulted in 17 potential covariates to estimate for each breeding population. Given the large number of covariates and the lack of *a priori* predictions about how the covariates may interact to influence wood thrush abundance, we chose to restrict our analysis to the additive effects of the covariates. To quantify the importance of the 17 covariates for predicting annual changes in abundance within each population, we modified the basic Link & Sauer [16] model as follows:

$$C_{i,j,t} \sim \mathrm{Pois}(\lambda_{i,j,t}) \tag{2.1}$$

and

$$\log(\lambda_{i,j,t}) = \alpha_j + \beta 1_j \times \mathrm{year}_t + \beta_2 \times \mathrm{novice}_{i,t} + \gamma_{3,j}\beta_{3,j} \times x_{1,t} + \ldots + \gamma_{n,j}\beta_{n,j} \times x_{n,t} + \omega_{i,t} + \varepsilon_{i,j,t}, \tag{2.2}$$

where $C_{i,j,t}$ is the observed number of wood thrush in year t at route i in population j, α_j and β_{1j} are a population-level intercept and linear trend, respectively, β_2 is the effect of novice observers, $\omega_{i,t}$ is a random effect indicating unique combinations of route and observer [16] and $\varepsilon_{i,j,t}$ is an over-dispersion parameter. For each population j, the coefficients for each of the n environmental predictors ($\beta_{n,j}$) are multiplied by an indicator variable ($\gamma_{n,j}$) that takes a value of 1 if predictor n is included in equation (2.2) and 0 if it is not [26]. As the MCMC algorithm updates, the posterior distribution for each indicator variable n tends towards 1 if the predictor n is an important predictor of wood thrush abundance in population j or tends towards 0 if it is not. The means of the indicator variable posteriors ($\dot{\gamma}$) provide an intuitive metric to gauge the relative importance of each predictor [27,28]. This indicator variable approach is preferable to using credible intervals because a variable with large posterior uncertainty may nonetheless have an important influence on wood thrush abundance [28].

An additional benefit of the indicator variable approach is that individual predictors for each population ($\beta_{n,j}$) can be removed from the model by fixing their indicator variables at 0, providing a flexible method for reducing type-I error and multi-collinearity while maintaining the hierarchical structure of equation (2.2). To reduce the number of predictors included our analysis, we used three approaches to eliminate predictors that either had no influence wood thrush abundance within each breeding population or were highly correlated with other predictors. First, we used single-predictor models to judge importance and remove unimportant predictors ($\dot{\gamma} \leq 0.25$) from subsequent models. Second, for all pairs of highly correlated predictors (Pearson's correlation coefficient (r) $> |0.7|$; electronic supplementary material, tables S3–S5), we set the indicator variable in the final model to 0 for the predictor with the lower. Third, we set indicator variables in all models to 0 for the non-breeding regions not connected to each breeding population [29,30] (figure 1).

The three screening methods allowed us to greatly reduce the number of covariates included in the final analysis (mean number of covariates for each population = 4; range 1–7). For both the single-predictor and full models, posterior distributions for each parameter were estimated using MCMC methods implemented in JAGS v. 3.4.0 [31] using the R2jags package [32] in R v. 3.0.2 [33]. See electronic supplementary material, appendix A, for details about MCMC settings and goodness-of-fit tests. Parameter estimates from the full model were used to determine the relative importance of each predictor on wood thrush abundance within each population. We considered covariates with $\dot{\gamma} \geq 0.75$ to be strong predictors and covariates with $0.25 \leq \dot{\gamma} < 0.75$ to be moderate predictors of wood thrush abundance in population j [28].

3. Results

Our analysis revealed that habitat loss and climate during both the breeding and non-breeding periods are significant drivers of wood thrush population dynamics. Overall, annual abundance in 13/17 of the demographic populations was strongly ($\dot{\gamma} \geq 0.75$) or moderately ($0.25 \leq \dot{\gamma} < 0.75$) correlated with at least one of the predictors included in our analysis (table 1). Non-breeding habitat loss was included as a predictor in the final model for nine populations (table 1) and was strongly or moderately correlated with annual breeding abundance for six of these populations. As expected, abundance was negatively correlated with non-breeding habitat loss for all six populations, indicating that abundance was reduced following years with high forest loss (figure 2). For all six populations, abundance was most strongly correlated with forest loss in southern Guatemala and western Honduras (region C). In general, the six populations linked to non-breeding habitat loss are clustered within the central and southeastern portions of the breeding distribution (figure 2). However, the magnitude of decline in these six populations was not correlated with either the estimates ($r = -0.53$, $p = 0.27$) or the β estimates ($r = 0.47$, $p = 0.35$) for non-breeding forest loss in region C, indicating the non-breeding forest loss has not driven the variation in population declines for these populations.

We also found evidence that annual variation in abundance was strongly or moderately correlated with climatic conditions experienced on the non-breeding, but not the breeding, grounds for six populations (table 1). For populations 2 and 9, breeding abundance was positively correlated with non-breeding EVI values from the preceding winter in the Yucatan peninsula (region B), whereas breeding abundance in population 6 was negatively correlated with non-breeding EVI from the preceding winter in eastern Honduras and Nicaragua (region D). For populations 7, 15 and 16, abundance was correlated with non-breeding EVI from the previous winter (i.e. year_{t-1}) in eastern Honduras and Nicaragua (region D) and non-Yucatan Mexico (region A; figure 3), respectively. This 1-year lag between non-breeding conditions and abundance indicates that, for these populations, non-breeding climate likely influenced breeding abundance via a seasonal interaction on reproductive success rather than through a direct impact on survival. Furthermore, non-Yucatan Mexico (region A) experienced a decline in EVI values between 2000 and 2013 (electronic supplementary material, table S1) and, therefore, this seasonal interaction may have contributed to the decline in abundance observed in populations 15 and 16.

For four of the populations, breeding abundance was strongly or moderately correlated with breeding habitat loss (table 1). Abundance was negatively correlated with breeding habitat loss, indicating that abundance declined following years with high forest loss. All four of these populations lost more than 3.5% of their 2000 forest cover during the study period, whereas only one (population 6) of the remaining 12 populations experienced greater than 3% loss.

(a) Contribution of breeding versus non-breeding habitat loss to observed population declines

Using estimates of net forest loss within each breeding populations, we found a strong relationship between the rate of annual population decline and the extent of breeding ground habitat loss ($\beta = -0.62 \pm 0.25$, $p = 0.026$; figure 4). This relationship remained even after removing three outlier populations (7, 8 and 10; $\beta = -0.60$, $p = 0.006$). Across all 17 populations, this relationship indicates that each 1% loss of breeding habitat resulted in a 0.62% (95% CI = 0.09 : 1.16) annual decline. Moreover, the y-intercept of this regression (−1.15%; 95% CI = −2.33 : 0.04) represents

Table 1. Covariates influencing annual abundance within wood thrush breeding populations: for each population and predictor, the left value is the posterior mean of the indicator variable ($\dot{\gamma}$) and the right value is the posterior mean of the regression coefficient, with 95% credible intervals in parentheses. For non-breeding predictors, the superscript indicates the region linked to variation in abundance for each population. Empty cells indicate that the predictor was not included in the full model. Only populations with at least one important predictor ($\dot{\gamma} \geq 0.25$) are shown.

population	non-breeding EVI_t	non-breeding EVI_{t-1}	non-breeding forest loss	breeding forest loss	breeding EVI_{t-1}
2	0.47^{B} 3.63 (0.59: 6.61)	0.14^{A} 2.42 (−1.01: 5.28)	—	0.03 −0.42 (−0.93: 0.11)	—
6	0.76^{D} −4.10 (−6.43: −1.40)	—	0.07^{E} −0.74 (−4.14: 5.40)	0.02 −0.24 (−0.64: 0.18)	0.11 −2.23 (−7.39: 3.15)
7	—	0.55^{D} −2.29 (−3.84: −0.70)	—	—	0.14 −1.95 (−4.05: 0.49)
8	—	0.09^{B} −1.29 (−2.94: 0.35)	0.76^{C} −5.44 (−8.53: −1.84)	0.24 6.37 (−5.52: 15.67)	0.38 2.07 (0.49: 3.89)
9	0.96^{B} 2.71 (1.25: 4.11)	0.06^{B} −1.29 (−2.85: 0.35)	0.99^{C} −7.05 (−9.50: −4.61)	—	—
10	—	—	0.51^{C} −4.35 (−7.43: −0.47)	0.76 −7.79 (−12.62: −2.36)	—
11	—	—	0.79^{C} −3.54 (−6.51: −0.54)	—	0.03 −019 (−1.90: 1.25)
12	0.09^{D} 1.75 (−0.33: 3.93)	—	0.99^{C} −7.39 (−10.91: −3.89)	0.98 −12.14 (−18.75: −5.59)	—
13	0.10^{B} 1.63 (−0.32: 3.72)	—	0.84^{C} −5.27 (−8.79: −1.77)	0.21 −1.53 (−2.87: −0.28)	—
14	0.10^{C} −1.92 (−4.87: 1.04)	—	0.22^{C} −2.47 (−6.47: 1.09)	0.94 −1.71 (−2.44: −0.94)	—
15	0.12^{C} −2.49 (−7.59: 4.21)	0.95^{A} 5.25 (2.37: 8.19)	—	—	—
16	0.06^{B} 0.72 (−2.37: 3.93)	0.92^{A} 4.08 (1.73: 6.46)	—	—	0.06 −1.17 (−4.03: 1.76)
17	—	0.07^{A} 0.49 (−4.12: 4.84)	0.09^{C} −1.53 (−3.95 : 0.77)	0.65 −2.41 (−3.95: −0.86)	—

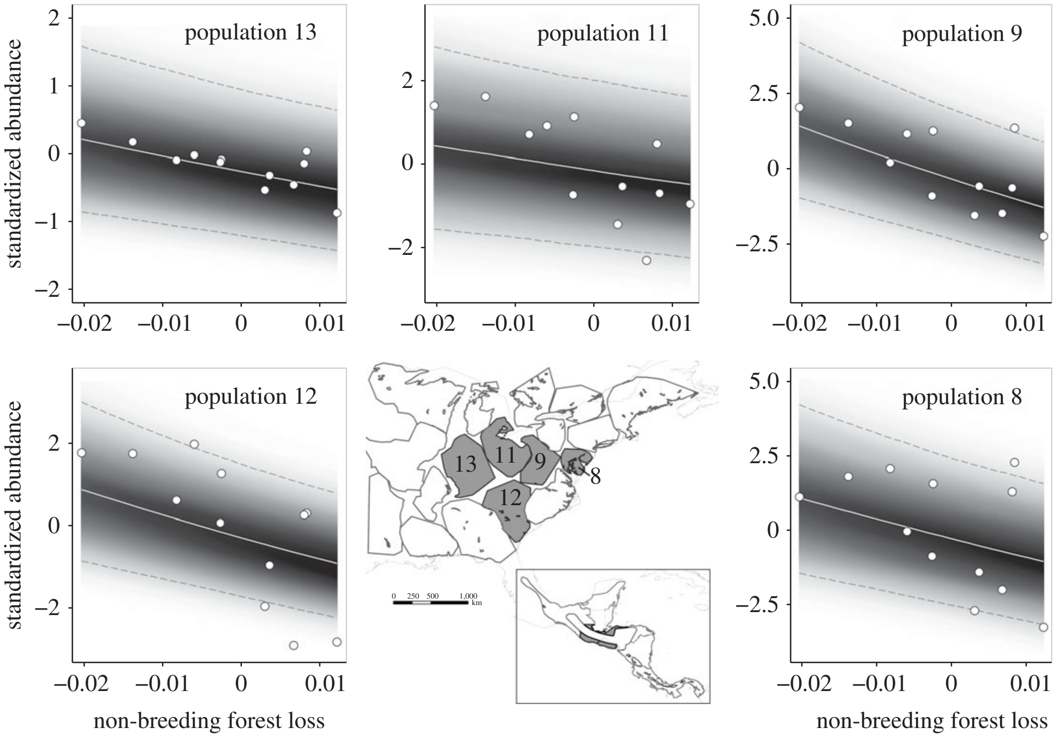

Figure 2. Estimated effect of forest loss in southern Guatemala and western Honduras (region C; shown in grey on map inset) on wood thrush abundance in the five breeding populations with $\dot{\gamma} \geq 0.75$ (shown in grey on the map). Note that different *y*-axis limits are used on each plot to account for differences in relative abundance. *X*-axis values are the residual forest loss estimates after accounting for the linear trend in forest loss. Thus, positive values indicate years with greater than expected forest loss and negative values indicate less than expected forest loss. Circles show the observed abundances within each population. White line is the posterior mean for the predicted abundance as a function of region C forest loss. Grey lines show the 95% posterior credible interval and shading is based on the posterior density for the estimated relationship. All observed and predicted abundances were mean-centred to aid in visual comparison across populations.

population decline attributable to all others factors (i.e. a population experiencing no breeding habitat loss). Given the observed rates of forest loss within the five non-breeding regions (approx. 6–12%), the 1.15% decline translates to maximum contribution of 0.1–0.2% annual decline per 1% loss of non-breeding forest (assuming that non-breeding forest loss has been the primary factor driving population declines). Thus, although non-breeding habitat loss has been substantial and has contributed to a sizeable proportion of the range-wide wood thrush decline, breeding habitat loss appears to have a relatively larger impact on abundance and is responsible for the steepest regional declines.

4. Discussion

Efforts to understand when population limitation occurs during the annual cycle of migratory birds is an area of active research, but these efforts are often hindered by insufficient data on migratory connectivity, missing information on range-wide demographic patterns and the paucity of range-wide environmental data. In this study, newly available data allowed us to overcome each of these issues to conduct a retrospective analysis of how factors operating across periods of the annual cycle influence breeding abundance within demographically distinct wood thrush populations. Our results suggest that the loss of non-breeding habitat plays a major role in range-wide wood thrush declines, but that the degree of habitat loss on the breeding grounds is the primary driver of the steepest regional declines. We also found regional consistency in the relative influence of habitat loss and climate on variation in breeding abundance, suggesting that these processes influence demographic rates over large spatial scales.

The ability to simultaneously quantify the effect of breeding and non-breeding environmental processes at range-wide scales provides several important insights into the factors that drive population dynamics of wood thrush. First, our results provide evidence that fluctuations in wood thrush breeding abundance are driven by multiple processes that operate throughout the annual cycle. Although there is a long-standing debate about whether migratory bird populations are limited by events on the breeding grounds *or* on the non-breeding grounds [4], theoretical models demonstrate that any decline in the amount or quality of habitat, whether on the breeding grounds or non-breeding grounds, will cause a decline in population size [3,11]. However, changes in population size are most responsive to habitat loss during the period in which populations are more severely limited [3]. Unfortunately, relatively few empirical studies provide quantitative evidence indicating whether population size of migratory species is more sensitive to the amount of breeding habitat or non-breeding habitat [7,34,35] and we are unaware of any study done at range-wide scales.

Here, we present empirical evidence that support the theoretical predictions of Sherry & Holmes [3] and Sutherland [11] showing that: (i) the breeding abundance of wood thrush is influenced by both breeding and non-breeding habitat and climate; and (ii) the availability of breeding habitat is the primary factor limiting population size. Habitat loss has been extensive throughout the wood thrush non-breeding range (figure 1) and all breeding populations have lost substantial winter habitat in recent decades. The strong correlation we found between annual breeding abundance and non-breeding habitat availability, especially within central populations,

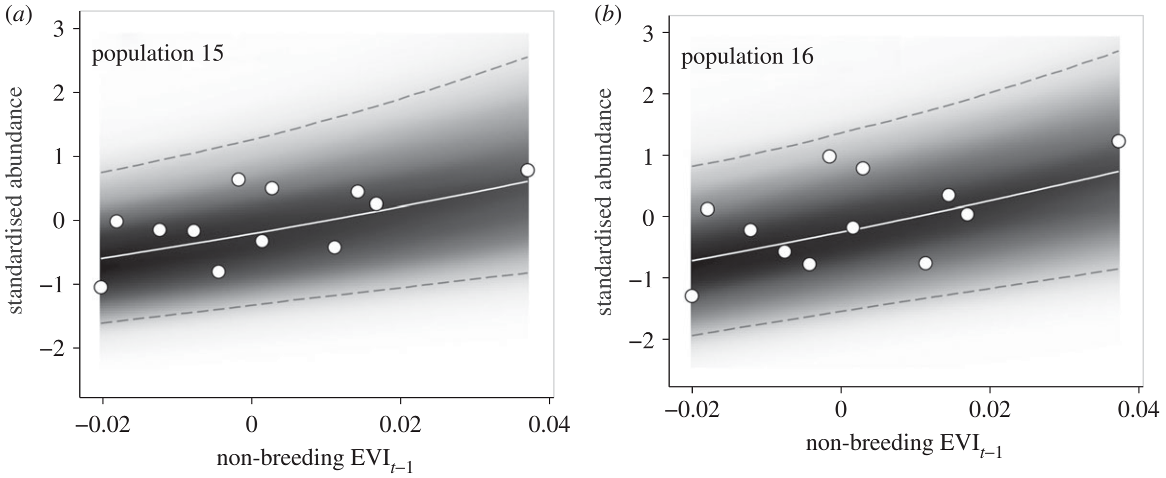

Figure 3. (*a*,*b*) Estimated effect of EVI$_{t-1}$ in non-Yucatan Mexico (non-breeding region A) on wood thrush abundance in the two breeding populations with $\dot{\gamma} \geq 0.75$. *X*-axis values are the residual EVI estimates after accounting for the linear decline in EVI values. Thus, positive values indicate years with greater than expected EVI and negative values indicate less than expected EVI. Circles show the observed abundances within each population. White line is the posterior mean for the predicted abundance as a function of region A *EVI*$_{t-1}$. Grey lines show that the 95% posterior credible interval and shading is based on the posterior density for the estimated relationship. All observed and predicted abundances were mean-centred to aid in visual comparison across populations.

supports the conclusion that non-breeding habitat loss is an important factor influencing the abundance of wood thrush across a large portion of the breeding range. However, despite relatively large differences in the rate of forest loss across the five non-breeding regions, we found no relationship between the loss of non-breeding habitat and the magnitude of breeding ground population declines.

In contrast, our results indicate that the extent of breeding habitat loss has a large impact on the rate of regional wood thrush population declines, despite the fact that this loss has been less extensive than the loss of non-breeding habitat. We also found that the relative impact of breeding habitat loss on breeding abundance is at least three to six times greater than the impact of equivalent non-breeding habitat loss. Based on the Sherry & Holmes [3] and Sutherland [11] models, these results are consistent with the hypothesis that breeding habitat is more strongly limiting than non-breeding habitat. This conclusion is supported by studies linking local wood thrush abundance to factors influencing reproductive success [36,37] and to our previous analysis showing that population trends are correlated with regional productivity rather than to annual survival [17].

Although habitat loss appears to be the primary factor driving wood thrush declines, our analysis indicates that the declines of several populations (15 and 16) are driven by the large-scale climatic variation and subsequent deterioration of non-breeding habitat in Mexico. Interestingly, non-breeding climate in this region appears to influence breeding abundance via a seasonal interaction rather than through a direct effect on survival. Although numerous studies have documented seasonal interactions operating at the individual level [38], our analysis provides the first evidence that conditions experienced during the non-breeding season can influence population-level demographic processes. As tropical areas continue to dry in the coming decades [39], it is imperative that the mechanisms behind and prevalence of these seasonal interactions receive further investigation.

An additional insight from our analysis is that although the factors influencing annual abundance differ among populations, the relative influence of habitat availability versus climate displayed regional consistency. In particular, populations linked to non-breeding habitat loss are primarily high-abundance populations located in the centre of the breeding range, whereas populations linked to non-breeding climate are primarily low-abundance populations on the periphery of the range. If high-abundance central populations occupy the most favourable habitat and operate close to their carrying capacity [9], the abundance of these populations is expected to be sensitive to habitat availability [40]. In contrast, low-abundance populations at the periphery of the range may occupy less favourable habitats, making them more susceptible to density-independent factors such as climatic conditions. Thus, our results are consistent with theoretical predictions that the dynamics of high-abundance populations will be governed more strongly by density-dependent regulation, whereas the dynamics of low-abundance populations are influenced more by density-independent processes [9,40].

Although our analyses provide evidence that habitat loss and climate are important drivers of wood thrush abundance, several limitations of our data and analysis could influence these conclusions. First, the correlative nature of our analysis combined with the low resolution of our migratory connectivity data increases the odds of spurious results. Although the consistency of the habitat loss results suggest these relationships are authentic, some of the conflicting patterns observed in the climate responses are difficult to account for. Better information about migratory connectivity could refine and focus our analyses to resolve these discrepancies. Second, the Hansen *et al.* [22] dataset does not distinguish between different forest types and therefore forest loss may have been overestimated if some of the loss occurred in forested habitats that are not suitable for wood thrush. On the non-breeding grounds, most recent forest loss is occurring within relatively mature forests [41] so at the regional scale of our analysis, the estimates of forest cover from Hansen *et al.* [22] are likely good proxies for wood thrush non-breeding habitat availability. In contrast, a large portion of forest loss on the breeding grounds, especially within the southeastern United States, is driven by commercial timber operations [23]. In these areas, some proportions of both the deforested and reforested patches are likely made up of timber plantations, which may not supported breeding wood thrush. Nonetheless, the

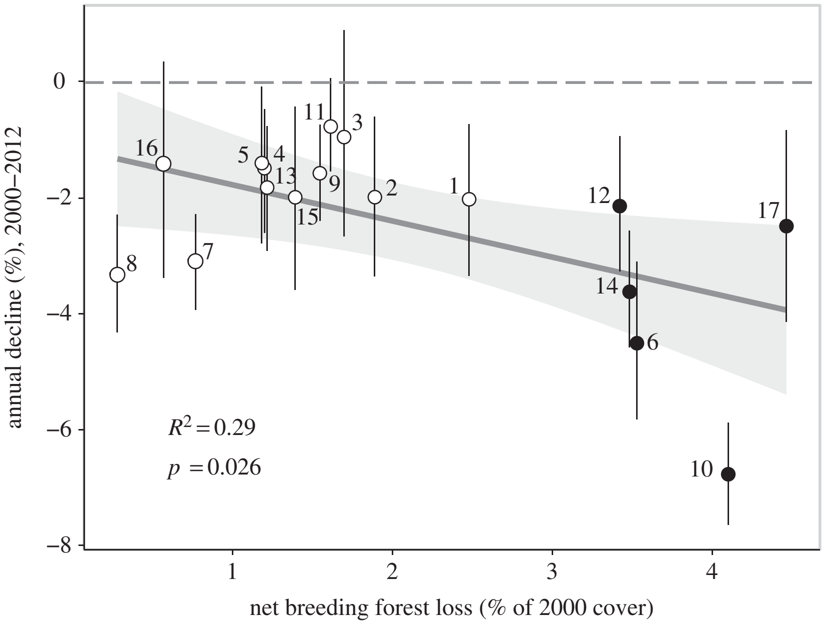

Figure 4. Estimated relationship between net forest loss between 2000 and 2013 and population trend over the same time period for 17 wood thrush populations. The negative slope indicates that, on average, populations that experienced more breeding habitat loss declined faster than populations that have lost less habitat. Closed circles indicate populations with significant correlations between annual breeding forest loss and annual abundance.

strong relationship between breeding forest loss and declining breeding abundance, especially within the southeastern populations, suggest that the large-scale forest dynamics captured by the Hansen *et al.* [22] dataset are representative of the dynamics that influence wood thrush demography.

A third limitation is that our model does not account for threats other than habitat loss and climate variability. Other factors likely influence wood thrush demographic rates, including habitat configuration [42], nest predation and parasitism [37], and native herbivores [43]. In addition, our model does not include all types of seasonal interactions [38], which may influence patterns of survival and productivity in complex ways. These factors could account for some of the unexplained variation in our analysis. For example, populations 7 and 8 have declined more than predicted based on the amount of breeding habitat loss alone (figure 4). These populations also occupy the highly urbanized corridor stretching from Washington, DC, to Boston, MA, suggesting that threats associated with urban habitats, including non-native predators [44] and collisions with anthropogenic structures [45], may play an important role in driving regional declines. Furthermore, annual abundance of several populations was not predicted by any of the covariates included in our model, suggesting other forces are driving declines in these areas.

Interestingly, a number of our conclusions differ from a recent analysis of wood thrush population dynamics [20], particularly with regard to the contribution of breeding habitat loss and climate to regional declines. These differences are likely the result of the contrasting methodological approaches used by two the studies. In particular, Taylor & Stutchbury [20] based their analysis on four large regions that are defined without regard to fine-scale spatial variation in demographic attributes that structure wood thrush populations [17]. In contrast, our analysis uses populations that inherently capture the spatial variation in wood thrush abundance and trend. The use of demographic populations enabled us to make more nuanced inferences about regional variation in breeding versus non-breeding population limitation. For example, the mid-west and southeast breeding regions used by Taylor & Stutchbury [20] are made up of multiple discrete demographic populations that show substantial variation in both recent population trends and the amount of breeding habitat loss [17]. As our analysis suggests, the ability to distinguish areas of high breeding forest loss from areas of low loss provided important insights into the role of breeding habitat loss, which are likely obscured within the larger regions used by Taylor & Stutchbury [20]. Additionally, our model was able to accommodate both climate effects and seasonal interactions, which revealed previously unknown effects of non-breeding climate on the declines of several populations. Although both studies agree that non-breeding habitat loss plays an important role in driving recent wood thrush declines, the use of demographic populations and additional climate variables highlight that a complex region-specific combination of habitat loss and climate across the annual cycle contribute to long-term population declines.

Our results suggest that conservation of wood thrush, and potentially other migratory birds, require a strategic combination of breeding and non-breeding management. On one hand, the rapid rate of forest loss in the Neotropics and the fact that most migrants are concentrated into a much smaller area in the winter than in the summer [46] suggests that conservation efforts should focus on slowing or reversing the destruction of non-breeding habitat. For wood thrush, our results suggest that forest loss in Guatemala and Honduras, and perhaps Nicaragua, have contributed to recent breeding declines, consistent with the results of Taylor & Stutchbury [20]. Moreover, significant forest loss in recent decades within the core of the species' non-breeding range (R. Rorbaugh 2015, personal communication) indicates that these regions may be an important target for future conservation efforts. On the other hand, and in contrast to Taylor & Stutchbury [20], our results indicate the breeding ground habitat loss may be the primary factor limiting wood thrush populations. As such, conservation efforts for some populations may be better focused on increasing habitat availability and productivity. Because productivity may be influenced directly by the availability of high-quality breeding habitat or indirectly via seasonal interactions from the non-breeding season, efforts to increase productivity may require management across the annual cycle. For example, populations in the southwestern portion of the breeding range (15–17) appear to be most limited by non-breeding climate and it remains possible that additional seasonal interactions not included in our model may be influencing regional productivity within other populations. For these populations, increasing productivity and abundance may require identifying and protecting non-breeding sites that will remain high quality in the face of climate change.

The complexity of conservation and management decisions for wood thrush and other migratory birds precludes simple judgements about where and how to invest conservation resources. With perfect knowledge of the system, the optimal investment would be the strategy that most efficiently achieves management objectives [47]. In reality, and for most species, managers have only limited understanding of the biological, economic, social and political systems that shape conservation actions. Effective conservation of wood thrush and other similar species requires moving beyond qualitative or anecdotal arguments about where species populations face the biggest threats and towards quantitative models to predict the effects of different management options on population dynamics. Although difficult, recent advances in full-annual-cycle population models provide powerful methods to link management actions to population dynamics [48]. Combined with decision-analytic approaches that can accommodate additional factors, such as cost, risk and uncertainty, these models can help inform strategic conservation plans that will yield greater return on investment [49]. For wood thrush, and likely many other species, our results suggest that a strategic approach to conservation should be region-specific and address the factors limiting the highest priority populations [50].

Data accessibility. All data used in this analysis are publicly available and can be accessed using the URL links found within the paper.

Authors' contributions. C.R., T.R. and P.M. conceived of the study. C.R. performed population modelling and analysed output data. C.R. and T.R. wrote the first draft of the manuscript and all authors contributed to the revisions.

Competing interests. We declare we have no competing interests.

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