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Spatial and temporal drivers of avian population dynamics across the annual cycle

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Abstract

Untangling the spatial and temporal processes that influence population dynamics of migratory species is challenging, because changes in abundance are shaped by variation in vital rates across heterogeneous habitats and throughout the annual cycle. We developed a full-annual-cycle, integrated population model and used demographic data collected between 2011 and 2014 in southern Indiana and Belize to estimate stage-specific vital rates of a declining migratory songbird, the Wood Thrush (*Hylocichla mustelina*). Our primary objective was to understand how spatial and temporal variation in demography contributes to local and regional population growth. Our full-annual-cycle model allowed us to estimate: 1) age-specific, seasonal survival probabilities, including latent survival during both spring and autumn migration, and 2) how the relative contribution of vital rates to population growth differed among habitats. Wood Thrushes in our study populations experienced the lowest apparent survival rates during migration and apparent survival was lower during spring migration than during fall migration. Both mortality and high dispersal likely contributed to low apparent survival during spring migration. Population growth in high-quality habitat was most sensitive to variation in fecundity and apparent survival of juveniles during spring migration, whereas population growth in low-quality sites was most sensitive to adult apparent breeding-season survival. These results elucidate how full-annual-cycle vital rates, particularly apparent survival during migration, interact with spatial variation in habitat quality to influence population dynamics in migratory species.

Keywords: population limitation; population dynamics; integrated population model; full annual cycle; migration; Wood Thrush

Introduction

Determining how and why populations change in abundance (i.e., population dynamics) has been a central focus of ecology since its inception. For most vertebrate populations, however, we still lack an understanding of how complex spatial and temporal processes interact to influence population growth and subsequent persistence (Oro 2013). Numerous theoretical models have been developed to examine how survival, reproductive output, emigration, and immigration contribute to temporal (Sutherland 1996, Runge and Marra 2005) and spatial (Pulliam 1988, Hanski 1999) variation in population growth, but these models rarely account for both spatial heterogeneity in habitat quality and temporal stochasticity in environmental conditions (Pearson and Fraterrigo 2011). Given the scale and severity of environmental change in terrestrial ecosystems (Pimm et al. 2014), developing a framework that can quantify the drivers of population dynamics across space and time will advance ecological theory and aid conservation.

The challenges of quantifying vital rates and their contribution to population dynamics are magnified for migratory animals because large-scale seasonal movements can induce complex spatiotemporal interactions that shape population processes (Nichols 1996). Understanding how demography affects population dynamics in these species is difficult because population limitation can occur at any stage of the annual cycle (i.e., breeding, winter, autumn and spring migration; Sherry and Holmes 1995, Sutherland 1996). To further complicate matters, stage-specific demographic and environmental processes often interact in such a manner that no single period can be understood outside the context of the entire cycle (Marra et al. 2015). Although some progress has been made in quantifying stage-specific survival for game species (Ward et al. 1997) and large-bodied species capable of carrying satellite transmitters (Klaassen et al. 2014, Lok et al. 2015), estimates of survival during spring and autumn migration are unavailable for the vast majority of migratory species. In addition, understanding how stage-specific vital rates influence population dynamics requires models that can integrate demographic data from across the annual cycle. Full-annual-cycle models have been developed for several well-studied waterfowl species (Mattsson et al. 2012, Robinson et al. 2016), but application of these frameworks to other migratory species has been hindered by the inability to

track individuals throughout the annual cycle, missing information on the linkages between breeding and wintering populations (i.e., migratory connectivity), and the lack of demographic monitoring data on the wintering grounds.

The relative contribution of vital rates to population dynamics is also unlikely to be uniform across space because migratory species typically inhabit heterogeneous habitats. A number of studies have documented habitat-specific vital rates (Holmes et al. 1996, Murphy 2001, Pereira and Novaro 2014) and population growth rates (Kreuzer and Huntly 2003, Getz et al. 2005), yet we know little about how vital rates contribute differentially to population growth in habitats that differ in quality. Many processes could influence the relative importance of vital rates to population growth among habitats that differ in quality, including dispersal driven by density dependence (e.g., Gundersen et al. 2001), reproductive failure (e.g., Pakanen et al. 2011), brood parasitism (e.g., Hoover and Reetz 2006), covariance among vital rates (Sæther and Bakke 2000, Sim et al. 2011), and seasonal interactions of vital rates (Runge and Marra 2005). The contribution of vital rates may also be scale-dependent such that certain rates may be more important at local scales and others at regional scales (Diez and Giladi 2011).

Integrated population models (IPMs) provide a powerful framework for combining multiple data sources (e.g., counts, mark-recapture, reproductive monitoring) to improve estimation of vital rates and their contribution to population growth. Recent applications of these models have provided insights into the demographic processes that drive population dynamics of several species (Schaub et al. 2007, Rhodes et al. 2011, Chandler and Clark 2014). To date, however, IPMs have focused solely on estimation of vital rates and their influence on population dynamics during a single stage of the annual cycle (e.g., breeding: Robinson et al. 2014, wintering: Weegman et al. 2016). Understanding how spatial and temporal factors drive population dynamics for migratory animals necessitates modeling demographic processes across the entire annual cycle (Hostetler et al. 2015).

Here, we present a full-annual-cycle IPM using habitat-specific demographic data from a long-distance migratory songbird, the Wood Thrush (*Hylocichla mustelina*), during the breeding and wintering periods. Wood Thrush are a species of high conservation concern due to a long-term decline of more than 60% over the past 50 years, but researchers lack a clear understanding of when during the annual cycle populations are limited (Rushing et al. 2016a). We integrated data collected across the annual cycle to test the hypothesis that temporal (i.e., stage-specific) and spatial (i.e., habitat-specific) demographic processes interact to drive variation in population growth rate (λ). Life history theory predicts that population growth of iteroparous species should be primarily influenced by survival (Sæther et al. 2004) and demographic analyses of passerine birds have supported this prediction (Sæther and Bakke 2000, Robinson et al. 2014). Therefore, we predicted that population dynamics of our study populations would be more sensitive to survival than to productivity. However, the contribution of survival during each stage of the annual cycle to population dynamics remains poorly understood, because most studies have focused on annual survival rates. Because mortality of migratory passerines is concentrated during the migratory periods (Sillett and Holmes 2002, Rockwell et al. 2016, Paxton et al. 2017), we further predicted that migration survival would make a larger contribution to variation in population growth than survival during the stationary periods. Source-sink theory suggests that populations are balanced by habitat-specific variation in mortality, fecundity and immigration dynamics (Pulliam 1988). As such, we predicted that survival would make a higher relative contribution in high-quality **or** source habitats, whereas immigration would be more important in low-quality **or** sink habitats. Finally, because the effects immigration and emigration on population dynamics are expected to be negligible compared to births and deaths at large spatial scales (Camus and Lima 2002), we predicted that immigration would have a large effect on population dynamics at local scales and have less effect at the regional scale.

Materials and Methods

Study species and sampling locations

Wood Thrush are long-distance migratory songbirds that breed in structurally diverse deciduous forests across most of the eastern United States (Evans et al. 2011). Like other thrushes, individuals are reproductively active at one-year of age and breed annually thereafter. Adults typically feed on the ground in the leaf litter and predominantly eat invertebrates during the breeding season. During the non-breeding season, Wood Thrushes reach their highest abundance in the understory of interior tropical broad-leaf forest from southern Mexico to western Panama (Conway et al. 1995). During the non-breeding season, Wood Thrushes have a more generalist diet, eating invertebrates, but also incorporating a much larger proportion of fruit into their diet (Blake and Loiselle 1992).

We collected demographic data from linked breeding and wintering Wood Thrush populations. Breeding fieldwork was conducted from 2011 to 2014 at 12 study sites across southern Indiana, USA (Fig. 1). Study plots ranged in size from 36 to 84 hectares (see Table S1). Habitat at all 12 sites was characterized as deciduous hardwood forest with consistent dominant canopy trees (*Quercus, Fagus, Carya, Populus, Ulnus,* and *Fraxinus* spp.) and understory shrub species (*Lindera, Viburnum, Hamamelis*, and *Sambucus* spp.), though the number of large trees (diameter at breast height > 30 cm) varied considerably across the plots (Table S1). This metric is highly predictive of Wood Thrush occupancy in southern Indiana (Valente *unpub.*) and we used it as the principal index of habitat quality of each plot.

Winter data were collected at the Belize Foundation for Research and Environmental Education (BFREE) and the Bladen Nature Reserve, both located in the Toledo District, Belize. Based on data from light-level geolocators and GPS tags deployed on Wood Thrushes at the southern Indiana breeding sites, we determined that our breeding birds winter in southeastern Mexico, northern Guatemala, and Belize (Stanley et al. 2014). These regions share similar habitat characteristics and climatic conditions with our study site (Karmalkar et al. 2011) and therefore, the demographic data collected from the Belize field sites should be representative of the winter conditions experienced by Wood Thrushes breeding in southern Indiana.

Integrated population model

We developed a female-only, two age-class IPM to quantify changes in breeding population size as a function of stage-specific vital rates. For a given study plot p, total female breeding abundance in each year ($N_{p,t}$) is composed of three classes of individuals: local recruits, surviving adults, and immigrants:

$$N_{p,t} = N_{p,t}^{L} + N_{p,t}^{Ad} + N_{p,t}^{Imm}$$

The number of individuals within each class changes annually as a function of fecundity, survival, immigration, and population size in the previous year:

$$N_{p,t}^{L} \sim Poisson\left(\frac{f_{p,t}\phi_{p,t-1}^{J}N_{p,t-1}}{2}\right)$$

$$N_{p,t}^{Ad} \sim Binomial\left(N_{p,t-1}, \phi_{p,t-1}^{Ad}\right)$$

$$N_{p,t}^{Imm} \sim Poisson(\gamma_{p,t})$$

where $f_{p,t}$ is the per capita fecundity in year $t – 1$ (divided by 2 assuming an equal nestling sex ratio), $\phi_{p,t-1}^{J}$ and $\phi_{p,t-1}^{Ad}$ are the apparent survival probabilities of juveniles and adults, respectively, from year $t – 1$ to year t, and $\gamma_{p,t}$ is the expected number of immigrants in year t, which was treated as a latent variable informed by the demographic rate estimates and the count data (Schaub and Fletcher 2015). Because we parameterized immigration as a count rather than a rate, we also derived the annual immigration rate for each plot as $\omega_{p,t} = \frac{N_{p,t}^{Imm}}{N_{p,t}}$.

The IPM consisted of six conditionally related sub-models that link demographic data to annual breeding abundance at each study site:

1) Population size

Data

From 2011 to 2014, we systematically surveyed each breeding site to locate all adult Wood Thrush pairs and nesting attempts. We used the total number of active nests on each plots an index of the number of breeding females in each year. To avoid overestimating the number of females due to failed nesting attempts and rebreeding, we only considered nests active in the first month of each breeding season; known renests of marked females in the first month were not counted.

Model structure

To account for imperfect detection of individuals in the population, we used a state-space model to link the true abundance on each plot, $N_{p,t}$, in each year to the observed number of females, denoted $C_{p,t}$, using a Poisson observation model :

$$C_{p,t} \sim Poisson(N_{p,t})$$

2) Fecundity

Data

All nests identified during our surveys (n = 946) were monitored approximately every three days. For each active nest, we recorded clutch initiation date, clutch size, Brown-headed cowbird parasitism rate, hatching success, and ultimate nest fate (fledge or fail). For successful nests, the number of offspring fledged was recorded as number offspring at the last nest check prior to fledge and, when possible, was visually confirmed on a follow-up visit during the post-fledgling period.

Model structure

To estimate fecundity, we modeled the total number of offspring per plot per year, denoted $J_{p,t}$, as a Poisson process based on the annual plot-level fecundity ($r_{p,t}$, i.e., the number of offspring per female) and total number of females in the population in year *t*:

$$J_{p,t} \sim Poisson(r_{p,t} N_{p,t})$$

We used a linear model with a random plot × year interaction to estimate spatial and temporal variation in $r_{p,t}$:

$$\log(r_{p,t}) = \mu_r + \epsilon_{r_{p,t}}$$

$$\epsilon_{r_{p,t}} \sim Normal(0, \sigma_r^2)$$

where μ_r is the mean fecundity across all years and all plots and σ_r^2 is the variance of fecundity across year and plots.

The estimated fecundity from nest-monitoring data potentially underestimates true fecundity due to movement between rebreeding or double brooding attempts. To account for this potential bias, we measured the total reproductive success of 77 female Wood Thrushes that were radio-tracked on our study plots as part of a separate study. To quantify the extent to which our nest monitoring data underestimated full reproductive success, we compared the mean reproductive success of the radio tracked individuals (2.45 fledglings/female) to the mean reproductive success of females from the nest monitoring data (1.69 fledglings/female). Only nests monitored on the same plots and in the same years as the radio-tracking data were used in this comparison. We used the ratio of these values (1.45) to correct the fecundity estimates from the nest-monitoring data. Specifically,

$$f_{p,t} = r_{p,t} \, \Delta_f$$

where $\Delta_f \sim Normal(1.4, 0.02)$. Variance for Δ_f was estimated based on variance in fecundity among known-fate re-breeding females.

3) Post-fledging survival

Data

Between 2011 and 2014, 210 late stage nestlings (day 8 post-hatching) were fitted with radio-transmitters (Model PipAg392, Lotek Wireless) to estimate post-fledging survival. Transmitters were attached using the standard backpack harness and weighed approximately 1.2g (~3% of the nestlings body weight). These tags have a battery life of approximately 9-weeks during which time fledglings were followed and located by homing every 2-3 days using a hand-held receiver (Biotracker, Lotek Wireless) and three-element flexible yagi antenna. During tracking, fledgling locations were either estimated using parental feeding or based on actual visual confirmations. The tracking data was converted into daily capture histories from day 1 post-fledging until either known-death or the

individual's fate became unknown (i.e., censored). Each individual was tracked until either known

death or day 30 post-fledging (the approximate time until independence from parents).

Model structure

For each year *t* and plot *p*, we modeled daily post-fledging survival probability as:

$$y_{i,p,t,d} \sim Bernouilli(\phi_{PF_{p,t,d}} y_{i,p,t,d-1})$$

$$logit\left(\phi_{PF_{p,t,d}}\right) = \mu_{\phi_{PF}} + \epsilon_{\phi_{PF_t}} + \rho_{\phi_{PF_{p,d}}}$$

$$\rho_{\phi_{PF_{p,d}}} \sim Normal(0, \sigma^2_{\phi_{PF}})$$

where $y_{i,p,t,d}$ is the known fate (dead or alive) of individual *i* on plot *p* in year *t* and occasion *d*, $\phi_{PF_{p,t,d}}$

is the survival probability from occasion *d - 1* to occasion *d* in year *t* on plot *p*, $\mu_{\phi_{PF}}$ is the mean daily

survival probability across all years and plots, $\epsilon_{\phi_{PF_t}}$ are fixed effects describing annual variation, and

$\rho_{\phi_{PF_{p,d}}}$ is a random plot × occasion interaction effect. Multiplying the daily survival probability by the

individual's state on the previous day ensures that dead individuals no longer contribute to the

likelihood of $\phi_{PF_{p,t,d}}$. Likewise, once individuals become censored either due to radio failure or

permanent emigration from the study plot, they no longer contributed to the estimation of post-

fledging survival. Annual post-fledging survival probability (i.e., survival to 30 days post-fledging)

was then estimated as the product of the daily survival probabilities.

4) Juvenile survival

Data

On each breeding plot, we used a combination of constant effort mist-netting through the Monitoring

Avian Productivity and Survival program (MAPS; Desante and Kaschube 2009) and target mist-

netting to capture independent hatch-year birds (n = 227). Upon initial capture, each individual was banded with a USGS aluminum leg band and a unique combination of colored leg bands. In subsequent years, we attempted to resight these individuals using systematic surveys of each study plot (see survey methods for adults below).

Model structure

We used a Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) and the juvenile mark-resight capture histories to estimate the apparent survival (hereafter survival) of juveniles from the end of their birth season to the next breeding season (i.e., September - April):

$$z_{i,p,t} \sim Bernoulli(z_{i,p,t-1}, \phi_{p,t-1}^J)$$

$$y_{i,p,t} \sim Bernoulli(z_{i,p,t}, d_t)$$

where $z_{i,p,t}$ is the true state (0 = dead, 1 = alive) of individual i on plot p in year t, $\phi_{p,t-1}^J$ is the survival probability of juveniles on plot p from year t - 1 to year t, $y_{i,p,t}$ is the observed state (0 = not observed, 1 = observed) of each individual, and d_t is the probability of detecting an individual in year t given that it is alive and on the plot.

We modeled spatial and temporal variation in juvenile survival as:

$$logit(\phi_{p,t}^J) = \mu_{\phi^J} + \epsilon_{\phi_t^J} + \rho_{\phi_p^J}$$

$$\epsilon_{\phi_t^J} \sim Normal(0, \sigma_{\phi^J}^2)$$

$$\rho_{\phi_p^J} \sim Normal(0, \varsigma_{\phi^J}^2)$$

where μ_{ϕ^J} is the mean juvenile survival probability across all plots and all years and $\sigma_{\phi^J}^2$ and $\varsigma_{\phi^J}^2$ are the annual and plot variances in juvenile survival probabilities, respectively. See description of adult CJS model for details of the detection model.

5-6) Adult survival

Data

Territorial adults (n = 1807) were captured in mist nets at each breeding site, banded with a USGS aluminum band and a unique combination of colored bands, aged (second-year or after second-year), and sexed using molt and plumage criteria. We conducted surveys every 3-5 days during breeding seasons to resight color-banded individuals. At each winter site, constant-effort mist-netting was conducted in five monthly pulses (November - March) each year from 2003 to 2013. During each pulse, birds were captured over two consecutive days with 16 mist nets. Individuals (n = 1388) were aged using plumage characteristics and fitted with a uniquely numbered USGS aluminum band (initial capture) or their band number was recorded (recaptures). Wood Thrushes cannot be reliably sexed during the winter so males and females were pooled for this analysis.

Model structure

For both the breeding and winter capture data, we used a modification of the standard CJS survival model to estimate the within- and between-season apparent survival probabilities while accounting for transient individuals and imperfect detection (Pradel et al. 1997). Because Wood Thrushes move extensively during the winter and, to a lesser extent, summer periods, the presence of transients in our capture histories violated the CJS assumption that all individuals have equal probability of surviving and being recaptured. The high probability of transience in our data is reflected in both capture datasets, with ~40% and ~72% of individuals captured only a single time in the summer and winter, respectively. We accounted for transients by creating two capture histories for each CJS model (Giavi et al. 2014): one containing the first capture and, if applicable, the first recapture of each individual (possible transients) and a second containing all subsequent recaptures for individuals captured more than once (i.e., known residents). Using this structure, monthly transient probability during each stationary period k (summer or winter) can be estimated as $\tau_{k,t,m} = 1 - \frac{\phi_{k,t,m1}}{\phi_{k,t,m2}}$ (Pradel et al. 1997), where $\phi_{k,t,m1}$ is the survival of possible transients from occasion $m – 1$ to m and $\phi_{k,t,m2}$ is the survival of known-residents during the same interval. Following Giavi et al. (2014), we parameterized

the model such that $\phi_{k,t,m2}$ and $\tau_{k,t,m}$ were directly estimated and $\phi_{k,t,m1}$ was derived. Specifically, we modeled transient probability during each month as:

$$logit(\tau_{k,t,m}) = \mu_{\tau_k} + \epsilon_{\tau_{k,t}} + \rho_{\tau_{k,m}}$$

$$\epsilon_{\tau_{k,t}} \sim Normal(0, \sigma^2_{\tau_k})$$

$$\rho_{\tau_{k,m}} \sim Normal(0, \varsigma^2_{\tau_k})$$

where $\tau_{k,t,m}$ is the transience probability in month m and year t for season k, μ_{τ_k} is the mean monthly transience probability in season k, and $\sigma^2_{\tau_k}$ and $\varsigma^2_{\tau_k}$ are the annual and monthly variance in transience probabilities, respectively. Initial fit of this model indicated that mean transient probabilities differed by < 3% across the 12 breeding plots so we did not include plot-level variation in summer transient probability. We also did not model transience between stationary periods as we consider these as normal dispersal movements rather than true transience.

In the original Pradel et al. (1997) model, $\phi_{k,t,m2}$ represents the apparent monthly survival of non-transients, which we treated as the monthly stationary period survival in our model (i.e., $\phi_{k_{t,m}}$ For the summer model, we modeled monthly survival as as:

$$logit\left(\phi_{Summer_{p,t,m}}\right) = \mu_{\phi Summer} + \epsilon_{\phi Summer_t} + \rho_{\phi Summer_{p,m}}$$

$$\epsilon_{\phi Summer_t} \sim Normal(0, \sigma^2_{\phi Summer})$$

$$\rho_{\phi Summer_{p,m}} \sim Normal(0, \varsigma^2_{\phi Summer})$$

where $\mu_{\phi Summer}$ is the mean monthly summer survival probability across all plots and all years and $\sigma^2_{\phi Summer}$ and $\varsigma^2_{\phi Summer}$ are the annual and month $\times$ plot variances in summer survival probablities, respectively. A similar model was used to estimate monthly winter survival probabilities ($\phi_{Winter_{t,m}}$) but without plot-level variation. Initial analysis of these data indicated no difference in monthly winter survival probability for juveniles and adults ($\phi^J_{Winter} = 0.95, 0.84: 0.99; \phi^{Ad}_{Winter} = 0.96, 0.84: 0.99$); therefore, we pooled these individuals and estimated a single overwinter survival probability. Because the winter capture data ended in 2013, we estimated monthly winter survival in

2014 as $\mu_{\phi_{Winter}} + \rho_{\phi_{Winter_m}}$. Thus, although we could not estimate an explicit year effect for the 2014

winter survival probabilities, this parameterization provided complete temporal overlap between our

two capture datasets.

In both seasons, we modeled monthly detection probability, denoted ，, as:

$$logit(d_{k,m}) = \mu_{d_k} + \rho_{d_{k,m}}$$

$$\rho_{d_{k,m}} \sim Normal(0, \varsigma_{d_k}^2)$$

where μ_{d_k} is the mean monthly detection probability in season k and $\varsigma_{d_k}^2$ is the monthly variance in

detection in season k. Variation across months allowed us to account for behavioral changes across

the season that may influence detectability. Because resighting efforts were extensive on each plot, we

chose not to model annual or plot-level variation in detection.

For each stationary period, survival across the entire season ($\phi_{k,t}$) was estimated as the

product of the m monthly survival probabilities.

Estimating migration and annual survival

The CJS models used to estimate stationary period survival provide estimates of apparent

survival from the end of the stationary period to the beginning of the next (i.e., September to April for

breeding model; April - October for winter model; Fig. 2). These between-season survival estimates

contain information about latent migration survival rates and when combined, the stationary period

and between-season survival estimates provide complementary information to estimate spring and

autumn migration survival. The plot-specific estimates of adult survival between breeding seasons

(denoted $\phi_{BB_{p,t}}^{Ad}$) are equivalent to:

$$\phi_{BB_{p,t}}^{Ad} = \phi_{Autumn_{p,t-1}}^{Ad} \phi_{Winter_{t-1}} \phi_{Spring_{p,t}}^{Ad}$$

where $\phi_{Winter_{t-1}}$ is the over-winter survival estimate from the winter CJS model, and $\phi_{Autumn_{p,t-1}}^{Ad}$

and $\phi_{Spring_{p,t}}^{Ad}$ are the estimated survival during autumn and spring migration, respectively. Likewise,

adult survival between winters ($\phi_{BW_t}^{Ad}$) is equivalent to:

$$\phi_{BW_t}^{Ad} = \hat{\phi}_{Spring_t}^{Ad} \hat{\phi}_{Summer_t} \hat{\phi}_{Autumn_t}^{Ad}$$

where $\hat{\phi}$ is the mean stage-specific survival estimate across all plots. For juveniles, survival between

breeding seasons ($\phi_{p,t}^{J}$) is parameterized in the same way as adults. However, once wintering

juveniles reach the breeding grounds, they become adults. Therefore, survival between winters for

juveniles is:

$$\phi_{BW_t}^{J} = \hat{\phi}_{Spring_t}^{J} \hat{\phi}_{Summer_t} \hat{\phi}_{Autumn_t}^{Ad}$$

For both juveniles and adults, the presence of each latent annual migration survival estimate in

multiple equations allows these rates to be estimated within the integrated framework (Fig. 2;

Appendix S1: Fig. S1). To aid comparison of mortality risk during each period, we scaled the

seasonal-survival estimates to their monthly equivalents by raising each seasonal estimate by

the inverse of season length (winter = 5 months, spring = 1 month, summer = 4 months, autumn

= 2 months; Sillett and Holmes 2002).

Apparent annual survival rates for each plot were estimated as a derived parameter composed

of the product of the 4 stage-specific survival estimates:

$$\phi_{p,t}^{Ad} = \phi_{Summer_{p,t}} \phi_{Autumn_{p,t}}^{Ad} \phi_{Winter_t} \phi_{Spring_{p,t}}^{Ad}$$

$$\phi_{p,t}^{J} = \phi_{PF_{p,t}} \phi_{Autumn_{p,t}}^{J} \phi_{Winter_t} \phi_{Spring_{p,t}}^{J}$$

Informative priors

We used capture-recapture data from each study site to estimate informative priors for each of the

stationary period survival parameters. Using the adult survival model described above and Wood

Thrush captures collected between 2003 and 2009 from the BFREE banding station, we estimated the

mean ($\mu_{\phi,Winter} = 0.95$), annual variation ($\sigma_{\phi,Winter}^{2} = 1.88$), and monthly variation ($\varsigma_{\phi,Winter}^{2} =$

5.19) of winter survival probability. Using Wood Thrush captures collected between 1994 and 2010

as part of the MAPS program (DeSante and Kaschube 2009) at our Indiana study sites, we estimated

the mean ($\mu_{\phi,Summer} = 0.98$), annual variation ($\sigma_{\phi,Summer}^{2} = 2.63$), and monthly variation

($\varsigma_{\phi,Summer}^{2} = 4.24$) of summer survival probability. We converted the mean survival estimates into

an informative Beta prior distribution (Lentini et al. 2015) with scale = 15 and shape = 0.9. We used half-Cauchy priors with scale parameters = 10 and 15 for the annual and monthly variance parameters, respectively (Gelman 2006). All other parameters were given uninformative priors. See supplementary information for JAGS code and further details regarding prior distributions and MCMC estimation.

Vital rate contributions to population growth

For each plot, annual population growth rates were measured as:

$$\lambda_{p,t} = f_{p,t-1}\phi_{p,t-1}^{J} + \phi_{p,t-1}^{Ad} + \omega_{p,t-1}$$

The total population growth rate of each plot across all years was measured as the geometric mean of the annual rates (Pulliam 1988):

$$\lambda_p = \left[\sum_{t=1}^{3} \lambda_{p,t}\right]^{1/3}$$

The above equations represent the total contribution of all three classes of individuals (local recruits, surviving adults, and immigrants) to local population growth. In some cases, populations that cannot support themselves through local recruitment processes may experience positive populations growth ($\lambda_{p,t} > 1$) due to high immigration rates. To measure the ability of each plot to maintain itself through retention and self-recruitment only, known as the self-recruitment rate (R, Runge et al. 2006), we also calculated:

$$R_{p,t} = f_{p,t-1}\phi_{p,t-1}^{J} + \phi_{p,t-1}^{Ad}$$

$$R_p = \left[\sum_{t=1}^{3} R_{p,t}\right]^{1/3}$$

Initial inspection of the values indicated that self-recruitment rate was highly correlated with the number of large trees (diameter at breast height > 30 cm) on the plot ($\rho = 0.80$, $P < 0.001$), which itself is highly predictive of Wood Thrush occupancy in southern Indiana (J.V. Valente & T.B.

Ryder *unpub. data*). Therefore, we considered R_p to be a demographic index of plot-level habitat quality.

We used life table response experiments (LTRE) to measure the contribution of each vital rate to annual population change while accounting for temporal variation in each rate and the covariance among rates (Caswell 2001, Robinson et al. 2014). We first estimated the posterior mean of the pair-wise covariance between vital rates and multiplied this mean matrix by the sensitivity matrices from each of the 30,000 posterior samples. The contribution of each rate was then estimated by summing the variances and covariances for each parameter and scaling the contributions to sum to 1 (Robinson et al. 2014). For each vital rate, we used the 95% highest posterior density interval (HPDI) to quantify uncertainty in contributions. We also estimated contributions from the overall rates typically used in most matrix population models (i.e. fecundity, juvenile apparent survival, apparent adult survival, and immigration). To understand how contributions varied across spatial scales, we estimated contributions of each vital rate at both the regional scale (using the mean rates across all plots) and at the local (i.e. plot) scale.

Results

When pooled across the 12 study plots, the regional population experienced overall positive growth during our study ($\lambda = 1.08$, 95% HPDI = 0.78:1.39). Population growth was partially driven by a high immigration rate ($\omega = 0.34$, 0.21:0.46), resulting in a self-recruitment rate < 1 ($R = 0.9$, 0.48:1.3). Thus, in the absence of continued immigration from outside sources, this population would likely have declined over the course of our study. Despite the importance of immigration in maintaining the regional population, annual variation in regional population growth was most strongly driven by adult and juvenile survival (Table 1).

Stage-specific vital rates and their contribution to population growth

Mean apparent adult survival was highest during winter ($\phi_{Winter}^{Ad} = 0.90$, 0.78:1.00), followed by survival during spring migration ($\phi_{Spring}^{Ad} = 0.89$, 0.71:1.00), autumn migration

(ϕ_{Autumn}^{Ad} = 0.85, 0.7:1.00), and summer (ϕ_{Summer}= 0.84, 0.69:0.97). Thus, spring and autumn

migration accounted for 21% and 29% of adult apparent mortality even though these stages

compose only 8% and 17% of the year. When scaled to the equivalent monthly survival rates,

adult survival was lowest during spring migration (Table 1).

Apparent survival of juveniles was highest during winter (ϕ_{Winter}^{J} = 0.90, 0.78:1.00),

followed by survival during autumn migration (ϕ_{Autumn}^{J} = 0.84, 0.59:1.00), post-fledging

survival (ϕ_{PF} = 0.65, 0.44:0.86), and survival during spring migration (ϕ_{Spring}^{J} = 0.48, 0.16:0.83).

Monthly survival probabilities for juveniles showed a similar pattern to the seasonal rates

(Table 1). As a result, spring migration and the post-fledging period accounted for 46% and

31% of juvenile apparent mortality, respectively, whereas autumn migration accounted for only

14%.

Stage-specific vital rates had different relative effects on λ. Apparent survival of

juveniles and adults during spring migration contributed most to variation in λ (Table 1). Adult

survival in summer, post-fledging survival, fecundity, and adult survival during autumn

migration each contributed more than 10%. The remaining vital rates, winter survival and

juvenile survival during autumn migration, each contributed < 6%.

Habitat-specific vital rates and their contribution to population growth

Mean vital rates, their relative contribution to λ, and λ itself varied among our 12 study plots

(Fig. 3; Appendix S1: Tables S3-S14). Populations in nine plots (75%) grew over the four years of the

study ($\lambda > 1$), but only four (33%) had self-recruitment rates > 1 (Appendix S2: Tables S1-S12). Self-

recruitment rate or R_p, a demographic proxy for habitat quality, was positively correlated with

fecundity (ρ = 0.71, 0.52:0.88) and adult apparent summer survival (ρ = 0.49, 0.15:0.78), and

negatively correlated with immigration rate (ρ = -0.48, 95% HPDI = -0.71:-0.23). Thus, high-quality

plots – those with high R_p – tended to have higher productivity, higher adult summer survival, and

lower immigration. The relative contributions of juvenile annual survival and fecundity tended to be

larger in plots with high R_p (juvenile survival: ρ = 0.87, 0.61:0.96; fecundity: ρ = 0.69, 0.24:0.92),

while the relative contribution of adult annual survival tended to be larger in plots with low self-recruitment rates (ρ = -0.91, -0.98:-0.77). These results were driven by a larger contribution of juvenile spring migration survival in higher-quality plots, and a larger contribution of adult summer survival in low-quality plots (Appendix S2: Tables S1-S12). The relative contribution of immigration to variation in λ was not correlated with R_p (ρ = -0.39, -0.79:0.23).

Discussion

Understanding the demographic processes that shape population dynamics is critical to advancing ecological theory and to designing effective management strategies for species of conservation concern. In this study, we combined breeding and wintering demographic data within a integrated population model to quantify full-annual-cycle vital rates and their contributions to population dynamics. Our analysis indicates that regional population dynamics of Wood Thrushes breeding in southern Indiana between 2011 and 2014 were most strongly driven by variation in apparent survival of juveniles and adults during spring migration. Our vital rate estimates are similar to published estimates of fecundity (0.20-2.5: Fauth 2000, Kaiser and Lindell 2007), post-fledging survival (0.42-0.79: Anders et al. 1997, Schmidt et al. 2008), monthly summer survival (0.91-0.94: Powell et al. 2000), over-winter survival (0.89-0.94: Rappole et al. 1989, Conway et al. 1995), and annual apparent survival of adults (0.53-0.62: Powell et al. 2000) from other Wood Thrush populations in the US, Belize, and southern Mexico.

Previous studies of three migratory songbird species, Black-throated Blue Warbler (*Setephaga caerulescens*), Kirtland's Warbler (*Setophaga kirtlandii*), and Willow Flycatcher (*Empidonax trailii*), indicated that apparent survival appears to be lowest during the migratory stages (Sillett and Holmes 2002, Rockwell et al. 2016, Paxton et al. 2017). These studies, however, were not designed to separate apparent survival during autumn and spring. For the Wood Thrushes in our study populations, apparent survival was lowest spring migration than during autumn migration. Interestingly, differences between apparent survival during spring and autumn migration from our analysis are comparable to differences in true migration survival of several larger-bodied bird

species that have been tracked using satellite transmitters. Klaassen et al. (2014) found that survival was ~8% lower in spring than autumn for Osprey (*Pandion haliaetus*), Marsh Harriers (*Circus aeruginosus*), and Montagu's Harriers (*Circus pygargus*). Similarly, Lok et al. (2015) found that survival during spring migration was ~16% lower in spring than in autumn for Eurasian Spoonbills (*Platalea leucorodia leucorodia*). This suggests that lower survival during spring migration than during autumn migration may be a general phenomenon across many migratory birds.

Two non-mutually exclusive hypotheses could explain the importance of spring migration in the annual cycle. Most species of Neotropical migratory birds depart their tropical wintering grounds on spring migration when precipitation and insect abundance are at their annual nadir (Janzen 1973). The scarcity of food resources in late winter limits the ability of individuals to build fat reserves prior to migration (Studds and Marra 2007) and makes them more susceptible to adverse conditions experienced during migration (Finch et al. 2014, Briedis et al. 2017). Additionally, because reproductive success is strongly tied to early arrival on the breeding grounds (Lozano et al. 1996), individuals are under severe time constraints during spring migration (Kokko 1999). Numerous studies have shown that individuals migrate faster in spring than in autumn (Stutchbury et al. 2009, Tøttrup et al. 2011, Nilsson et al. 2013) and the urgency to reach the breeding grounds may further limit the ability of individuals to rest en route. These constraints appear to impose substantial mortality risks on migratory birds in spring. Our results suggest that these risks may be especially severe for juveniles if habitat segregation forces less dominant individuals into poor-quality winter habitat (Rappole et al. 1989).

Alternatively, low survival during spring migration, especially for juveniles, may be an artifact of dispersal. Juvenile Wood Thrushes, and to a lesser extent adults, disperse over large distances between breeding seasons (Tittler et al. 2006). Accumulating evidence indicates that dispersal decisions of migratory songbirds are influenced by conditions experienced during the preceding winter (Studds et al. 2008) or spring migration (Hušek et al. 2014, Rushing et al. 2015). If dispersal decisions made by Wood Thrushes are similarly influenced, annual variation in dispersal

may explain the contribution of this period to variation in population growth. Without explicit estimates of dispersal probabilities, our data do not allow us to disentangle the contribution of true survival and dispersal decisions made during spring migration to the dynamics of our study populations. Nonetheless, the ability to separately estimate apparent survival during spring and autumn migration is important given the differential contribution of these vital rates to population dynamics in our study populations. Apparent survival of juveniles and adults during spring migration had the largest effects to population growth, cumulatively accounting for ~38% of the variation in λ.

Vital rates during the breeding season (adult survival, fecundity, and post-fledging survival) cumulatively accounted for nearly as much variation in regional λ as that attributed to apparent survival during spring migration (37% vs 38%; Table 1). This finding corroborates previous research indicating that Wood Thrush populations in southern Indiana are limited by productivity and recruitment (Rushing et al. 2016a, 2016b, Ahrestani et al. 2017). It also emphasizes that spatial variation in breeding habitat quality influences the contribution of vital rates to variance in λ. Environmental heterogeneity and habitat-specific demography have long been hypothesized to be central to spatial variation in population growth (Holt 1984, Pulliam 1988, Dias 1996, Hanski 1999). Our work highlights a subtle but important extension: the relative contribution of vital rates to λ can vary significantly among habitats that differ in quality. Juvenile survival and fecundity of Wood Thrush in Indiana contribute more to λ in high-quality habitats, whereas adult survival contributes more to λ in low-quality habitats.

Although our field methods were not designed to collect the data required to differentiate between mortality and permanent emigration, we propose that the breeding habitat-related differences in the relative contribution of vital rates to λ are driven primarily by high permanent emigration of adults in low-quality plots following reproductive failure (Part and Gustafsson 1989, Haas 1998). Specifically, reproductive failure due to nest predation rates or parasitism by Brown-headed Cowbirds (*Molothrus ater*) has been shown to reduce site fidelity and apparent survival in Wood Thrush (Ladin et al. 2016) and other songbirds (Hoover and Reetz 2006). As a result, Wood Thrush populations in

low-quality habitats that experience high rates of nest predation and parasitism generally have lower apparent survival and lower population growth rates than populations in high-quality patches (Trine 1998, Ladin et al. 2016). Consistent with our hypothesis, the self-recruitment rate of our study populations was negatively correlated with the proportion of nests that failed due to predation or parasitism (= -0.11, -0.18:-0.06; C.S. Rushing & T.B. Ryder *unpub.*). Identifying the external drivers of population growth and understanding how they contribute to spatial variation in demography will require additional modeling efforts.

Our results also indicate that the contribution of immigration to population dynamics was scale-dependent. At the regional scale, annual variation in immigration had a small contribution to variation in λ, despite a relatively high overall immigration rate (Table 1). At the plot-scale, however, the contribution of immigration was large (range: 9-49%; mean = 22%; Table 1) and in some cases larger than the contributions of other vital rates (Fig. 3). These results are consistent with theoretical predictions that the effects of emigration and immigration on population dynamics can be comparable to fecundity and survival at local scales but are largely redistribution processes at regional scales (Camus and Lima 2002). Despite the contribution of immigration to λ at the plot-level, we found no evidence that immigration explained a larger portion of the variance in population growth in high-quality than in low-quality habitats. This finding is contrary to the predictions of source-sink theory (Pulliam 1988, but see Gundersen et al. 2001) and highlights the need to directly estimate the contribution of immigration to population dynamics when assessing how demographic processes contribute to source-sink dynamics.

Apparent survival of adults and juveniles during winter and autumn migration collectively accounted for only ~12% of the variation in λ, but our estimates of the contribution of these stages may underestimate their influence on population dynamics. First, many Wood Thrushes move within the stationary winter period and these transient individuals have lower and more variable survival than stationary individuals (Rappole et al. 1989). We were unable to estimate the survival of transient individuals and therefore could

not account for their influence on λ. If the overwinter survival of our breeding populations was lower and more variable due to the presence of transients, the true contribution of overwinter survival to λ may be larger than our results indicate. Second, many studies have revealed the ubiquitous nature of seasonal carry-over effects in migratory species (reviewed in Harrison et al. 2011). Biotic or abiotic conditions experienced during autumn or winter may be important in limiting Wood Thrush populations via indirect effects on spring migration survival, fecundity, or dispersal decisions (Wilson et al. 2011, Rushing et al. 2015). Accounting for these carry-over effects might reveal that the winter period has a larger effect on breeding population dynamics than the vital rate contributions indicate, but requires longer-term demographic data than were available for this study.

Historically, studies of population limitation in migratory species have not been replicated across heterogeneous habitats (Pearson and Fraterrigo 2011) and have focused primarily on the breeding period (Marra et al. 2015). Our full-annual-cycle IPM provides a framework for exploring additional questions about the influence of habitat-and season-specific vital rates on population dynamics in migratory species. For example, by modeling vital rates as a function of covariates, this framework can be used to estimate the relative importance of carry-over effects (e.g., winter habitat quality) versus within-season factors (e.g., weather, availability of stopover habitat, collisions) on migration survival and population growth. Given the flexibility of IPMs to accommodate multiple types of data and sub-model structure, this framework could also be modified to estimate habitat- and season-specific dispersal probabilities to isolate the effects of true seasonal survival and permanent emigration on population dynamics (Gilroy et al. 2012, Chandler and Clark 2014). Expanding this model to aggregate data sources over larger spatial and temporal scales (Ahrestani et al. 2017) will be especially important in understanding the causes of long-term population declines (which may differ from the drivers of annual variation in abundance, e.g., Johnston

et al. 2016) and for predicting the consequences of environmental change or management strategies. The model we present here provides a flexible framework for testing hypotheses about how spatial and temporal variation in demography shape population dynamics, and for identifying when and where populations are limited.

Acknowledgements

Data Availability

All demographic data used in this analysis are archived in the Smithsonian Digital Data Repository: https://doi.org/10.5479/data_nzp/10088/32800

Supplementary Information

Appendix S1: Details of MCMC estimation, model parameters, priors, and migration survival estimation

Appendix S2: Plot-level demographic rate estimates and contributions

Data S1: JAGS code

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Table 1: Vital rate estimates and contributions to variation in population growth for Wood Thrushes breeding in southern Indiana (2011-2014). Seasonal survival estimates have been scaled to their equivalent monthly survival rates to aid comparison. The annual range provides the posterior means for minimum and maximum annual estimates across the four years of our study. Coefficient of variation is measured as the standard deviation of the annual vital rate estimates divided by the mean. Note that winter survival was not estimated as a function of age and therefore only one estimate is provided. Because the contribution of juvenile winter survival was negligible (posterior mean = 0.002, 95% HPDI = 0:0.0005), it is not shown.

Vital Rate	Mean (95% HDPI)	Annual range	Coef. Variation	Contribution to Var(λ) (95% HPDI)
Overall				
Fecundity (f)	1.84 (1.25-2.46)	1.43-2.25	0.21	0.11 (0.06-0.17)
Immigration (ω)	0.34 (0.21-0.46)	0.33-0.36	0.04	0.06 (0.04-0.09)
Juvenile annual survival (ϕ^J)	0.24 (0.17-0.32)	0.16-0.33	0.35	0.37 (0.29-0.45)
Adult annual survival (ϕ^{Ad})	0.58 (0.46-0.69)	0.56-0.61	0.05	0.46 (0.35-0.57)
Seasonal				
Adult summer survival (ϕ_{Summer})	0.96 (0.91-0.99)	0.95-0.96	0.02	0.14 (0.07-0.22)
Winter survival (ϕ_{Winter})	0.98 (0.95-1.00)	0.98-0.98	0.01	0.06 (0.03-0.10)
Adult autumn survival (ϕ_{Autumn}^{Ad})	0.92 (0.84-1.00)	0.92-0.93	0.01	0.11 (0.05-0.17)
Adult spring survival (ϕ_{Spring}^{Ad})	0.89 (0.71-1.00)	0.85-0.92	0.04	0.14 (0.07-0.23)
Post-fledging survival (ϕ_{PF})	0.65 (0.44-0.86)	0.54-0.78	0.16	0.12 (0.07-0.19)
Juvenile autumn survival (ϕ_{Autumn}^J)	0.92 (0.77-1.00)	0.91-0.92	0.01	0.01 (0.00-0.01)
Juvenile spring survival (ϕ_{Spring}^J)	0.48 (0.16-0.83)	0.38-0.58	0.23	0.24 (0.1-0.37)

List of figures:

Fig. 1: Map of the study sites and demographically linked populations of Wood Thrush. (A) Wood Thrush breeding range is shown in green and the winter range in blue. Population linkages (migratory connectivity) were estimated from light-level geolocators (Stanley et al. 2015) and the kernel density plot shows the estimated probability distribution of wintering Wood Thrushes tracked from our breeding population. The approximate autumn (red) and spring (yellow) migration route of one individual is shown. The orange star represents the winter study location at Belize Foundation for Research and Environmental Education. (B) Regional forest cover shown in green and the distribution of the 12 breeding study plots distributed across southern Indiana, USA. Orange points denote the geographic location of study plots in southern Indiana and point size indicates the count of trees > 30 cm DBH, a proxy for Wood Thrush habitat quality.

Fig. 2: Conceptual overview of the linked summer and winter CJS models. (A) Within each stationary period, apparent survival is estimated both within and between seasons (BB = between-breeding; BW = between-winter). The between-season survival estimates contain information about the latent survival rates during spring and autumn migration. (B) Using the estimated survival rates in each CJS model (black), the latent migration survival rates (gray) can be estimated. Lines under each latent survival rate highlight shared parameters in each equation.

Fig. 3: Posterior distributions of the relative contribution of (A) fecundity, (B) immigration, (C) juvenile survival, and (D) adult survival to plot-level variation in annual population growth for Wood Thrushes breeding in southern Indiana, USA. For each demographic rate, the white line indicates the posterior mean and the dark grey and light grey areas indicate the 50% and 95%

highest posterior density intervals, respectively. Vertical dashed lines show the relative

contribution of each vital rate to regional population growth. Plots are ranked on the y-axis by

their self-recruitment rate (R), which is strongly positively correlated with the count of trees >
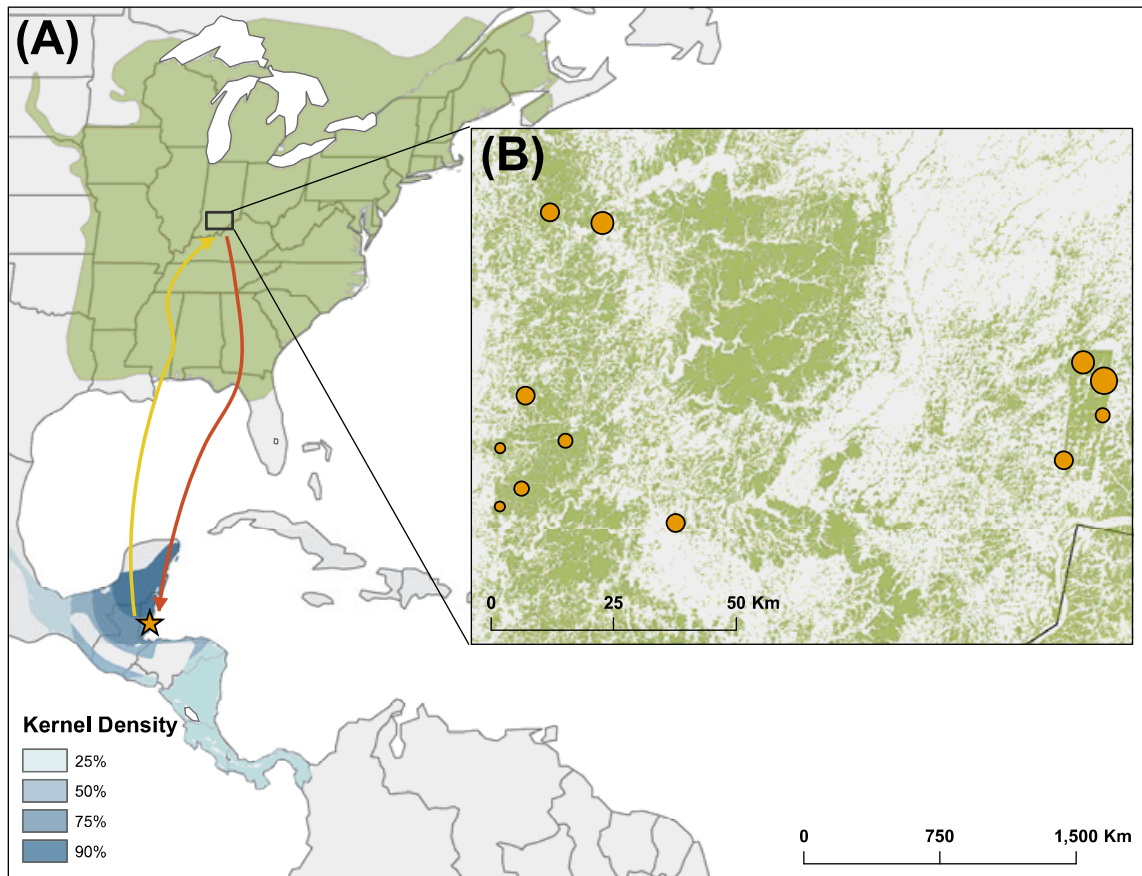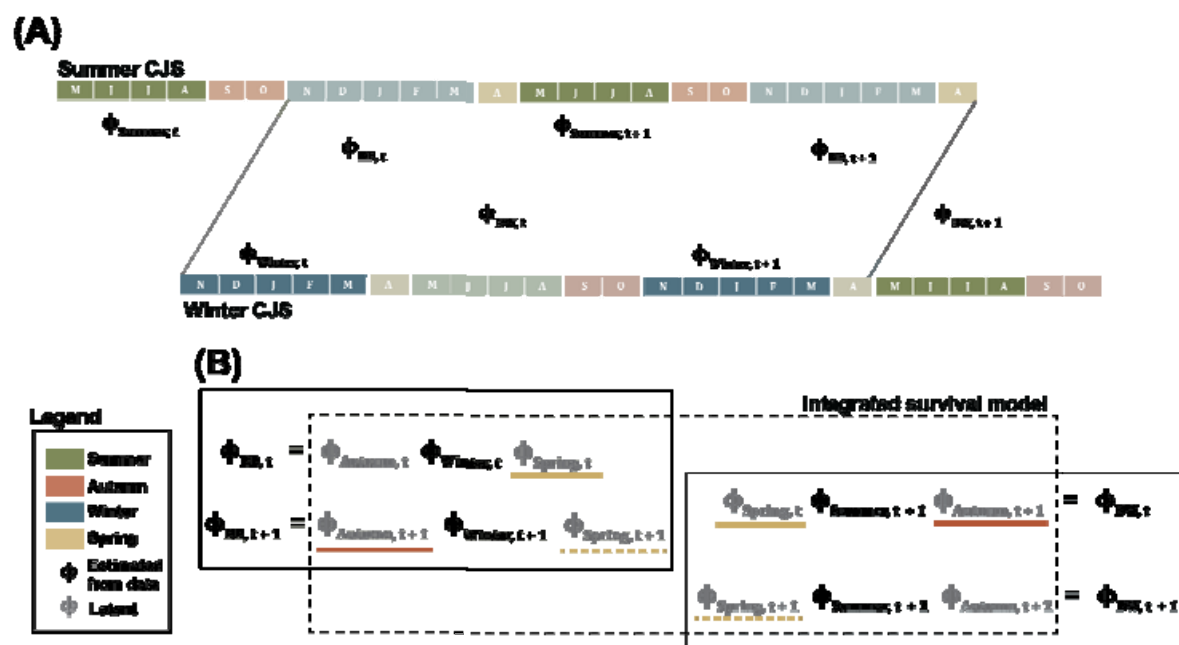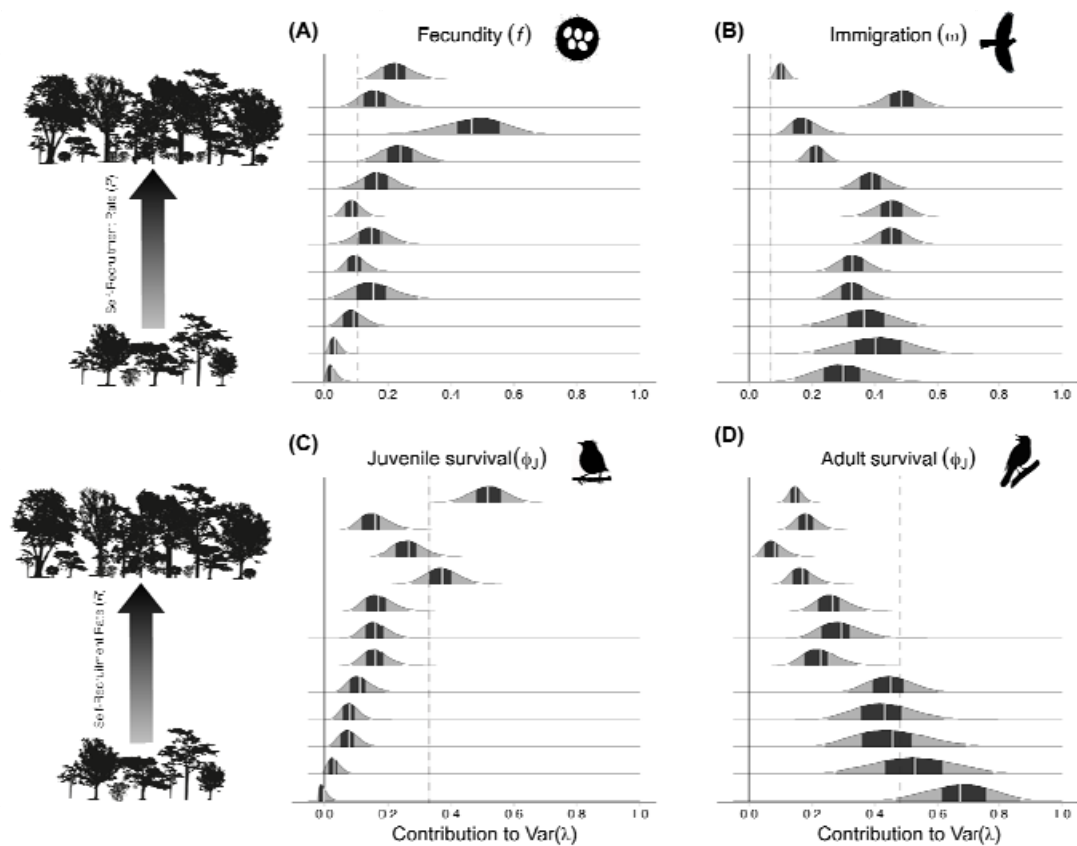
30 cm DBH on each plot.

Fig. 1

Fig. 2

Fig. 3