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APPLICATION

mignette: An R package for creating and visualizing migratory network models

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Abstract

1. A prominent challenge for managing migratory species is the development of conservation plans that accommodate spatiotemporally varying distributions throughout the year. Migratory networks are spatially-explicit models that incorporate migratory assignment and seasonal abundance data to define patterns of connectivity between stages of the annual cycle. These models are particularly useful for widespread application because different types of migratory data can be used to quantify individual and population-level movement across the annual cycle of migratory species. While there are clear benefits of combining migratory assignment and abundance data for the development of conservation strategies, there is a concurrent need for corresponding user-friendly software to facilitate the integration of these data for conservation.
2. Here, we present *mignette* (migratory network tools ensemble), an R package for developing migratory network models to estimate network connectivity among migratory populations. We demonstrate the functionality of *mignette* with three empirical examples that highlight the use of different types of tracking data for migratory assignment.
3. *mignette* facilitates the modelling of migratory networks by providing R functions to: (1) define breeding and nonbreeding nodes, (2) assemble abundance and assignment data and (3) model the migratory network. Additionally, *mignette* provides R functions to visualize modelled migratory networks.
4. With increasing availability of migratory assignment and abundance data, *mignette* represents a valuable tool for developing effective conservation strategies for migratory species.

Matthew G. DeSaix and Christen M. Bossu contributed equally.

KEYWORDS
Bayesian methods, connectivity, conservation prioritization, genoscape, JAGS, migratory ecology, network model

1 | INTRODUCTION

Migratory species occupy multiple habitats throughout the year that can be geographically separated by vast distances. A prominent challenge for the conservation and management of these species is addressing population decline in the face of spatiotemporally varying distributions and incomplete knowledge of migratory connectivity (Runge et al., 2014). While research addressing population declines in migratory species has historically been hindered by a bias of research toward the breeding season (Marra et al., 2015), advancements in the development of species abundance data across the annual cycle as well as migratory assignment and tracking methods (hereafter referred to as 'assignment') are facilitating full annual cycle research aimed at informing conservation efforts. Although there are clear benefits of combining assignment and abundance data for the design of conservation strategies, the availability of user-friendly software that facilitates the modelling of migratory population dynamics with these data has been limited (but see Cohen et al., 2018).

Current methods excel at quantifying the 'strength' of migratory connectivity of a species—a metric that defines the correlation of distances between individuals or populations across stages of the annual cycle (Cohen et al., 2018). The strength of migratory connectivity is a valuable metric for conservation and management efforts as it informs the extent to which individuals or populations experience similar environmental conditions or stressors throughout the year, and such methods are currently implemented in R packages (e.g. *MigConnectivity*; Cohen et al., 2018). Here, we present *mignette* (migratory network tools ensemble), a complementary approach to existing methods by quantifying the 'pattern' of connectivity (i.e. network connectivity), which describes the proportion of a species' global population that migrates between breeding and nonbreeding populations. *mignette* expands upon a previously published network model (Ruegg et al., 2020), which was designed initially for use with genetic assignment data, by accommodating any type of migratory assignment or tracking data (from here on referred to as assignment data) that can be used to confidently assign individuals to cross-season populations. In this paper, we walk-through a description of *mignette* and then provide three examples demonstrating the use of different types of assignment data (genetic only, banding only, genetic and geolocator combined), typically available for migratory species.

2 | PACKAGE DESCRIPTION

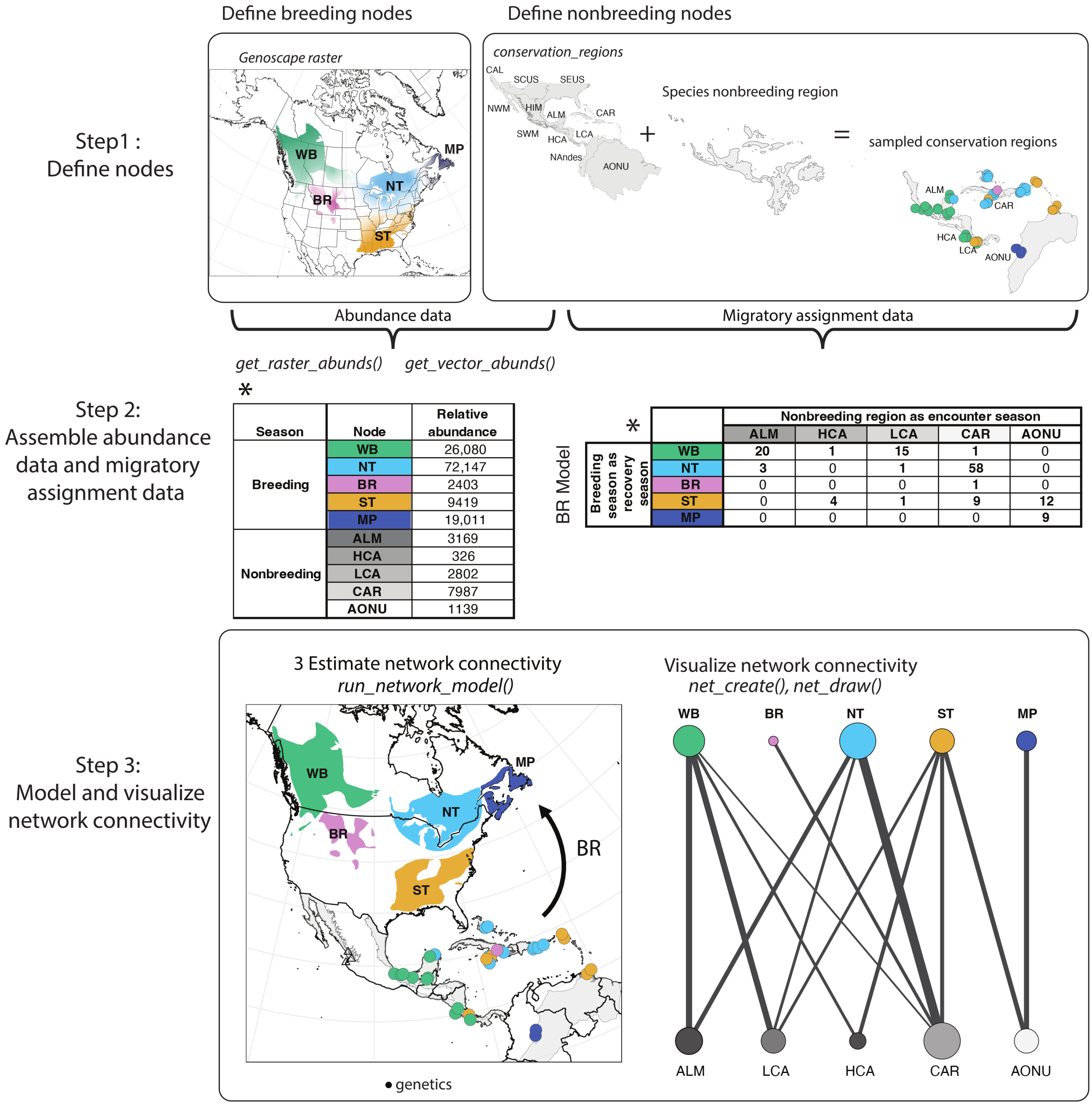
mignette is a package in the R programming language (R Core Team, 2023) applicable for any study of migratory species that has basic information on migratory movement and abundance. We outline a general workflow for estimating network connectivity with *mignette* (Figure 1): (1) define breeding and nonbreeding nodes, (2) assemble abundance and assignment data and (3) model network connectivity. Assignment data is directional—that is, there is an 'encounter' season and a 'recovery' season (Procházka et al., 2017; Figure 2). For assignments generated from extrinsic markers, individuals are initially captured or tagged during the encounter season, and during the recovery season they are re-captured or re-sighted. In the case of geolocators or GPS trackers, the recovery season is where individuals are inferred to have been. For genetic data, the encounter season is nonbreeding and the recovery season is the breeding origin inferred from a genetic analysis of the individual using population assignment methods.

mignette implements a Bayesian connectivity model using JAGS, a software for Markov Chain Monte Carlo simulation (Depaoli et al., 2016; Plummer, 2004) and runs JAGS using the R packages *rjags* (Plummer, 2019) and *jagsUI* (Kellner, 2019). *mignette* is designed for working with spatial data in R using *terra* (v1.7-39; Hijmans, 2021) and data manipulation is performed with *tidyverse* (Wickham et al., 2019). The *mignette* functions and data sets are provided in Supporting Information (Tables S1 and S2). Information on how to install and use *mignette* is provided in an online vignette (https://mgdesaix.github.io/connectivity-book/).

2.1 | Step 1: Define nodes

The migratory network model is a graph-based model where populations are spatially distinct regions defined as nodes and the links between nodes (network connectivity) are defined as edges (Taylor & Norris, 2010). In *mignette*, we provide vector data of conservation regions, stored as conservation_regions, which can be used to delineate terrestrial breeding or nonbreeding nodes in the Western Hemisphere (Figure S1). These regions were delineated based largely on US Environmental Protection Agency Level I ecoregion boundaries and geopolitical borders (Commission for Environmental Cooperation, 1997; Griffith et al., 1998). Development of *mignette* was motivated by our studies of Neotropical migratory landbirds, and we combined some smaller adjacent and biogeographically similar regions, as well as some larger regions containing relatively few nonbreeding Neotropical migratory landbird species. Geopolitical borders were used to split some of the larger conservation regions, as such divisions may be more practical for conservation purposes. Although these conservation regions may be also applicable for other terrestrial migratory species, *mignette* users can alternatively provide vector data for spatially delineating nodes that are relevant to their study system and objectives.

For *mignette* users with genetic data, breeding nodes can also be defined using population structure analyses that spatially delineate



Season	Node	Relative abundance
Breeding	WB	26,080
	NT	72,147
	BR	2403
	ST	9419
	MP	19,011
Nonbreeding	ALM	3169
	HCA	326
	LCA	2802
	CAR	7987
	AONU	1139

		Nonbreeding region as encounter season				
		ALM	HCA	LCA	CAR	AONU
Breeding season as recovery season	WB	20	1	15	1	0
	NT	3	0	1	58	0
	BR	0	0	0	1	0
	ST	0	4	1	9	12
	MP	0	0	0	0	9

FIGURE 1 Workflow for creating a migratory network model in mignette. Data shown are from the American Redstart example in the text.

populations (Ruegg et al., 2020). While it is outside the scope of *mignette* to perform population genetics analyses, there are numerous reviews on approaches for delineating populations with genetic data (e.g. Hohenlohe et al., 2021).

2.2 | Step 2a: Assemble relative abundance data

We provide functions in *mignette* that take range-wide abundance estimates in raster format and calculate the relative abundance for each node (Table S2). From such raster data, the *mignette* user can calculate the relative abundance in each node either by supplying a vector (a *terra* spatVector object) with polygons delineating population boundaries using the *mignette* function get_vector_abunds(), or by supplying a raster (a *terra* spatRaster object where each layer is a raster for a given node) in which each cell has a probability of membership to a given node and using the *mignette* function get_raster_abunds(). This latter function is used for genetically distinguished populations, such as a genoscape (Ruegg et al., 2020), which are created from spatially determining population genetic

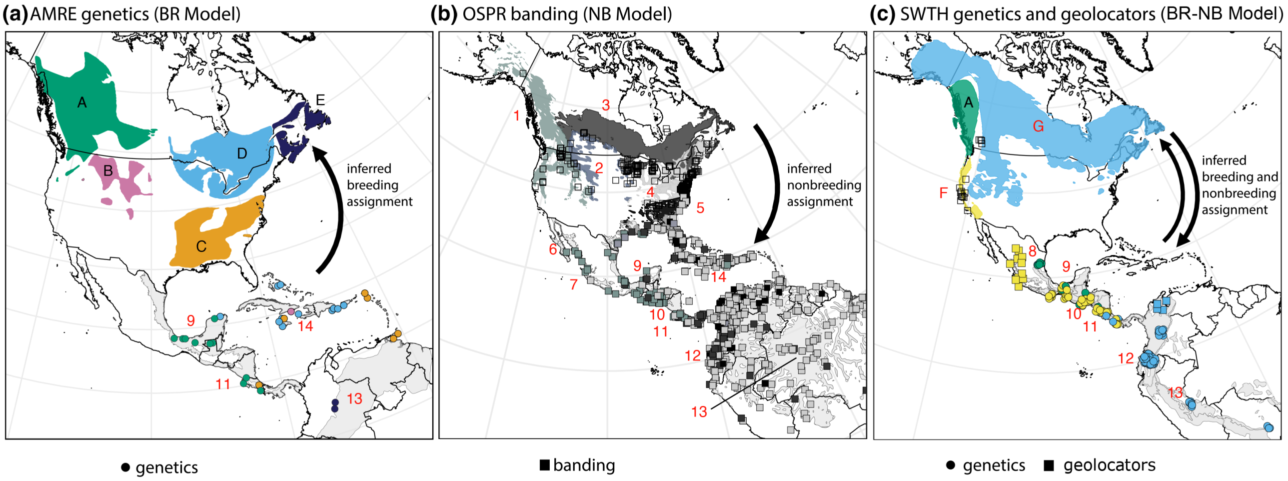


FIGURE 2 Examples of the directionality of assignment data and the corresponding model in mignette. (a) Genetic data from American Redstart (AMRE) uses the breeding assignment model (BR); (b) Banding data from Osprey (OSPR) uses the nonbreeding assignment model (NB); (c) Genetic data (breeding assignment) and geolocator data (nonbreeding assignment) for Swainson's Thrush (SWTH) is the bi-directional model (BR-NB).

structure. get_raster_abunds()uses the membership probabilities of different populations from the raster data to then calculate the abundance of each population by weighting each cell in the abundance raster by the corresponding cell of membership probability to the given node.

2.3 | Step 2b: Assemble assignment data

In *mignette*, we specifically refer to 'assignment data' as a matrix specifying the number of individuals sampled from each node in the 'encounter' season that are assigned to nodes in the 'recovery' season (Procházka et al., 2017). An assignment matrix requires data from a single type of tracking method in a single direction. One current limitation is that the network model does not account for node assignment uncertainty. Therefore, the assignment data solely consists of individuals that can be confidently assigned to a single node and it is essential for users to consider appropriate sample selection and node size delineation to address the geographic uncertainty in their assignment method. Individuals with low confidence of assignment to a given node should be pruned. Node size can also be increased to accommodate the geographic uncertainty of assignment.

Since the network model accounts for sampling effort in the encounter season, we provide different model variations in *mignette* based on the directionality of the data: Breeding Assignment Model (BR) = a single assignment matrix where the nonbreeding season is 'encounter' (columns) and the breeding season is 'recovery' (rows); *Nonbreeding Assignment Model (NB)* = a single assignment matrix where the breeding season is 'encounter' (rows) and the nonbreeding season is 'recovery' (columns); and Multi-directional Assignment Model (BR-NB) = two assignment matrices, one of the BR model type and one of the NB model type (Figure 2).

While sampling design recommendations for a migratory connectivity study will likely vary according to the particular system (see Vickers et al., 2021), we performed basic simulations to highlight how sample sizes, in relation to different migratory connectivity scenarios, affect estimates of network connectivity (Figures S2 and S3; see Supporting Information for details). We found that sampling as few as five individuals per encounter node can result in consistently accurate estimates of connectivity (i.e. 95% credible intervals overlapping with the true connectivity value) for weak migratory connectivity scenarios (Figure S3). In scenarios where an encounter node has strong connectivity to a single recovery node and weak connectivity to other recovery nodes, the network model can also consistently estimate the strong connectivity values accurately with sample sizes as low as 5 but may inaccurately estimate the weak connectivity values as zero, even when sample sizes are as high as 10 or 20 individuals, due to a lack of sampling of less frequent individuals that migrate to the weaker connectivity node (Table S3).

2.4 | Step 3: Model network connectivity

mignette expands on a published network model (Ruegg et al., 2020; Supporting Information). In short, we assumed individuals assigned to recovery season nodes sampled at a given encounter season node (specified in the assignment matrix) followed a multinomial distribution with probabilities proportional to the corresponding recovery season column. Similarly, we assumed the individuals found at each recovery season node from a given encounter season node followed a multinomial distribution with probabilities equal to the corresponding rows of encounter season nodes weighted by the sampling effort at each recovery season node. Sampling effort was estimated as the proportion of the total number of individuals sampled at a given encounter season node. Finally, we assumed the population size indices (i.e. abundance) for the encounter and recovery season nodes were drawn from a multinomial distribution with node probabilities derived from the connectivity matrix.

The migratory network is created using the *mignette* function run_network_model(). This function is a wrapper for the *jagsUI* autojags() function (Kellner, 2019) and will accept the same arguments for the MCMC parameters (Table S1). Additionally, the run_network_model() function requires the abundance data, assignment data and model type to be specified by the corresponding arguments. The function returns a list object with four components. The first component, [["conn"]], is an R tibble object of the mean connectivity estimates. These values are interpreted as the proportion of individuals within the global population that migrate between the corresponding nodes, such that all values in the connectivity matrix sum to one. The second component, [["jags_out"]], is a list object of the output from *jagsUI* autojags(). The final two components, [["brnode_names"]] and [["nbnode_names"]], store the node names corresponding to the rows and columns, respectively, of the connectivity matrix.

After running the network model, convergence and fit need to be assessed to ensure that the model provides reasonable inferences (Conn et al., 2018). Gelman-Rubin diagnostic statistics (Gelman & Rubin, 1992), $\hat{R}$, for all parameters of the connectivity matrix can be accessed from the autojags() output. $\hat{R}$ values <1.1, combined with traceplots showing that stationary distributions have been reached, can provide evidence of adequate convergence. MCMC specifications can be adjusted and the model re-run to address any apparent convergence issues (Kellner, 2019). In *mignette*, we implement posterior predictive checks using the Freeman-Tukey discrepancy statistic to compare the fit of the observed data to data simulated from the model (Conn et al., 2018). The function get_FT_fit() produces a density plot of the Freeman-Tukey statistics for qualitatively comparing observed and simulated data, and outputs the Bayesian *p*-value of the goodness-of-fit.

Visualization of different features of the migratory network is implemented in *mignette*. Statistical uncertainty in the network connectivity estimates is characterized by the credible intervals provided in the network model output for the conn parameter. The *mignette* function plot_network_CI() plots the mean and 95% credible intervals for network connectivity which allows users to assess the uncertainty in the estimates. The mean connectivity estimates can be plotted as a migratory network using a two-step process of preparing the network output with the function net_create() and then plotting the network with net_draw(). The network model can produce extremely small connectivity values for unsampled migratory connections and setting the connected_tol parameter in net_create will set a threshold for plotting only robust connections.

3 | EXAMPLE APPLICATIONS

Here, we create migratory networks for three species of migratory birds to highlight the three directionality models in *mignette*. In the first example, we demonstrate the use of *mignette* with genetic assignment data from a study on the American Redstart (*Setophaga ruticilla*; DeSaix et al., 2023). In the second example, we use breeding Osprey (*Pandion haliaetus*) banding and re-encounter records (Celis-Murillo et al., 2022). Finally, we combined geolocator data (Cormier et al., 2013; Delmore et al., 2012) with genetic assignment data (Turbek et al., 2024) to estimate network connectivity for Swainson's Thrush (*Catharus ustulatus*). In the subsequent sections, all species' examples are described while code examples are provided only for American Redstart.

3.1 | Data preparation

For American Redstart, we used the five genetically delineated populations from DeSaix et al. (2023) as breeding nodes (Table 1). For nonbreeding nodes, we used the intersection of sampling coordinates for 135 individuals from the stationary nonbreeding range with the conservation regions (Table 1; Figure 2a). For Osprey, we intersected conservation regions with coordinates for 683 individuals banded during the breeding season to define five breeding nodes and defined eight nonbreeding nodes from the resight coordinates (Table 1; Figure 2b). For Swainson's Thrush, we used three genetically distinct breeding populations of Swainson's Thrush as breeding nodes and identified six nonbreeding nodes from both genetic data ($n=122$) and geolocator data ($n=15$) (Table 1; Figure 2c).

To calculate relative abundance, we obtained seasonal abundance data from the eBird Status and Trends dataset (Fink et al., 2022) using the *ebirdst* package in R (Strimas-Mackey et al., 2022). To estimate the breeding node abundance for American Redstart and Swainson's Thrush, we used the get_raster_abunds() function in *mignette* with a raster object of the breeding population structure (i.e. genoscape) and the *ebirdst* raster object of the breeding range abundance. For the breeding node abundance of Osprey and the nonbreeding node abundance of all species, we used the get_vector_abunds()function with the node vector object and an *ebirdst* raster object of the breeding and nonbreeding range abundance as inputs, respectively.

3.2 | Creating the migratory network

The assignment and abundance data are the two main inputs into the migratory network model (Figure 1). For the American Redstart example, individuals were sampled on the nonbreeding grounds and assigned to breeding populations so we use the BR Model.

```
```
network_model <- run_network_model(abundance=amre_abundance,
 nb2br_assign=amre_assign,
 model="BR")
```
```

We used similar coding to run the model for Osprey and Swainson's Thrush, specifying the corresponding abundance

TABLE 1 Node labels, names, season and species for the three example species: American Redstart (AMRE), Osprey (OSPR) and Swainson's Thrush (SWTH).

Genetic node label	Genetic node name	Season	Species
A	Pacific Northwest	Breeding	AMRE, SWTH
B	Basin Rockies	Breeding	AMRE
C	Southern Temperate	Breeding	AMRE
D	Northern Temperate	Breeding	AMRE
E	Maritime Provinces	Breeding	AMRE
F	Pacific Coast	Breeding	SWTH
G	East/West Boreal	Breeding	SWTH
Conservation node label	**Conservation node name**	**Season**	**Species**
1	Northwestern Forested Mountains (NWFM)	Breeding	OSPR
2	Great Plains (GP)	Breeding	OSPR
3	Northern Forests (NF)	Breeding	OSPR
4	Eastern Temperate Forests (ETF)	Breeding	OSPR
5	Southeastern US (SEUS)	Breeding, Nonbreeding	OSPR
6	Northwest Mexico (NWM)	Nonbreeding	OSPR
7	Southwest Mexico (SWM)	Nonbreeding	OSPR
8	Highland Interior Mexico (HIM)	Nonbreeding	SWTH
9	Atlantic Lowland Mexico (ALM)	Nonbreeding	AMRE, OSPR, SWTH
10	Highland Central America (HCA)	Nonbreeding	OSPR, SWTH
11	Lowland Central America (LCA)	Nonbreeding	AMRE, OSPR, SWTH
12	Andes	Nonbreeding	OSPR, SWTH
13	Amazon/Orinoco-Northern Uplands (AONU)	Nonbreeding	AMRE, OSPR, SWTH
14	Caribbean (CAR)	Nonbreeding	AMRE, OSPR

(Tables S4 and S5) and assignment data (Tables S6 and S8). The Osprey connectivity model is based on breeding season banding data (with band resights on the nonbreeding grounds), therefore we use the NB Model (Table S6), whereas the Swainson's Thrush model uses both genetic and geolocator data (deployed on breeding grounds with inferred nonbreeding locations), so we use the BR-NB Model, which requires two separate assignment matrices (breeding and nonbreeding assignment; Tables S7 and S8).

For genetic data, we followed standard practice in genetic assignment tests to use assignment consistency of ≥0.8 as the threshold for confidently assigning an individual to a node (DeSaix et al., 2023, 2024). Assignment from banding/re-encounter data can reasonably be assumed accurate so long as individual identification is not an issue. For geolocator data we used the centroids of the inferred nonbreeding location to assign conservation regions. While light-level geolocator inference can have high geographic uncertainty, our data had inferred locations on the periphery of the Swainson's Thrush nonbreeding range and inspection of error bars and kernel densities supported confident assignment of each individual to a single node. In the absence of being able to reliably prune individuals for assignment uncertainty, we recommend generating assignment matrices from assignment probabilities and estimating connectivity for each generated matrix to assess that similar results are produced (Supporting Information).

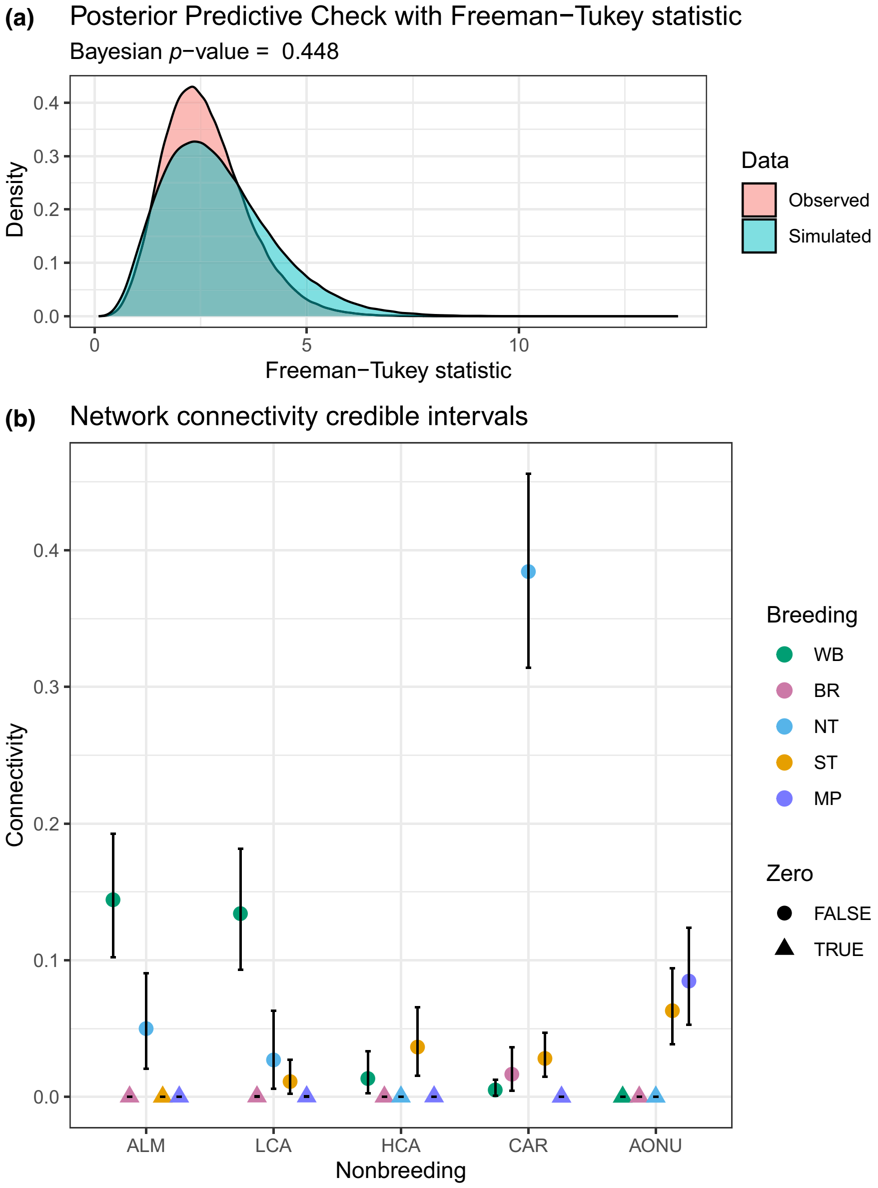
3.3 | Model checking of the migratory network

We check that all parameters converged by looking at the Rhat column in network_model$jags_out as well as visually assessing chains for convergence with jagsUI::traceplot(network_model$jags_out, “conn”) (Figure S4). Below, the posterior predictive check of the American Redstart model shows largely overlapping distributions of the Freeman-Tukey discrepancy statistics for the observed and simulated data, with a corresponding Bayesian *p*-value of 0.45—indicating sufficient goodness of fit (Figure 3a).

```
get_FT_fit(network_model)
```

The Osprey and the Swainson's Thrush models also converged, and had overlapping Freeman-Tukey statistic distributions in the posterior predictive check, suggesting reasonable goodness of fit

FIGURE 3 American Redstart network model results from (a) posterior predictive check from the get_FT_fit() function and (b) 95% credible intervals from plot_network_CI() where shape specifies estimates with a posterior mass at zero.



(Osprey: Bayesian p-value = 0.23 [Figure S5]; Swainson's Thrush: Bayesian p-value = 0.45 [Figure S6]).

3.4 | Visualizing the migratory network

We plot the mean and 95% CI of the connectivity estimates with the plot_network_CI() function (Figure 3b).

```
plot_network_CI(network_model)
```

We also plot the connectivity estimates as a network (Figure 1; Table 2).

```
amre_net <- net_create(network_model)
net_draw(amre_net)
```

Visualization of the migratory network can be readily expanded upon for users to produce graphical interpretations to best suit their needs (Figure 4).

4 | CONCLUSIONS

With the development of *mignette*, we present a tool for quantifying population-level migratory connections across the annual cycle. This tool can provide crucial information for conservation

TABLE 2 American Redstart mean connectivity estimates, where rows refer to breeding nodes and columns refer to nonbreeding nodes. Node names are provided in Table 1.

	ALM	LCA	HCA	CAR	AONU
WB	0.14212	0.13901	0.01346	0.00507	0.00002
BR	0.00010	0.00021	0.00008	0.02082	0.00004
NT	0.05680	0.00041	0.00013	0.38276	0.00006
ST	0.00003	0.01345	0.03618	0.03902	0.06453
MP	0.00013	0.00036	0.00022	0.00002	0.08496

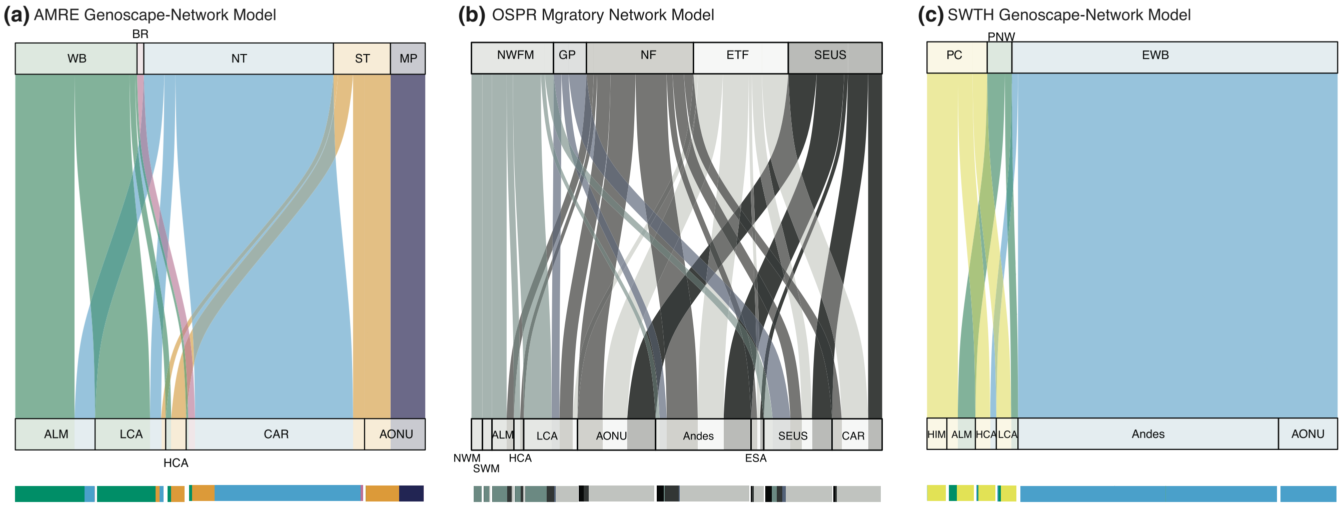


FIGURE 4 Alluvial plots of the connectivity estimates for the three species examples (a–c). The bars are coloured by breeding node and the width of the bars corresponds to the mean connectivity estimates.

decision-making concerning migratory species (Ruegg et al., 2020) and supplements existing methods that quantify the strength of migratory connectivity (Cohen et al., 2018). *mignette* allows visualization of the resulting migratory network using both the standard network plot from *mignette* (Figure 1) and the alluvial plot (Figure 4), both which can provide clarity in identifying migratory connections. These visualizations represent an important first step in the process of developing full annual cycle conservation strategies for migratory species. For instance, wildlife managers in northwestern North America (e.g. Alaska or British Columbia) can discern that their breeding American Redstarts are part of the larger Western Boreal (WB) breeding population and thereby focus on the nonbreeding connections with WB, which is connected almost equally to the Atlantic Lowland Mexico and Lowland Central America conservation regions (47.5% and 46.5%, respectively, of the WB breeding population). Consequently, should persistence of breeding populations become a priority in the future, conservation efforts could involve the development of partnerships with conservation practitioners in the two nonbreeding regions. Similarly, the Boreal population of Swainson's Thrush are primarily connected to two conservation regions, with 79.3% of Boreal breeding individuals estimated to migrate to the Andes and 18.0% to the Orinoco/Amazon region. In contrast, if the persistence of Boreal breeding Osprey was of concern, the estimated diffuse network connectivity suggests that conservation efforts could involve partnerships across a much broader area of Central America, North America and the Caribbean.

The *mignette* R package provides a valuable addition to the conservation practitioners toolbox, since mapping migratory connectivity is a critical step when attempting to implement management strategies for migratory species. Future development of *mignette* will include extending the model to more than two stages of the annual cycle as well as incorporating individual assignment uncertainty. These extensions will further improve the generalizability of the network model and allow users to retain a larger sample size without pruning individuals due to low assignment probability.

AUTHOR CONTRIBUTIONS

Kristen C. Ruegg, Caz M. Taylor, James F. Saracco, Ryan J. Harrigan, Christen M. Bossu and Matthew G. DeSaix conceived the study. Kristen C. Ruegg and Julie C. Hagelin acquired the funding for the study. The specific methods were developed by Caz M. Taylor, James F. Saracco, Ryan J. Harrigan and Marius Somveille. Matthew G. DeSaix developed the R package, and the package was tested by Christen M. Bossu and Ryan J. Harrigan. Christen M. Bossu and Matthew G. DeSaix performed the analyses and led the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14455.

DATA AVAILABILITY STATEMENT

The *mignette* package is available at https://github.com/mgdesaix/mignette and archived on Zenodo (https://doi.org/10.5281/zenodo.13931780; DeSaix, 2024). An online vignette is available at https://mgdesaix.github.io/connectivity-book/. Data used in this manuscript is publicly available from previous studies for the different species: American Redstart (DeSaix et al., 2023); Osprey (Celis-Murillo et al., 2022); Swainson's thrush (Cormier et al., 2013; Delmore et al., 2012; Turbek et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Additional details of analyses and model.

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