

# Hierarchical computing for hierarchical models in ecology

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## Funding information

Division of Graduate Education, Grant/Award Number: 1840343; Division of Environmental Biology, Grant/Award Number: 1927177; Division of Mathematical Sciences, Grant/Award Number: 1614392

Handling Editor: Robert B. O'Hara

## Abstract

1. Bayesian hierarchical models allow ecologists to account for uncertainty and make inference at multiple scales. However, hierarchical models are often computationally intensive to fit, especially with large datasets, and researchers face trade-offs between capturing ecological complexity in statistical models and implementing these models.
2. We present a recursive Bayesian computing (RB) method that can be used to fit Bayesian models efficiently in sequential MCMC stages to ease computation and streamline hierarchical inference. We also introduce transformation-assisted RB (TARB) to create unsupervised MCMC algorithms and improve interpretability of parameters. We demonstrate TARB by fitting a hierarchical animal movement model to obtain inference about individual- and population-level migratory characteristics.
3. Our recursive procedure reduced computation time for fitting our hierarchical movement model by half compared to fitting the model with a single MCMC algorithm. We obtained the same inference fitting our model using TARB as we obtained fitting the model with a single algorithm.
4. For complex ecological statistical models, like those for animal movement, multi-species systems, or large spatial and temporal scales, the computational demands of fitting models with conventional computing techniques can limit model specification, thus hindering scientific discovery. Transformation-assisted RB is one of the most accessible methods for reducing these limitations, enabling us to implement new statistical models and advance our understanding of complex ecological phenomena.

## KEYWORDS

Bayesian filtering, MCMC, parallel computing, recursive, transformation

## 1 | INTRODUCTION

Ecological systems are characterized by dynamics and uncertainty at many scales, but observing all relevant scales may be difficult or impossible (Wiens, 1989). Instead, we must use models to scale and connect processes across multiple levels (Levin, 1992), such as from the scale of observation to the hypothesized scale of biological

process, or from a single individual or species to a population or community. For example, in movement ecology, we often collect telemetry data and observe movement at the individual level, but wish to make inference on the population as a whole, like to better understand responses to environmental conditions that are similar among individuals (Hooten et al., 2016). Alternatively, modelling ecosystems or ecological communities often involves joint analysis of many taxonomic groups as well as the processes that connect them (Levin, 1992; Warton et al., 2015). Finally, conducting

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ecological studies introduces additional uncertainty, including sampling and detection uncertainty as well as spatial and temporal variation between study sites and years, which must be considered when specifying ecological models (Beissinger et al., 2016; Royle & Dorazio, 2008).

Bayesian hierarchical modelling has become a popular tool in ecology, facilitating scaling by relating process models at one level to parameters at another level (Hobbs & Hooten, 2015; Royle & Dorazio, 2008). Hierarchical models are flexible and facilitate the inclusion of multiple sources of uncertainty in the data, process and parameter components (Berliner, 1996; Cressie et al., 2009). For example, many integrated population models (IPMs) use a Bayesian hierarchical framework to integrate multiple data sources to understand population dynamics and demographic processes (Schaub & Abadi, 2011). However, IPMs and other hierarchical models can quickly become large and time-consuming to fit.

Ecological science has seen a rapid increase in the availability of big data, advanced statistical techniques and collaborative research, and our ability to specify ecological models that capture more of the complexity of natural phenomena has improved substantially as a result (McCallen et al., 2019). However, many ecologists have also reached the point where computational demands limit what can be modelled. Furthermore, as ecologists are increasingly interested in long-term monitoring and prediction (Dietze et al., 2008), statistical models must be fit each time data are added. Collaborations with computer and data scientists and new software packages for efficient computing have introduced sophisticated computational techniques (e.g. distributed computing) in ecological science, but barriers to wide implementation of these approaches are a bottleneck for advancing ecological modelling (Hampton et al., 2017; Visser et al., 2015). Therefore, more accessible approaches for reducing computational limitations are needed to support progress in ecological modelling and understanding.

Recursive computing techniques, also known as batch or modular computing or Bayesian filtering, are used to fit a statistical model in a series of steps (Särkkä, 2013). These techniques simplify computing at each step, without modifying the original model specification or

resulting inference. One recursive Bayesian computing (RB) method, introduced by Lunn et al. (2013), leverages the properties of Markov chain Monte Carlo (MCMC) sampling (Gelfand & Smith, 1990) to lessen the computational burden of fitting hierarchical models. The authors used RB to reconcile the results of several independent studies in a meta-analysis (Lunn et al., 2013), and the method has been applied in ecological contexts to facilitate online updating (Hooten et al., 2020), model individual and group variation in physiological measurements (Hooten & Heey, 2019), and scale movement and resource-selection models from individuals to populations (Gerber et al., 2018; Hooten et al., 2016). While not unique to ecology, RB is a natural computational technique for ecologists to consider because the RB framework mirrors many ecological study designs and hierarchical models.

Consider a study of invasive cheatgrass *Bromus tectorum* occurrence in grasslands in Montana, in the northwestern United States (Pearson et al., 2018). Cheatgrass occurrence was monitored at 20 grassland sites by sampling 20 randomly selected 1-m<sup>2</sup> plots within each site. Suppose we want to model the probability of cheatgrass occurrence  $y_{ij}$  in Montana grasslands using a Bernoulli generalized linear mixed model (GLMM) specified as

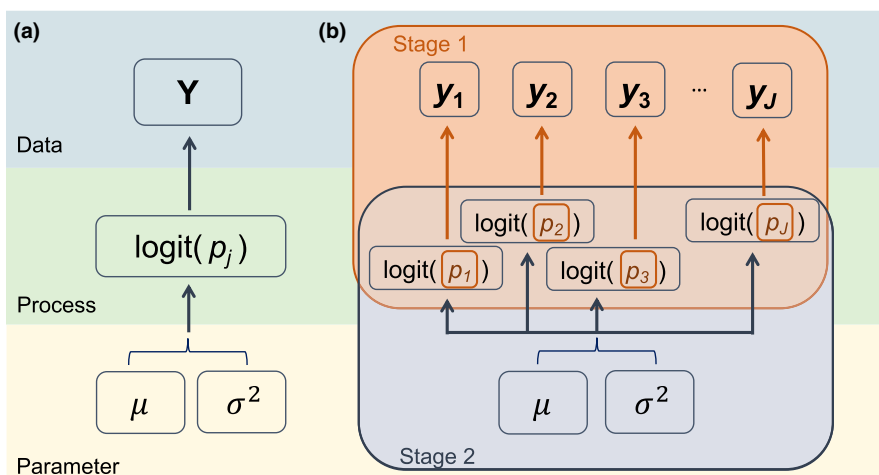
$$y_{ij} \sim \text{Bern}(p_j), \quad i = 1, \dots, N, j = 1, \dots, J, \quad (1)$$

$$\text{logit}(p_j) \sim N(\mu, \sigma^2), \quad (2)$$

$$\mu \sim N(\mu_0, \sigma_0^2), \quad (3)$$

$$\sigma^2 \sim \text{IG}(q, r), \quad (4)$$

where  $j$  indexes sites and  $i$  indexes plots within each site. In this model,  $p_j$  is the probability of cheatgrass at site  $j$ , and  $\text{logit}(p_j)$  arises from a Gaussian distribution with study-wide parameters  $\mu$  and  $\sigma^2$ , arising from Gaussian and inverse gamma distributions, respectively (Figure 1). Thus,  $p_j$  are 'random effects' because they will vary for each site but will arise from a single underlying distribution. We use Gaussian random effects, with the logit link function to constrain  $p_j$  to the proper support, and seek inference on  $\mu$ . The full-conditional distributions for the  $\text{logit}(p_j)$  are not analytically tractable, so the



**FIGURE 1** (a) Directed acyclic diagram (DAG) for Bernoulli GLMM of cheatgrass occurrence in Montana (1)–(4) and (b) schematic for partitioning DAG according to the TARB framework. In (a),  $\mathbf{Y}$  is the matrix whose columns are the data vectors  $\mathbf{y}_j$  for the sites  $j = 1, \dots, J$ . In stage 1, the data  $\mathbf{Y}$  are partitioned by site and fit to obtain the posterior distributions for the  $p_j$ . In stage 2, samples from these posterior distributions are used to sample  $\text{logit}(p_j)$ ,  $\mu$ , and  $\sigma^2$

$\text{logit}(p_j)$  cannot be sampled using Gibbs updates and will need to be tuned individually to fit the model (Gelfand & Smith, 1990). This minimal example could be fit in a single, conventional MCMC algorithm, but we describe the procedure to fit it recursively to demonstrate RB methods.

We could fit this model using RB by first partitioning the data by site,  $\mathbf{Y} = (\mathbf{y}'_1, \dots, \mathbf{y}'_J)'$ . These individual partitions would be analysed independently in a first-stage MCMC algorithm with a temporary prior for  $\text{logit}(p_j)$  to obtain temporary posterior distributions for the parameters  $\text{logit}(p_j)$ . Then, the resulting temporary posterior distributions would be used as proposals in the second-stage algorithm to update the study-wide parameters  $\mu$  and  $\sigma^2$ , and the  $\text{logit}(p_j)$  given  $\mu$  and  $\sigma^2$  (Lunn et al., 2013). However, we would still need to tune the updates for each  $\text{logit}(p_j)$  by hand in the first stage because the full-conditional distributions are not analytically tractable. This would slow model fitting and may be difficult.

Instead, we propose a modification of RB, which we call transformation-assisted RB (TARB), to eliminate tuning in the first stage and ease model fitting with unsupervised algorithms and efficient Gibbs updates. In what follows, we demonstrate how to implement RB and TARB to fit ecological models and apply TARB to a hierarchical movement model for avian migration to make individual- and population-level inference. Additionally, we discuss the implementation of TARB to other ecological models to illustrate its wide applicability.

## 2 | MATERIALS AND METHODS

Our Bernoulli GLMM is a hierarchical model comprised of data, process and parameter components (Berliner, 1996), with a set of latent random effects  $\theta_j = \text{logit}(p_j)$  for  $j = 1, \dots, J$  (Figure 1). The group-level parameters  $\boldsymbol{\psi} = (\mu, \sigma^2)'$ , which correspond to the full study area in our example, describe the distribution underlying the partition-level (e.g. site-level) parameters  $\theta_j$ . For data partitioned  $\mathbf{Y} = (\mathbf{y}'_1, \dots, \mathbf{y}'_J)'$ , this can be written

$$\mathbf{y}_j \sim [\mathbf{y}_j | \theta_j], \quad j = 1, \dots, J, \quad (5)$$

$$\theta_j \sim [\theta_j | \boldsymbol{\psi}], \quad (6)$$

$$\boldsymbol{\psi} \sim [\boldsymbol{\psi}]. \quad (7)$$

Note that square brackets  $[\cdot]$  denote probability distributions (Gelfand & Smith, 1990).

In general,  $\theta_j$  could be an  $m \times 1$  vector that describes the partition-level process with  $m$  covariates. The data partitions  $\mathbf{y}_j$  do not need to be equal-sized, and can represent any natural data subset such as different field sites as in our example, telemetry fixes for distinct individuals, results from several studies in a meta-analysis or data on different species in a community, as long as dependence within the data partitions is accounted for in the data or process models.

The RB approach presented by Lunn et al. (2013) is carried out by specifying prior distributions  $[\theta_j]$  in the first stage to obtain a sample from the posterior distributions  $[\theta_j | \mathbf{y}_j] \propto [\mathbf{y}_j | \theta_j][\theta_j]$  for each partition  $j = 1, \dots, J$  independently. Next, the hierarchical model in Equations 5–7 is fit using a second-stage MCMC algorithm with Metropolis–Hastings (MH) updates for  $\theta_j$ , in which random samples from the temporary, first-stage posterior distributions for  $\theta_j$  are used as the proposals  $\theta_j^{(s)}$ . This eliminates the need for tuning in the second-stage MH updates. Also in the second-stage algorithm, the group-level parameters  $\boldsymbol{\psi}$  are updated based on their full-conditional distributions  $[\boldsymbol{\psi} | \cdot] \propto (\prod_{j=1}^J [\theta_j | \boldsymbol{\psi}])[\boldsymbol{\psi}]$ . The MH acceptance probability for each  $\theta_j^{(s)}$  is  $\min(r_j^{(s)}, 1)$  where

$$r_j^{(k)} = \frac{[\mathbf{y}_j | \theta_j^{(s)}] [\theta_j^{(s)} | \boldsymbol{\psi}^{(k-1)}] [\theta_j^{(k-1)} | \mathbf{y}_j]}{[\mathbf{y}_j | \theta_j^{(k-1)}] [\theta_j^{(k-1)} | \boldsymbol{\psi}^{(k-1)}] [\theta_j^{(s)} | \mathbf{y}_j]}, \quad (8)$$

$$= \frac{[\mathbf{y}_j | \theta_j^{(s)}] [\theta_j^{(s)} | \boldsymbol{\psi}^{(k-1)}] [\mathbf{y}_j | \theta_j^{(k-1)}] [\theta_j^{(k-1)}]}{[\mathbf{y}_j | \theta_j^{(k-1)}] [\theta_j^{(k-1)} | \boldsymbol{\psi}^{(k-1)}] [\mathbf{y}_j | \theta_j^{(s)}] [\theta_j^{(s)}]}, \quad (9)$$

$$= \frac{[\theta_j^{(s)} | \boldsymbol{\psi}^{(k-1)}] [\theta_j^{(k-1)}]}{[\theta_j^{(k-1)} | \boldsymbol{\psi}^{(k-1)}] [\theta_j^{(s)}]}, \quad (10)$$

for MCMC iteration  $k = 1, \dots, K$ . Notably, neither the MH ratio (10) nor the full-conditional distributions for  $\boldsymbol{\psi}$  involve the data  $\mathbf{y}$ . For the data model to cancel in the numerator and denominator of the MH ratio (10), the proposals  $\theta_j^{(s)}$  should be independent draws from the first-stage posterior distributions for  $\theta_j$ . Thus, in practice, we sample  $\theta_j^{(s)}$  randomly with replacement from the first-stage Markov chains so that the samples are uncorrelated (Hooten et al., 2020; Lunn et al., 2013).

If the hierarchical model is specified such that the conditional distributions for  $\theta_j$  are not analytically tractable, like in our GLMM, then the first stage of the model must be fit using MH or importance sampling (Geweke, 1989) which must be tuned by the user for each partition (Hooten et al., 2016). Thus, rather than specifying a first stage-prior directly on  $\theta_j$ , we use TARB and specify a prior  $[\mathbf{g}(\theta_j)]$  on a transformation  $\mathbf{g}(\theta_j)$  of the parameters  $\theta_j$ . It is most advantageous to specify  $\mathbf{g}$  so that the first-stage priors on  $\mathbf{g}(\theta_j)$  are conjugate with the data model to allow us to use an automated Gibbs sampler in the first stage. In GLMMs and other hierarchical models, we often specify models so that parameters and random effects arise from Gaussian distributions, and use a link function to constrain these parameters to the appropriate support. Thus, in these cases,  $\mathbf{g}$  will likely be a back-transformation (i.e. the inverse of the link function) that allows us to specify conjugate first-stage priors. However, unlike if we were to specify a different model to facilitate conjugacy, using TARB allows us to incorporate prior knowledge and obtain inference in terms of the original model specification. For example, if we let  $\mathbf{g}(\theta_j) = \text{logit}^{-1}(\theta_j)$  in our cheatgrass example, then we can specify a temporary beta prior on  $p_j$  in the first stage. In this example, the benefit of doing so extends beyond conjugacy to a first-stage posterior

distribution that can be written analytically, and therefore does not require MCMC to sample. We provide the complete procedure to fit the cheatgrass GLMM using TAR, with code, in the Supporting Information (Appendix A in Supporting information).

We need to use the resulting first-stage posterior distribution as a proposal distribution in the second-stage MCMC algorithm, but the first-stage posterior distribution  $[\mathbf{g}(\theta_j)|\mathbf{y}_j]$  is on the transformed parameters  $\mathbf{g}(\theta_j)$ . Thus, to account for the first-stage prior on transformed parameters, we must modify the MH ratio (10) and use a change of variables technique to ensure the proposal is on the same transformation that appears in the process component (6) of the original hierarchical model. While we could easily use the first-stage posterior distribution to obtain a *sample* from the desired posterior distribution  $[\theta_j|\mathbf{y}_j]$ , the MH ratio requires us to evaluate the probability density function  $[\theta_j|\mathbf{y}_j]$  rather than sample from it. There are many possible methods for obtaining this distribution, including analytical change of variable techniques and numerical approaches. For continuous random variables, we use a change of variables technique where

$$[\theta_j|\mathbf{y}_j] = [\mathbf{g}(\theta_j)|\mathbf{y}_j] |\mathbf{J}(\mathbf{g}(\theta_j))|, \quad (11)$$

in which  $\mathbf{J}(\mathbf{g}(\theta_j))$  is the Jacobian matrix defined as

$$\mathbf{J}(\mathbf{g}(\theta_j)) \equiv \begin{bmatrix} \frac{\delta g_{11}(\theta_j)}{\delta \theta_{j,1}} & \dots & \frac{\delta g_{1p}(\theta_j)}{\delta \theta_{j,p}} \\ \vdots & \ddots & \vdots \\ \frac{\delta g_{ps}(\theta_j)}{\delta \theta_{j,1}} & \dots & \frac{\delta g_{ps}(\theta_j)}{\delta \theta_{j,p}} \end{bmatrix}. \quad (12)$$

The Jacobian matrix consists of partial derivatives of each element of  $\mathbf{g}(\theta_j)$  with respect to each element of  $\theta_j$ . Its determinant  $|\mathbf{J}(\mathbf{g}(\theta_j))|$  maps the change in the transformed variables to the change in the non-transformed variables ( $d\mathbf{g}(\theta_j)$  onto  $d\theta_j$ ), yielding the correct probability distribution of the non-transformed variable when multiplied to the probability distribution of the transformed variable. Thus, substituting (11) for the proposal in the second-stage MH ratio (10) results in

$$r_j^{(k)} = \frac{[\mathbf{y}_j|\theta_j^{(s)}] [\theta_j^{(s)}|\boldsymbol{\psi}^{(k-1)}] [\theta_j^{(k-1)}|\mathbf{y}_j]}{[\mathbf{y}_j|\theta_j^{(k-1)}] [\theta_j^{(k-1)}|\boldsymbol{\psi}^{(k-1)}] [\theta_j^{(s)}|\mathbf{y}_j]}, \quad (13)$$

$$= \frac{[\theta_j^{(s)}|\boldsymbol{\psi}^{(k-1)}] [\mathbf{g}(\theta_j)^{(k-1)}] |\mathbf{J}(\mathbf{g}(\theta_j)^{(k-1)})|}{[\theta_j^{(k-1)}|\boldsymbol{\psi}^{(k-1)}] [\mathbf{g}(\theta_j)^{(s)}] |\mathbf{J}(\mathbf{g}(\theta_j)^{(s)})|}. \quad (14)$$

The data component of the hierarchical model cancels in the MH ratio (14) associated with the second-stage MCMC algorithm regardless of the transformation used in the first-stage temporary prior, and we account for the transformation via the determinant of the Jacobian in the modified TAR ratio (14). In our cheatgrass GLMM, because  $\theta_j = p_j$  is a scalar, the Jacobian simplifies to the derivative of  $g = \text{logit}^{-1}(p_j)$  with respect to  $\text{logit}(p_j)$  (Appendix A in Supporting information). Thus, we

can use TAR to create unsupervised first-stage algorithms that can be easily parallelized and a second-stage MCMC algorithm that does not rely on the data model. This results in substantial computational savings when the data model is complex or there are many data models to fit and allows the second stage to be updated easily if new data partitions become available.

### 3 | APPLICATION: WHITE STORK MIGRATION

To demonstrate TAR, we developed a hierarchical animal movement model for the migratory behaviour of white storks *Ciconia ciconia* in western Europe to obtain individual- and population-level inference for migration characteristics. We analysed data from  $J = 15$  individuals tracked with GPS units from 30 July 2018 to 29 September 2018 (Figure 2; Cheng et al., 2019; Fiedler et al., 2019 data). These data are available in the R package 'MOVEVis' (Schwalb-Willmann et al., 2020).

#### 3.1 | Model statement

We specified a continuous-time hierarchical model for stork movement with the data component

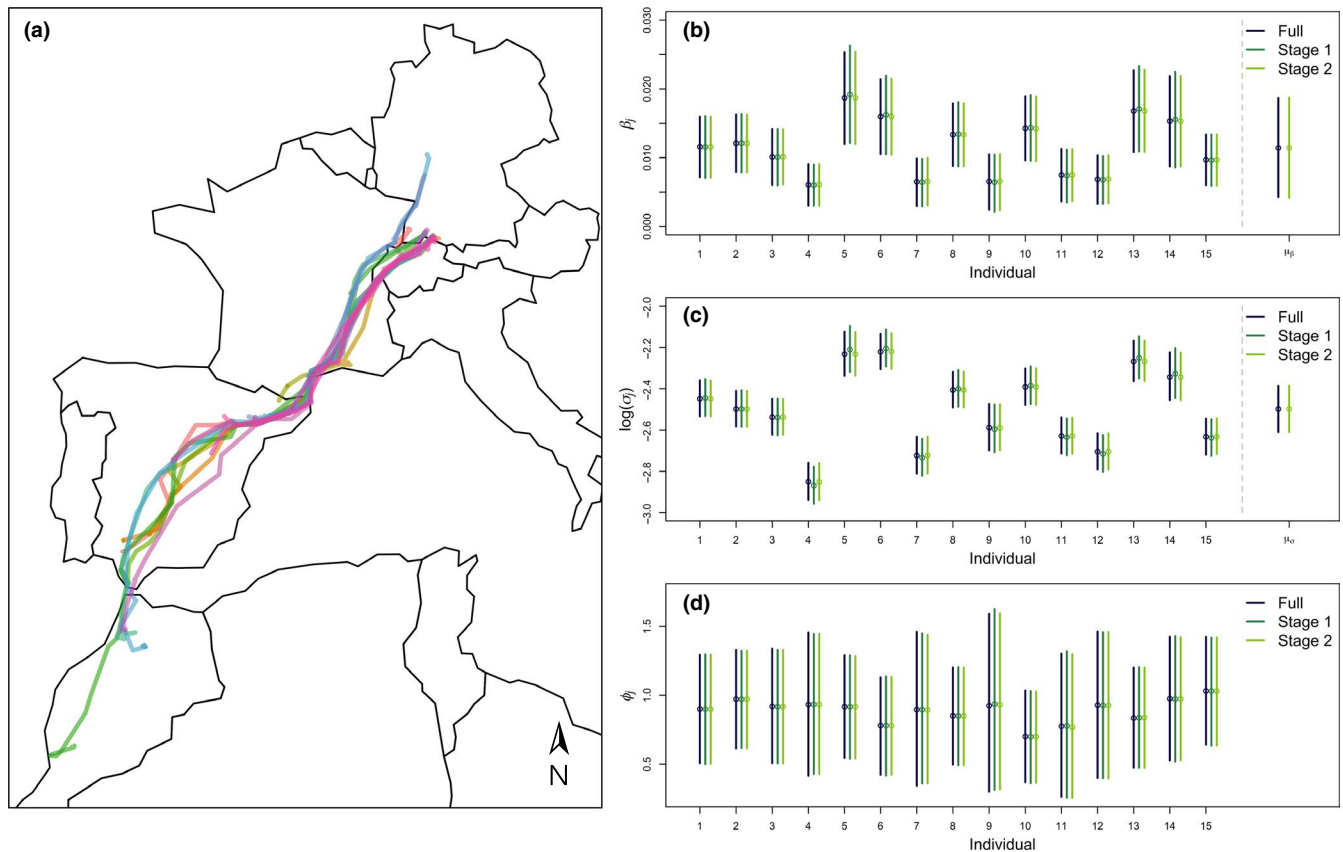
$$\mathbf{s}_j(t_i) \sim N(\mathbf{s}_j(t_{i-1}) - \nabla p(\mathbf{s}_j(t_i), \boldsymbol{\beta}_j) dt_i, \sigma_j^2 dt_i), \quad (15)$$

where  $\mathbf{s}_j(t_i)$  is the measured position of individual  $j$  at time  $i$  (for  $j = 1, \dots, J$  and  $i = 1, \dots, n_j$ ). We defined the potential function in (15) as  $p(\mathbf{s}, \boldsymbol{\beta}_j) \equiv \mathbf{x}'(\mathbf{s})\boldsymbol{\beta}_j$ , which describes a surface upon which an individual is more likely to move 'downhill' (Brillinger, 2010; Hooten et al., 2017). In our specification, this surface is a linear function of covariates  $\mathbf{x}(\mathbf{s})$  and will influence the speed and directional persistence of movement. The term  $dt_i$  represents the change in time between successive positions  $\mathbf{s}_j(t_{i-1})$  and  $\mathbf{s}_j(t_i)$ , and  $\mathbf{I}$  is the  $2 \times 2$  identity matrix. The statistical model in (15) converges to the stochastic differential equation (SDE)

$$\mathbf{s}_j(t) = -\nabla p(\mathbf{s}_j(t), \boldsymbol{\beta}_j) dt + \sigma_j d\mathbf{b}_j(t), \quad (16)$$

as  $dt \rightarrow 0$ , where  $d\mathbf{b}_j(t)$  is bivariate Gaussian white noise.

In the data model (15), the parameters  $\sigma_j^2$  relate to the speed of the migrating individuals and will vary around a group-level speed. However, due to the positive support of the variance components  $\sigma_j^2$ , we chose to model the individual-level process relating to migration speed in the transformation  $\text{log}(\sigma_j)$  so that the support is unbounded and can be suitably modelled with a Gaussian distribution. Otherwise, to create Gibbs updates for  $\sigma_j^2$  directly in a single-stage algorithm, we would need to specify a conjugate inverse gamma process model on  $\sigma_j^2$ , and specifying hyperpriors on the associated shape and scale parameters would be neither trivial nor biologically intuitive. Thus, we specified a process model for  $\text{log}(\sigma_j)$  instead of  $\sigma_j^2$ , implying the transformation function  $\sigma_j^2 = \mathbf{g}(\text{log}(\sigma_j)) = e^{2\text{log}(\sigma_j)}$ .



**FIGURE 2** (a) Migratory trajectories for  $J = 15$  white storks tracked via GPS loggers in fall 2018, with each individual represented by a different colour, and (b)–(d) posterior means (points) and 95% credible intervals for model parameters resulting from fitting our hierarchical movement model to  $n = 1,675$  telemetry locations from  $J = 5$  white storks as a single hierarchical algorithm and in two stages using TARB. It is important to note here that we show the posterior distributions for the first-stage estimates to illustrate how some individual-level parameters borrow strength from the group-level parameters in stage 2, but in practice, the first-stage posterior estimates would not be used to make inference

In our example, we expected migration to occur primarily in a single direction and specified  $\mathbf{x}(\mathbf{s}) = s_2$  where the second component of position  $\mathbf{s}$  corresponds to latitude and the coefficient vector is comprised of a single parameter  $\beta$ . Thus, the negative gradient of the potential function in (15) simplifies to  $-\nabla p(\mathbf{s}_j(t), \beta_j) = -(0, \beta_j)'$ . However, this simplification is based on the assumption that all individuals will migrate in a north/south orientation. To allow for individual variation in the bearing, we multiplied the potential function in (15) by the rotation matrix

$$\mathbf{M} \equiv \begin{pmatrix} \cos(\phi_j) & -\sin(\phi_j) \\ \sin(\phi_j) & \cos(\phi_j) \end{pmatrix}, \quad (17)$$

where  $\phi_j$  is the angle from south of a migratory path, resulting in the data model

$$s_j(t_i) \sim N(s_j(t_{i-1}) - \beta_j \begin{pmatrix} \sin(\phi_j) \\ \cos(\phi_j) \end{pmatrix} dt_i, \sigma_j^2 dt_i \mathbf{I}), \quad (18)$$

Assuming that the variability in  $\beta_j$  and  $\log(\sigma_j)$  across individuals can be accounted for as Gaussian random effects and that individual

variability in  $\phi_j$  does not arise from an underlying group-level distribution, we have  $\beta_j \sim N(\mu_\beta, \sigma_\beta^2)$ ,  $\log(\sigma_j) \sim N(\mu_\sigma, \sigma_\sigma^2)$ , and  $\phi_j \sim \text{Unif}(0, \pi)$ , where population-level means  $\mu_\beta$  and  $\mu_\sigma$  are modelled with Gaussian priors and  $\sigma_\beta^2$  and  $\sigma_\sigma^2$  arise from inverse gamma priors (full model in Supporting Information, Appendix B in Supporting information).

### 3.2 | Two-stage implementation

We fit our model to a subset of the stork migration data (approximately two observations per day per individual) using TARB. In the first stage, we specified individual-level models using the temporary prior  $[\beta_j, \sigma_j^2] = [\beta_j] [\sigma_j^2]$ , where  $\beta_j \sim [\beta_j] \equiv N(\mu_0, \sigma_0^2)$  and  $\sigma_j^2 \sim [\sigma_j^2] \equiv \text{IG}(q_0, r_0)$  for  $j = 1, \dots, J$ . Thus, in the first stage, we sample from the posterior distribution

$$[\beta_j, \sigma_j^2, \phi_j | \mathbf{S}_j] \propto \prod_{i=2}^{n_j} [s_j(t_i) | \beta_j, \sigma_j^2, \phi_j] [\beta_j] [\sigma_j^2] [\phi_j], \quad (19)$$

for each individual  $j = 1, \dots, J$ . We sampled sequentially from the conjugate full-conditional distributions  $[\beta_j]$  and  $[\sigma_j^2]$  using Gibbs updates and from  $[\phi_j]$  using a MH update in an MCMC algorithm in R (version

3.6.1) that we parallelized over individuals with the 'PARALLEL' package (R Core Team 2019).

To use samples from the first-stage models as proposals in the second-stage algorithm, we calculated the Jacobian determinant in (14). Letting  $\theta_j \equiv (\beta_j, \log(\sigma_j))'$ , and the  $2 \times 1$  vector transformation  $\mathbf{g}(\theta_j)$  be comprised of components  $\mathbf{g}_1(\theta_j) = \beta_j$  and  $\mathbf{g}_2(\theta_j) = e^{2\log(\sigma_j)}$ , we calculated the Jacobian

$$\mathbf{J}(\mathbf{g}(\theta_j)) \equiv \begin{bmatrix} \frac{\delta \mathbf{g}_1(\theta_j)}{\delta \beta_j} & \frac{\delta \mathbf{g}_1(\theta_j)}{\delta \log(\sigma_j)} \\ \frac{\delta \mathbf{g}_2(\theta_j)}{\delta \beta_j} & \frac{\delta \mathbf{g}_2(\theta_j)}{\delta \log(\sigma_j)} \end{bmatrix} \equiv \begin{bmatrix} 1 & 0 \\ 0 & 2\sigma_j^2 \end{bmatrix}, \quad (20)$$

which has the determinant  $|\mathbf{J}(\mathbf{g}(\theta_j))| = 2\sigma_j^2$ . Thus, the second-stage MH ratio from (14) to update  $\beta_j$ ,  $\log(\sigma_j)$ , and  $\psi_j$  for individual  $j$  is

$$r_j^{(k)} = \frac{\left[ \beta_j^{(*)} | \mu_\beta^{(k-1)}, \sigma_\beta^{2(k-1)} \right] \left[ \log(\sigma_j^{(*)}) | \mu_\sigma^{(k-1)}, \sigma_\sigma^{2(k-1)} \right] \left[ \beta_j^{(k-1)} \right] \left[ \sigma_j^{2(k-1)} \right] \left[ \phi_j^{(*)} \right] \times \sigma_j^{2(k-1)}}{\left[ \beta_j^{(k-1)} | \mu_\beta^{(k-1)}, \sigma_\beta^{2(k-1)} \right] \left[ \log(\sigma_j^{(k-1)}) | \mu_\sigma^{(k-1)}, \sigma_\sigma^{2(k-1)} \right] \left[ \beta_j^{(*)} \right] \left[ \sigma_j^{2(*)} \right] \left[ \phi_j^{(k-1)} \right] \times \sigma_j^{2(*)}}. \quad (21)$$

The scalar multiple of 2 from the Jacobian determinant cancels in the numerator and denominator of (21). In the second-stage algorithm, we used the MH ratio in (21) to accept our proposals for  $\beta_j^{(*)}$ ,  $\log(\sigma_j^{(*)})$  and  $\phi_j^{(*)}$  which we sampled jointly at random (with replacement) from our first-stage MCMC sample. Then, we sampled the group-level model parameters ( $\mu_\beta$ ,  $\sigma_\beta^2$ ,  $\mu_\sigma$ , and  $\sigma_\sigma^2$ ) sequentially from their full-conditional distributions using Gibbs updates (Appendix B in Supporting information).

Alternatively, it is possible to fit the full hierarchical model using a standard MCMC algorithm with Gibbs updates for  $\beta_j$ ,  $\mu_\beta$ ,  $\sigma_\beta^2$ ,  $\mu_\sigma$  and  $\sigma_\sigma^2$ . However, we would need to use MH updates for  $\log(\sigma_j)$  and  $\phi_j$ , and in cases where the number of individuals  $J$  is large, we may have to tune a prohibitively large number of proposal distributions to yield optimal acceptance rates in the MCMC algorithm. Nonetheless, to demonstrate that we obtain the same inference with TARB as compared to a single MCMC algorithm, we also fit the full model with a single algorithm, updating  $\beta_j$  and  $\log(\sigma_j)$  sequentially for each individual with Gibbs and MH updates, respectively, and the remaining model parameters as above.

### 3.3 | Results

We fit our movement model to a subset of  $n = 1,675$  stork telemetry observations across  $J = 15$  individuals using TARB with  $K = 100,000$  MCMC iterations for each stage, computing the first stage in parallel over 8 cores, and using a single hierarchical MCMC algorithm with  $K = 100,000$  MCMC iterations. The recursive approach required 2.95 min and the single algorithm required 9.87 min; thus computation was over three times faster using TARB. With a larger dataset of  $n = 155,161$  locations for 15 individuals and  $K = 60,000$  MCMC iterations, computation time to fit the model recursively, in parallel over 15 cores, was 49 min, compared to 88 min to fit the model as a single algorithm.

Both computational approaches resulted in the same 95% credible intervals and posterior means for  $\beta_j$  and  $\log(\sigma_j)$  and the same population-level means  $\mu_\beta$  and  $\mu_\sigma$  (Figure 2). The stage-two posterior credible intervals for the  $\beta_j$  and  $\log(\sigma_j)$  for each individual  $j$  indicate individual variation in speed and directional persistence of migration, but the population is centred around  $\mu_\beta$  and  $\mu_\sigma$ . First-stage credible intervals are included only to visualize the relationship between stage one and stage two in Figure 2, and are not used for inference. The shrinkage in interval width between the first- and second-stage posteriors of  $\beta_j$  and  $\log(\sigma_j)$  indicates individual-level inference was informed by group-level parameters in the second stage, although this effect was relatively minor in this example. Furthermore, fitting the model to simulated data shows that both computational approaches do equally well recovering 'true' simulated parameters (Appendix C in Supporting information).

## 4 | DISCUSSION

In our application, we illustrated how TARB can be used to efficiently fit a hierarchical animal movement model to telemetry data, but TARB could be implemented in many ecological models to improve computational efficiency. In Table 1, we highlight several studies from the ecological literature in which the authors used a Bayesian hierarchical model (or desired to, barring computational limitations, as in Breed et al., 2009) that could be fit with TARB. To demonstrate the application of TARB to existing ecological models, we discuss two examples in detail, outlining how the models can be specified in the two-stage framework for faster computation.

### 4.1 | Harbour seal counts

Cressie et al. (2009) specified a Bayesian hierarchical model to explicitly account for uncertainty at the data and process levels while estimating abundance of harbour seals *Phoca vitulina* from census data (Ver Hoef & Frost, 2003) in Prince William Sound

$$y_{ij} \sim \text{Pois}(\lambda_{ij}), \quad (22)$$

$$\log(\lambda_{ij}) \sim \text{N}(\mu_{ij}, \sigma_{ij}^2), \quad (23)$$

$$\mu_{ij} = \theta_{0j} + \mathbf{x}'_{ij}\theta_j, \quad (24)$$

$$\theta_j \sim \text{N}(\boldsymbol{\mu}_\theta, \boldsymbol{\Sigma}), \quad (25)$$

where  $y_{ij}$  is the number of hauled-out seals counted from photographs during each aerial survey  $i$  conducted at site  $j$ . In the observation

**TABLE 1** Examples of ecological studies with Bayesian hierarchical models that could be implemented in a transformation-assisted recursive Bayesian framework

| Discipline                   | Study                     |
|------------------------------|---------------------------|
| Fish & Wildlife Ecology      | Burton et al. (2012)      |
|                              | Cressie et al. (2009)     |
|                              | Breining et al. (2019)    |
|                              | Kuhnert et al. (2005)     |
|                              | Monroe et al. (2017)      |
|                              | Moore and Barlow (2011)   |
| Integrated Population Models | Cleasby et al. (2017)     |
|                              | Eacker et al. (2017)      |
|                              | Raiho et al. (2015)       |
|                              | Schaub et al. (2013)      |
| Animal Movement              | Breed et al. (2009)       |
|                              | Eckert et al. (2008)      |
|                              | Jonsen et al. (2006)      |
|                              | McClintock et al. (2013)  |
|                              | Muff et al. (2019)        |
| Forestry & Plant Ecology     | Dietze et al. (2008)      |
|                              | Evans et al. (2012)       |
|                              | Hanks et al. (2011)       |
|                              | Iijima and Otsu (2018)    |
|                              | Vieilledent et al. (2010) |
| Ecosystem Ecology            | Borsuk et al. (2001)      |
|                              | Coll et al. (2019)        |
|                              | Shelton et al. (2016)     |

model (22), counts arise from a Poisson distribution with intensity parameter  $\lambda_{ij}$  that represents the expected number of haul-outs in a given survey and location. The expected number of haul-outs ( $\lambda_{ij}$ ) arises from a normal distribution with mean  $\mu_{ij}$  that is a function of covariates  $\mathbf{x}_{ij}$  with variance parameters  $\sigma_{ij}^2$  for each survey and location. Site-level coefficients  $\theta_j$  arise from a population-level multivariate Gaussian distribution, where  $\Sigma$  is a diagonal matrix with population-level variance parameters along the diagonal. Thus, the hierarchical model in (22)–(25) is a special case of a generalized linear mixed model.

Surveys were conducted several times per year at each site. Thus, in the first stage of the TARB framework, counts could be modelled independently for each site with the model

$$y_{ij} \sim \text{Pois}(\lambda_{ij}), \quad (26)$$

$$\lambda_{ij} \sim \text{Gamma}(\alpha, \beta), \quad (27)$$

where a temporary gamma prior on  $\lambda_{ij}$  is conjugate with the data model (22) in the first stage so that the MCMC algorithm is unsupervised and could be parallelized over the sites. To complete model fitting in stage two, log-transformed first-stage samples for  $\lambda_{ij}$  would

be used as proposals in the MH update for  $\log(\lambda_{ij})$  in a second-stage algorithm,

$$[\log(\lambda_{ij})]_{\cdot} = \frac{[\log(\lambda_{ij}^{(s)}) | \mu_{ij}, \sigma_{ij}^2] [\lambda_{ij}^{(k-1)} | \alpha, \beta] \lambda_{ij}^{(k-1)}}{[\log(\lambda_{ij}^{(k-1)}) | \mu_{ij}, \sigma_{ij}^2] [\lambda_{ij}^{(s)} | \alpha, \beta] \lambda_{ij}^{(s)}} \quad (28)$$

where  $\frac{d}{d \log(\lambda_{ij})} e^{\log(\lambda_{ij})} = \lambda_{ij}$ . All other parameters in the second stage would be updated in the same manner as in a conventional algorithm.

## 4.2 | Host plant genetics

Evans et al. (2012) conducted a common garden experiment to determine the effects of cottonwood host (*Populus* spp.) genotype on the abundance of herbivorous mite *Aceria parapopuli* galls on trees. In our notation, their model was

$$y_{imt} \sim \text{Pois}(\theta_{imt}), \quad (29)$$

$$\log(\theta_{imt}) \sim \text{N}(\mu_{imt}, \sigma^2), \quad (30)$$

$$\mu_{imt} = \beta_i + \mathbf{x}'_{tm} \alpha, \quad (31)$$

$$\alpha \sim \text{N}(\mu_\alpha, \Sigma_\alpha), \quad (32)$$

$$\beta_i \sim \text{N}(0, \tau^2), \quad (33)$$

$$\tau^2 \sim \text{IG}(a_\tau, b_\tau), \quad (34)$$

$$\sigma^2 \sim \text{IG}(a_\sigma, b_\sigma), \quad (35)$$

where  $y_{imt}$  is the number of galls on tree  $i$  with genotype  $m$  in year  $t$ . The intensity parameter  $\theta_{imt}$  is a log-linear function of fixed effects  $\alpha$  for year and genotype and random effect of tree,  $\beta_i$ . Modifying the process model to

$$\theta_{imt} \sim \text{Gamma}(\gamma_1, \gamma_2), \quad (36)$$

and using temporary priors on  $\gamma_1$  and  $\gamma_2$  results in an unsupervised first-stage algorithm. We make a similar adjustment to the second-stage MH ratio as in (28) for recursive computation.

## 4.3 | Conclusion

Transformation-assisted RB is one of the most accessible approaches for fitting ecological models recursively with improved computational efficiency and ease. Transformation allows us to extend the benefits of RB to more model specifications, and the demonstrated approach with change of variables can be implemented for most continuous random variables. The ability to incorporate prior information into analyses is a well-known feature of Bayesian analysis, but it can be difficult to determine how to do so in a robust way, and TARB is a natural approach for using

posterior estimates from a previous study as prior information in subsequent studies. Finally, TARB leverages the parallel computing capacity of modern multi-core computers (Visser et al., 2015) to reduce the computational bottleneck created by large datasets and conventional sampling techniques.

Decreased computation time is a major advantage of fitting hierarchical models using TARB, but reducing tuning and partitioning the data in the first stage are equally, if not more, advantageous. This is especially true for large hierarchical models where one might otherwise have to individually tune dozens or hundreds of individual-level parameters to achieve convergence, which would require repeatedly fitting the model. Furthermore, because the first-stage algorithm is used to fit data partitions independently and the second-stage algorithm does not rely on the data directly, we expect additional computational gains. Finally, by design, TARB accommodates uneven sample sizes of partitions, because the first-stage posterior distributions will reflect the uncertainty associated with different sample sizes, thus implicitly weighting the partitions according to sample size in the second stage.

In many cases, the first-stage algorithms of RB and TARB approaches could be implemented in an existing package like JAGS, Stan or NIMBLE (NIMBLE Development Team, 2019; Plummer, 2003; Stan Development Team, 2018), but the second-stage algorithm cannot be easily implemented in this software. However, using TARB, it may be possible to fit models that are not feasible using these software packages at all. While automated software is convenient and well-suited to a wide range of models, it cannot accommodate all model specifications and users do not always have control over tuning. Although software packages can often fit large models quickly, this may be achieved via computation in C++ rather than R (e.g. Stan; Stan Development Team, 2018) or by making approximate inference (e.g. INLA; Rue et al., 2009). Recursive techniques like TARB can also be implemented in C++ via R and `rcpp` for greater computational efficiency, and the results can be used to obtain both marginal and joint inference.

While TARB can be implemented for a broad range of hierarchical models, there are some cases for which TARB, as presented here using the Jacobian to perform a change of variables, is not ideal for model fitting. For example, hierarchical models that have common parameters at the data level, in addition to partition-level parameters, such as GLMMs with both fixed and random effects, are not easily implemented using TARB. In this case, prior-proposal RB may be helpful (Hooten et al., 2020). Additionally, the Jacobian approach for computing transformed densities is well-suited for transforming continuous random variables, but alternate approaches must be used for discrete random variables. We demonstrated TARB using this technique because it serves as a good introduction into recursive techniques with transformation. For other random variables or applications, there are many useful generalizations of this approach that could be used to obtain valid transformations.

Hierarchical models are powerful tools for understanding complex ecological systems, but the computational demands of fitting ecologically realistic models can make them impractical or impossible to implement. Recursive Bayesian computing techniques address these computational demands, and partitioning model fitting

into stages is natural in many ecological applications. For example, in adaptive management, RB and TARB would allow managers to fit first-stage individual-, year- or site-level models as data are collected, and add new partitions to existing results by subsequently updating the second stage. Additionally, because the second-stage algorithm only requires first-stage posterior samples, partitions could represent data collected by different researchers during ongoing projects, and researchers could fit population-wide models without needing to share data (Hooten et al., 2020). Thus, in the current era of big data and complex modelling in ecology, TARB is an approachable technique that reduces the computational limitations on the ecological models ecologists can specify and fit.

## ACKNOWLEDGEMENTS

The authors thank the editor and anonymous reviewers whose insights improved the manuscript, and J. Tipton for early discussions on this work. This research was funded by NSF DMS 1614392, NSF DEB 1927177 and NSF GRF 1840343. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

## AUTHORS' CONTRIBUTIONS

M.B.H. and A.B.F. designed the modelling methodology, and H.M.M. and M.B.H. designed the case study and performed the analysis; H.M.M. and A.B.F. wrote the first version of the manuscript, and all authors contributed to revisions of the manuscript.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13513>.

## DATA AVAILABILITY STATEMENT

The R code used in our analyses is available at <https://doi.org/10.5281/zenodo.4075393> (McCaslin et al., 2020). The white stork dataset is available on Movebank (Fiedler et al., 2019, <https://doi.org/10.5441/001/1.v1cs4nn0>) and in the R package 'moveVis' (Schwalb-Willmann et al., 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** McCaslin HM, Feuka AB, Hooten MB. Hierarchical computing for hierarchical models in ecology. *Methods Ecol Evol.* 2021;12:245–254. <https://doi.org/10.1111/2041-210X.13513>