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Bridging gaps in demographic analysis with phylogenetic imputation

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Abstract: Phylogenetically informed imputation methods have rarely been applied to estimate missing values in demographic data but may be a powerful tool for reconstructing vital rates of survival, maturation, and fecundity for species of conservation concern. Imputed vital rates could be used to parameterize demographic models to explore how populations respond when vital rates are perturbed. We used standardized vital rate estimates for 50 bird species to assess the use of phylogenetic imputation to fill gaps in demographic data. We calculated imputation accuracy for vital rates of focal species excluded from the data set either singly or in combination and with and without phylogeny, body mass, and life-history trait data. We used imputed vital rates to calculate demographic metrics, including generation time, to validate the use of imputation in demographic analyses. Covariance among vital rates and other trait data provided a strong basis to guide imputation of missing vital rates in birds, even in the absence of phylogenetic information. Mean NRMSE for null and phylogenetic models differed by <0.01 except when no vital rates were available or for vital rates with high phylogenetic signal (Pagel's $\lambda > 0.8$). In these cases, including body mass and life-history trait data compensated for lack of phylogenetic information: mean normalized root mean square error (NRMSE) for null and phylogenetic models differed by <0.01 for adult survival and <0.04 for maturation rate. Estimates of demographic metrics were sensitive to the accuracy of imputed vital rates. For example, mean error in generation time doubled in response to inaccurate estimates of maturation time. Accurate demographic data and metrics, such as generation time, are needed to inform conservation planning processes, for example through International Union for Conservation of Nature Red List assessments and population viability analysis. Imputed vital rates could be useful in this context but, as for any estimated model parameters, awareness of the sensitivities of demographic model outputs to the imputed vital rates is essential.

Keywords: conservation modeling, demographic models, extinction risk, generation time, parameter estimation, population dynamics, population growth rate, survival

Cerrando Brechas en los Análisis Demográficos con Imputación Filogenética

Resumen: Los métodos de imputación guiados filogenéticamente se han aplicado con poca frecuencia para estimar los valores faltantes en los datos demográficos, aunque pueden ser una herramienta poderosa para la reconstrucción de tasas vitales de supervivencia, maduración y fecundidad de especies de importancia para la conservación. Las tasas vitales imputadas podrían usarse para generar parámetros en los modelos demográficos para explorar cómo responden las poblaciones cuando se perturban las tasas vitales. Utilizamos estimaciones de tasas vitales estandarizadas para 50 especies de aves para analizar el uso de la imputación filogenética para llenar

los vacíos en los datos demográficos. Calculamos la certeza de imputación para las tasas vitales de las especies focales excluidas del conjunto de datos por sí solas o en combinación y con y sin datos de filogenia, masa corporal y características de historia de vida. Usamos las tasas vitales imputadas para calcular las medidas demográficas, incluyendo el tiempo de generación, y así validar el uso de la imputación en los análisis demográficos. La covarianza entre las tasas vitales y otros datos de características proporcionó una base sólida para orientar la imputación de tasas vitales faltantes en las aves, incluso la ausencia de información filogenética. El NRMSE medio para los modelos nulo y filogenético difirió por <0.01 salvo cuando no hubo tasas vitales disponibles o para tasas vitales con una señal filogenética alta (λ de Pagel > 0.8). En estos casos, la inclusión de la masa corporal y las características de historia de vida compensó la falta de información filogenética: el error cuadrático medio de la raíz normalizada media (NRMSE) para los modelos nulo y filogenéticos difirió por <0.01 para la supervivencia adulta y <0.04 para la tasa de maduración. Las estimaciones de las medidas demográficas fueron sensibles a la certeza de las tasas vitales imputadas. Por ejemplo, el error medio en el tiempo generacional se duplicó en respuesta a las estimaciones imprecisas del tiempo de maduración. Las medidas y datos demográficos certeros, como el tiempo generacional, son necesarios para orientar los procesos de planeación de la conservación; por ejemplo, a través de las valoraciones de la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza y los análisis de viabilidad poblacional. Las tasas vitales imputadas podrían ser útiles en este contexto, pero como para cualquier tipo de parámetro de modelo estimado, el conocimiento de las sensibilidades del rendimiento del modelo demográfico es esencial para las tasas vitales imputadas.

Palabras Clave: dinámicas poblacionales, estimación de parámetros, modelado de la conservación, modelos demográficos, riesgo de extinción, supervivencia, tasa de crecimiento poblacional, tiempo de generación

摘要: 基于系统发育信息的插补模型很少用于估计种群统计数据中的缺失值, 但这种方法可能是重建受保护物种生存率、性成熟和繁殖力等生命统计数据的有力工具。估算的数据可以用于获得种群模型参数, 以探索当生命统计指标受到扰动时种群的响应。本研究使用五十种鸟类的标准化生命统计估计值, 评估了系统发育插补法在填补种群统计数据空缺中的应用。我们对排除在数据集之外的关注物种计算了插补准确率, 其中包括单独或联合计算, 纳入或不纳入系统发育、体重和生活史特征数据。接下来, 我们使用插补的生命统计数据计算了种群统计指标, 包括世代时长, 以验证数据插补在种群统计分析中的作用。结果显示, 生命统计指标和其它性状数据之间的协方差为估算鸟类缺失的生命统计数据提供了有力的依据, 即使在缺乏系统发育信息的情况下也是如此。除了无可用生命统计数据或有高系统发育信号的生命统计数据 (Pagel's λ > 0.8) 的情况之外, 无系统发育模型和系统发育模型的平均标准均方根误差相差小于 0.01 。在这些情况下, 纳入体重和生活史特征数据可以弥补系统发育信息的不足:成鸟存活率的无系统发育模型和系统发育模型的平均标准均方根误差相差不到 0.01, 而成熟率的相差小于 0.04 。种群统计指标的估计对插补获得的生命统计数据准确性很敏感。例如, 对性成熟时间估计不准确会导致世代时长估计的平均误差增加一倍。准确的种群统计数据和指标 (如世代时长) 可以为保护规划提供信息, 例如通过《国际自然保护联盟红色名录》评估和种群生存力分析。插补得到的生命统计数据在这方面可以发挥作用, 但是对于任何估算的模型参数都要认识到种群模型输出对生命统计数据插补的敏感性。

【翻译: 胡怡思; 审校: 聂永刚 】

用系统发育插补模型填补种群统计分析的空缺

保护模型, 人口模型, 参数估计, 世代时长, 种群增长率, 种群动态, 存活, 灭绝风险

Introduction

Understanding population responses to human-induced threats, such as habitat loss and degradation, climate change, and overexploitation (Brook et al. 2003; Parmesan 2006; Maclean & Wilson 2011; Maxwell et al. 2016), is crucial for identifying at-risk species and to guide conservation interventions (e.g., Bruna et al. 2009; Dahlgren et al. 2016; Lunn et al. 2016). Population models parameterized with estimates of vital rates of survival, development, and reproduction can be used to generate predictions about how a population will respond to pressures that cause changes to vital rates (Selwood et al. 2015).

Obtaining the vital rate estimates necessary to populate demographic models requires investment of resources and time, which may be lacking in a critical conservation setting. The most at-risk species may be those for which information is most lacking (Beissinger & Westphal 1998; Coulson et al. 2001; González-Suárez et al. 2012), due to geographical, taxonomic, or other biases in recording (Roberts et al. 2016; Troudet et al. 2017; dos Santos et al. 2020) or to logistical barriers to collecting complete demographic data (Menges 2000; Weimerskirch 2001; Pike et al. 2008; Clutton-Brock & Sheldon 2010). Consequently, complete empirical demographic data are available for only a small and biased subset of species (Lebreton et al. 2012; Salguero-Gómez et al. 2015, 2016; Conde et al. 2019).

When data are missing for a focal species, ad hoc imputation methods are commonly used to fill in such gaps for demographic modeling (Beissinger & Westphal 1998). Parameter estimates may be derived from empirical data

for other species based on relatedness (Heinsohn et al. 2004; Koenig 2008) or trait similarity (McCarthy et al. 1999; Valle et al. 2018). Other approaches include combining estimates from populations to form a representative model for a species (Sæther & Bakke 2000) and parameterization of models based on a range of plausible values (Rodríguez et al. 2004) or on data from captive individuals (e.g., Young et al. 2012). Such approaches produce bias (Schafer & Graham 2002), and their use raises concerns about the reliability of model outputs and the ability to make robust conclusions (Sæther & Engen 2002; Ellner & Fieberg 2003; McGowan et al. 2011). Therefore, formal methods for estimating missing vital rates and quantifying uncertainty in such estimates are needed.

Many ad hoc methods of imputing missing values are based on the expectation that the vital rates of the focal species will be similar to closely related species (Felsenstein 1985; Pagel 1999). By accounting more formally for evolutionary history, it may be possible to improve the imputation of missing vital rates. Phylogenetic imputation methods use phylogeny, together with an evolutionary model describing the divergence of trait values (Martins & Hansen 1997; Pagel 1999; Freckleton et al. 2002), to estimate missing values in species-based data. Traits may be more or less labile, leading to differences in how well trait values may be predicted by evolutionary relationships (Freckleton et al. 2002; Blomberg et al. 2003). Phylogenetic signal, a measure of the strength of phylogenetic dependence of trait values (Pagel 1999; Blomberg & Garland 2002), may determine the benefit of using phylogenetic information when imputing trait values (Penone et al. 2014). If phylogenetic signal is strong, phylogenetically informed methods can potentially improve imputation performance.

Phylogenetic imputation has been proposed for filling gaps in functional trait data in plants (Swenson 2014) and mammals (Guénard et al. 2013; Penone et al. 2014). Such methods have rarely been applied to demographic data, although hierarchical approaches incorporating taxonomy have been used to estimate life-history parameters in fish (Thorson et al 2017). We focused on demographic traits, namely vital rates of survival, maturation, and fecundity. In plants, imputation of single vital rates suggests that neither fecundity nor the survival of different life stages are strongly predicted by phylogeny or species-level traits (Che-Castaldo et al. 2018), reflecting weak phylogenetic signal in plant vital rates (Burns et al. 2010). In vertebrates, strong phylogenetic signal in characteristics that covary with vital rates (body size, morphology, and life-history traits) has been interpreted as being informative about evolutionary processes, such as the strength of stabilizing selection and evolutionary lability (Blomberg et al. 2003; but see Revell et al. 2008).

Whatever the exact evolutionary processes involved, the tendency of vital rates to covary with body size (Stearns 1983) and life-history traits (e.g., age at maturity and clutch size, Sæther & Bakke 2000) suggests that they will also have strong phylogenetic signal, which would be useful in an applied setting to infer vital rates for related species. The inclusion of covarying allometric and life-history trait data may inform the imputation of vital rates (e.g., Shine & Charnov 1992; Brawn et al. 1995).

Imputed vital rates provide a means by which demographic characteristics of a population may be derived. Demographic metrics of interest in a conservation setting include population growth rate and its sensitivity and elasticity to underlying vital rates (Benton & Grant 1999) and life-history metrics such as generation time. Sensitivity analysis identifies vital rates with the most capacity to produce change in population growth rate. Accurate imputation of vital rates to which population growth rate is sensitive would be valuable for making well-founded demographic predictions to guide conservation interventions. Generation time is used by international conservation bodies, such as the International Union for Conservation of Nature (IUCN), to produce indicators for conservation decision-making (Mace et al. 2008). When underlying life-history data are missing or sparse, demographic metrics may be estimated using proxies based on life-history traits such as reproductive lifespan (Fung & Waples 2017; Staerk et al. 2019) or imputed either directly (Fagan et al. 2013; Cooke et al. 2018) or by means of underlying life-history traits (Pacifici et al. 2013; Bird et al. 2020). Demographic metrics derived using phylogenetically imputed vital rates could improve accuracy over these alternative methods.

We used existing vital-rate data for birds to assess the feasibility of using phylogenetic imputation to fill gaps in demographic analysis. Although many avian demographic data sets have been compiled (Sæther & Bakke 2000; Lebreton et al. 2012; Salguero-Gómez et al. 2016), information about vital rates is missing for many species of conservation concern (e.g., survival is missing for 82% of bird species, Conde et al. 2019). We used demographic data for 50 species to derive standardized vital rates and apply a multivariate imputation framework that incorporates phylogenetic covariance among vital rates to impute missing values. We determined how accurately values excluded from the vital-rate data can be imputed, either singly or in combination. Further, we assessed the value of including body mass and life-history trait data (clutch size and female age at maturity) when imputing missing vital-rate data. We used original and imputed vital rates to calculate demographic metrics that inform assessments of population performance and extinction risk.

Methods

All analyses were carried out in R (version 3.6.3, R Core Team 2020).

Standardized Vital Rate, Body Mass, and Life-History Trait Data

We extracted matrix population models for birds from the COMADRE Animal Matrix Database (version 3.0.1, COMADRE 2019) and other sources (Sæther & Bakke 2000). We screened the data to avoid models with errors in construction (Kendall et al. 2019) and to ensure valid structure for the subsequent analysis (Appendix S1). The resulting set of matrix population models represented 50 bird species across 15 orders and a range of avian life histories. We identified prebreeding and postbreeding census models and categorized each life history as early maturation (individuals mature and breed after 1 year) or delayed maturation (individuals remain as nonbreeding juveniles for 1 or more years; Fujiwara & Diaz-Lopez 2017). Allowing for the different representation of early- and delayed-maturation species in prebreeding and postbreeding census models, we collapsed prereproductive and reproductive stages (Salguero-Gómez & Plotkin 2010) and derived a set of standardized vital rates representing first-year survival (s_0), adult survival (s_a), fecundity (f), and maturation rate (m) from the resulting matrices. To ensure a full set of standardized vital rates in the imputation analysis, we restricted the main analysis to 40 species with postbreeding census models (Appendix S2). We combined the standardized vital rates with avian body mass, clutch size, and female age at maturity (Wilman et al. 2014; Myhrvold et al. 2015) and transformed all variables to satisfy the requirements of the imputation model (Appendix S1).

Phylogeny

We downloaded a sample of 1,000 full avian phylogenetic trees (Hackett backbone) from the BirdTree website (www.birdtree.org, Jetz et al. 2012), pruned to match the species in the standardized vital-rate data. The tree topology was well supported (3 nodes with posterior probability <0.95), so we used the least squares consensus method (Lapointe et al. 1997; phytools version 0.7-20, Revell 2012) to create an average tree for phylogenetic imputation analysis (Appendix S3). This method creates a consensus tree for which the sum-of-squares patristic (node-to-node) distances to the set of trees in the sample is minimized. We compared outputs from imputation in the consensus tree with results for a sample of 50 trees from the posterior distribution to demonstrate that our results were insensitive to phylogenetic uncertainty (Appendix S5).

Phylogenetic Signal

Phylogenetic signal is a measure of pattern derived by comparing observed trait distributions with expectations from a specified model of evolution. Pagel's λ is a transformation of the phylogeny, obtained by maximum likelihood, that produces the best fit of the data to a Brownian motion model of evolution. Pagel's λ takes values from 0 (complete phylogenetic independence) to 1 (patterns of similarity observed in the data are proportional to shared evolutionary history) or above (traits are more similar among species than expected) (Pagel 1999; Freckleton et al. 2002). We used phytools (version 0.7-20) (Revell 2012) to estimate mean Pagel's λ for each standardized vital rate across 1,000 phylogenetic trees obtained from BirdTree to account for any residual uncertainty in branch lengths. In addition, we used Rphylopars (version 0.2.12) (Goolsby et al. 2016) to estimate Pagel's λ for each of the trait data sets to characterize phylogenetic dependence in the data, taking into account covariance among the data.

Phylogenetic Imputation

We carried out a multistage analysis to assess the use of phylogenetic imputation to reconstruct missing values introduced systematically into the standardized vital-rate data (Fig. 1). Phylogenetic imputation predicts missing values based on covariance among the data, supplemented by phylogeny and a model for evolution. We used Rphylopars (version 0.2.12, Goolsby et al. 2016), which implements maximum likelihood estimation of missing trait values in a phylogenetic generalized least squares framework, assuming normally distributed continuous variables. We combined the consensus phylogeny with a null model of evolution, in which phylogeny does not influence trait values, and a Pagel's λ model, in which the phylogeny is scaled to account for phylogenetic dependence in the data (phylogeny, Fig. 1). We created 3 trait data sets: standardized vital rates only; vital rates and body mass data; and vital rates, body mass, and life-history trait data (trait data sets, Fig. 1). Within each trait data set, we introduced a known structure of missing values among the vital rates for a focal species. We removed vital rate values in all possible combinations of single and multiple vital rates, resulting in 15 data sets per species (missing data combinations, Fig. 1). We imputed missing values assuming either model of evolution. After transformation to the original scale for each vital rate, we used the normalized root mean square error (NRMSE),

$$\text{NRMSE} = \frac{\sqrt{\frac{\sum_i (X_i^* - X_i)^2}{n}}}{(X_i) - \min_i(X_i)} \quad (1)$$

to assess imputation accuracy for each vital rate, missing vital rate combination, trait data set, and evolutionary model (error calculation, Fig. 1). Here, X_i^* and X_i are
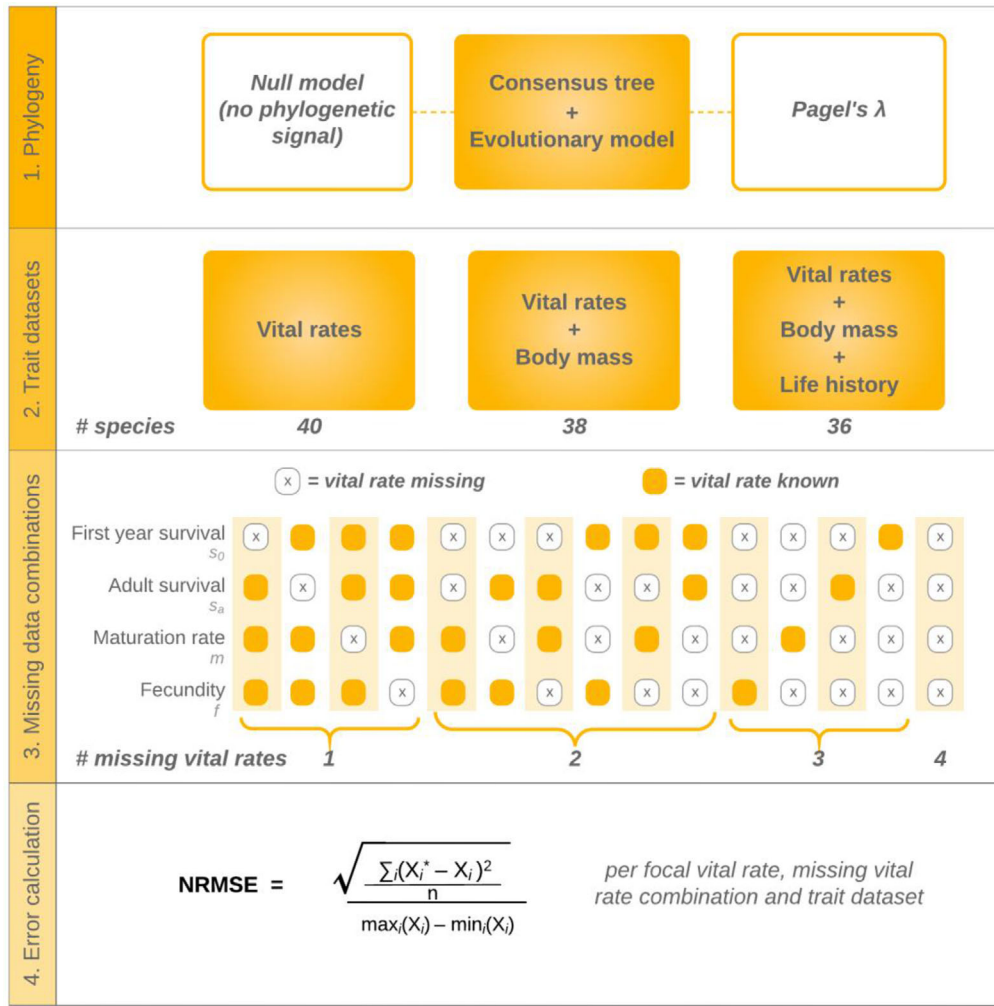
Figure 1. Process for applying phylogenetic imputation to vital rate, body mass, and life-history trait data to assess the accuracy of predicting vital rates for use in demographic models (NRMSE, normalized root mean square error; X_i^* and X_i, imputed and original values, respectively, of a vital rate for species i; n, number of species).

imputed and original values, respectively, of a vital rate for species *i*. Normalization by the range of observed values for the vital rate allows comparison of errors across vital rates.

We used species means to estimate phylogenetic covariance (Goolsby et al. 2016) to avoid conditioning problems in the data sets that included body mass and life-history trait data. We imputed values both with and without phenotypic variation for the vital-rate data to demonstrate that excluding phenotypic covariance from the analysis was not detrimental to the estimation of phylogenetic covariance (Appendix S6).

Demographic Metrics

We represented avian life histories with stage-structured, postbreeding census models with an annual time step (Caswell 2001) parameterized with s_0, s_a, f, and m imputed under the phylogenetic model. For early-

maturation species,

$$A = \begin{bmatrix} s_0 \, f & s_a \, f \\ s_0 & s_a \end{bmatrix} \quad (2)$$

and for delayed-maturation species,

$$A = \begin{bmatrix} 0 & m \, s_a \, f & s_a \, f \\ s_0 & (1-m) \, s_a & 0 \\ 0 & m \, s_a & s_a \end{bmatrix} \quad (3)$$

We used these population models to generate population growth and life-history metrics (Table 1). For each missing data combination and trait data set, we calculated the normalized root mean square error (Eq. 1) to compare estimates of these demographic metrics from models parameterized with imputed and original vital rates. We inspected differences in the sensitivity and elasticity of population growth rate to each vital rate for bias (systematic differences) or increased variance.

Table 1. Demographic metrics of population growth and life history used in an assessment of the effect of imputed parameters on demographic model outputs.

Metric	*Description*
Population growth	
asymptotic population growth rate	long-term performance of a population
sensitivity and elasticity of population growth rate	response of population growth rate to changes in underlying vital rates
Life history	
generation time	time required for population to increase by a factor equal to net reproductive rate
mean age at maturity	average time taken to enter reproductive stage
mean lifespan	average age of individuals at death

Results

Phylogenetic Signal

For postbreeding census data, mean Pagel's λ was weak for first-year survival (0.246 [SD 0.013]), intermediate for fecundity (0.532 [0.018]), and strong for adult survival (0.889 [0.016]) and maturation rate (0.923 [0.116]). Mean values for prebreeding census data were similar (s_a: 0.817 [0.019]; m: 0.934 [0.094]). High phylogenetic signal suggested that adult survival and maturation rate should be successful targets for phylogenetic imputation but high variance in Pagel's λ for maturation rate suggested greater phylogenetic uncertainty in maturation rate.

For postbreeding census models, Pagel's λ was 0.488 for the vital-rate data, increasing to 0.702 when body mass was added and decreasing to 0.684 when life-history trait data were included; the pattern was similar for prebreeding census data. These results indicate that body mass improves the characterization of phylogenetic dependence among vital rates, but that life-history trait data do not produce further improvement and may even act slightly negatively on phylogenetic signal.

Imputed Vital Rates

Adult survival and fecundity were the most accurately imputed vital rates in the postbreeding census data: mean NRMSE of 0.169 (SD 0.039) and 0.172 (0.019), respectively. Imputed first-year survival (mean NRMSE: 0.248 [0.010]) and maturation rate (mean NRMSE: 0.346 [0.055]) were less accurate.

For first-year survival and fecundity, the phylogenetic model was no more accurate than the null model (Fig. 2). However, phylogenetic information helped to improve imputation accuracy for adult survival and maturation rate, particularly for multiple missing vital rates. Including body mass and life-history trait data improved imputation accuracy for adult survival and maturation rate (Fig. 2) and reduced the difference in accuracy between phylogenetic and null models for adult survival.

Life-History Metrics

Generation time calculated with a single imputed vital rate had a similar accuracy across trait data sets for first-year survival, adult survival, and fecundity (mean NRMSE: 0.075 [SD 0.011]) (Fig. 3), despite differences in imputation accuracy for these vital rates (Fig. 2). For maturation rate, mean NRMSE was higher (0.140 [0.073]) and NRMSE was markedly higher when body mass and life-history trait data were included, due to 2 outliers for which imputed maturation rate was underestimated, leading to overestimation of generation time (Appendix S17).

Mean age at maturity was sensitive to imputed adult survival because we assumed juvenile survival to be equal to adult survival, but it was relatively well characterized when adult survival was imputed (mean NRMSE: 0.041 [SD 0.007]) (Fig. 3). For imputed maturation rate, mean age at maturity was not well estimated (mean NRMSE: 0.234 [0.035]) and, as for generation time, mean age at maturity was less accurate when life-history trait data were included due to 2 outliers for which the metric was overestimated (Appendix S18).

Mean lifespan had similar accuracy when either first-year or adult survival were unknown (mean NRMSE: 0.121 [SD 0.007] and 0.118 [0.011], respectively) and was not influenced by adding body mass and life-history trait data.

Population Growth Metrics

When maturation rate was imputed, population growth rates matched the original values reasonably well (mean NRMSE: 0.051 [SD <0.001]) (Fig. 4). Population growth rate was less accurate when first-year or adult survival was imputed (mean NRMSE: 0.125 [0.010] and 0.126 [0.014], respectively). The least accurate results arose when fecundity was imputed (mean NRMSE: 0.221 [0.039]) driven by overestimation of fecundity for a single species (Appendix S20).

Estimates of the sensitivity of population growth rate to the underlying vital rates varied in accuracy across missing vital rates and focal vital rate for the sensitivity
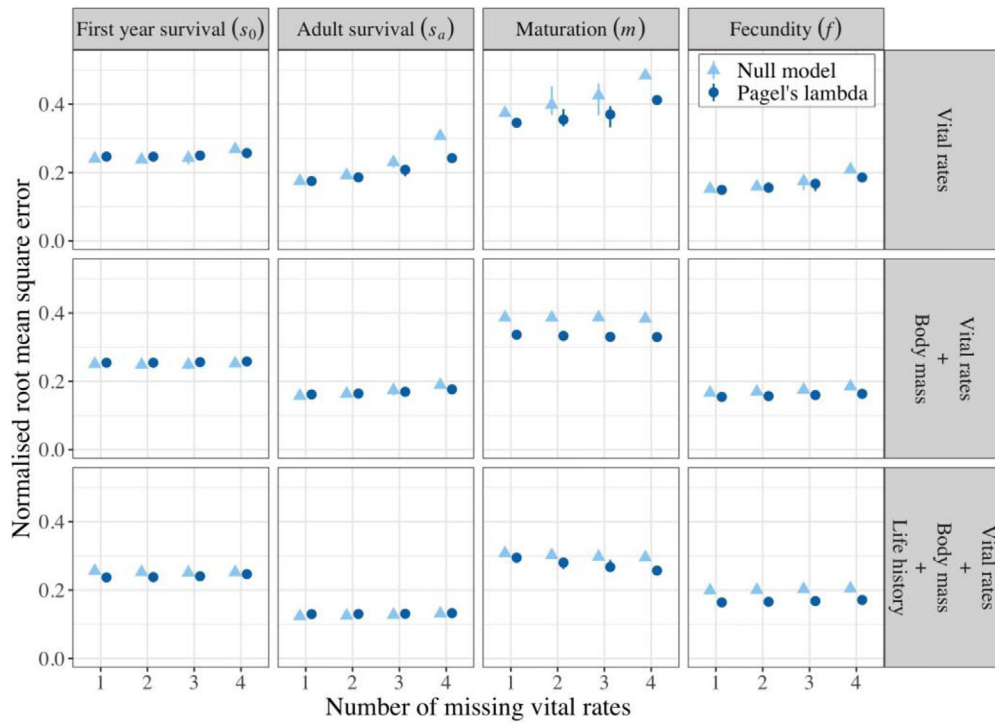
Figure 2. Accuracy of vital rates imputed from demographic data for different numbers of missing vital rates, trait data set, and evolutionary model (points, mean error across combinations of the same number of missing vital rates; whiskers, range of normalized root mean square error for different missing vital rate combinations).
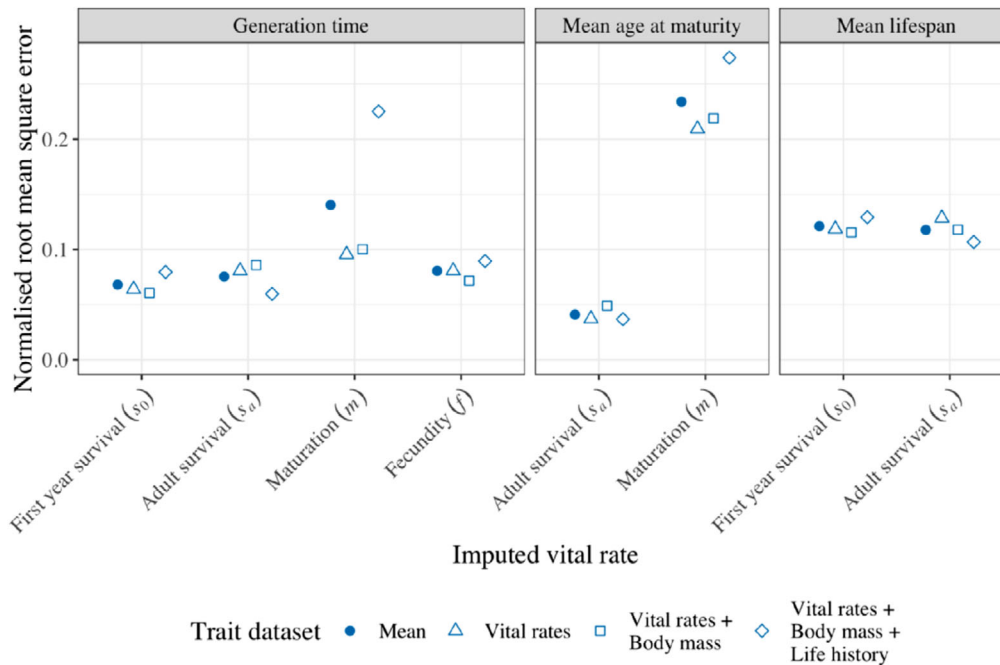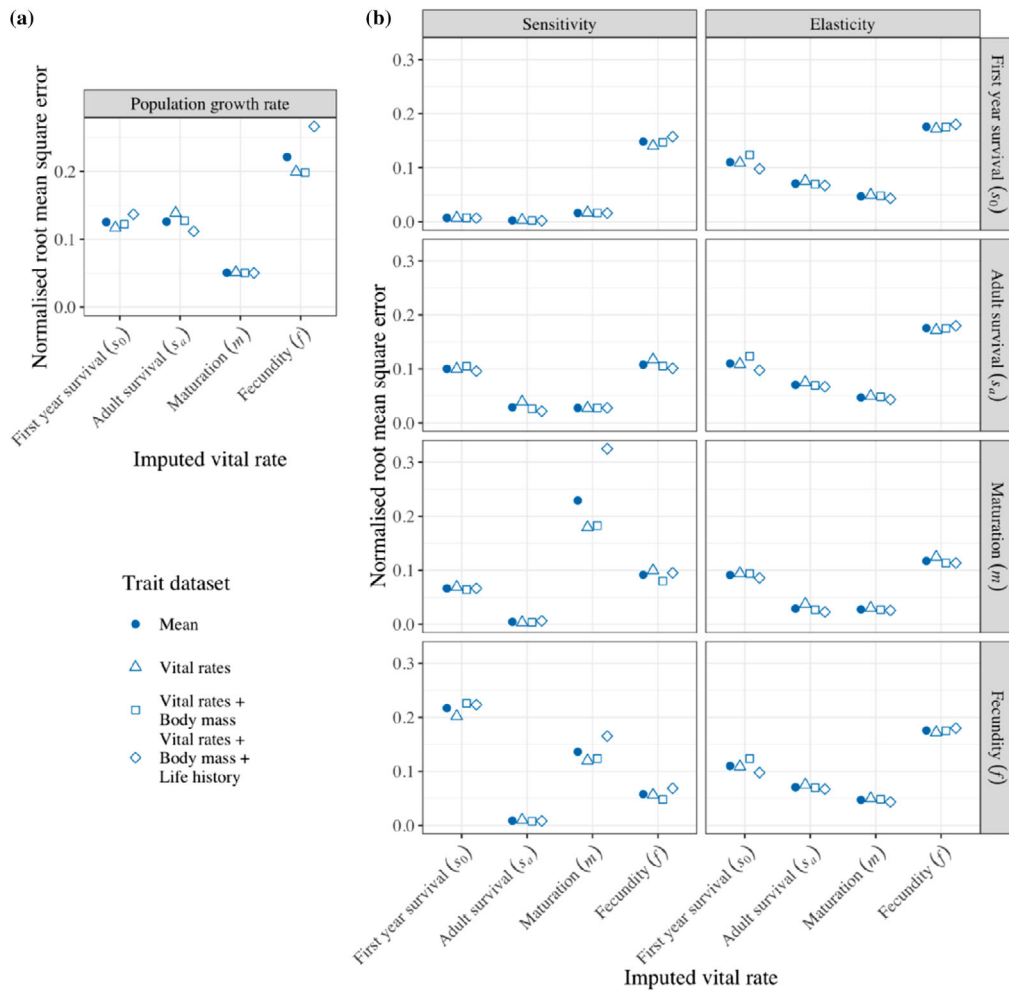

Figure 3. Accuracy of life-history metrics calculated from matrix population models parameterized with imputed vital rates (filled symbols, mean error across trait data sets; open symbols, error for individual trait data sets). Imputed vital rates that did not have an effect on the estimate of the life-history metric are not shown.

Figure 4. Estimates of (a) population growth rate and (b) sensitivity and elasticity of population growth rate to underlying vital rates (filled symbols, mean error across trait data sets; open symbols, error for individual trait data sets).

calculation (Fig. 4). Responses to imputed vital rates were more consistent across vital rate elasticities; maturation rate (mean NRMSE: 0.042 [SD 0.009]) and adult survival (mean NRMSE: 0.060 [0.019]) were the most accurate and first-year survival (mean NRMSE: 0.105 [0.013]) and fecundity (mean NRMSE: 0.161 [0.027]) were the least accurate. Errors in sensitivities and elasticities were unbiased except when maturation rate was imputed (Appendix S21 and S22).

Discussion

Detailed understanding of species' responses to global change, which is needed to address the current biodiversity crisis, is limited by gaps in the demographic data needed to predict population trajectories (Kindsvater et al. 2018; Conde et al. 2019). Efforts such as the IUCN Red List (IUCN 2020) are designed to make the most of limited information (Rodrigues et al. 2006; Mace et al.

2008), but the use of proxies to compensate for missing data can result in bias and under- or overestimation of extinction risk (Fung & Waples 2017; Staerk et al. 2019). Accurate estimation of vital rates, particularly those for which elasticity of population growth rate is high, such as adult survival in long-lived species, is important for reliable predictions of population performance. We found that applying a multivariate framework that accounted for covariance among rates of survival, reproduction, and maturation allowed us to impute some missing vital rates relatively well, even in the absence of phylogenetic information. Including phylogenetic relationships improved the accuracy of imputed values in some cases. However, auxiliary trait data also tended to improve imputation accuracy for multiple vital rates and compensated for lack of phylogeny in most cases.

Imputation accuracy did not reflect the ranking of vital rates by phylogenetic signal. However, vital rates with the strongest phylogenetic signal, adult survival and maturation rate, improved in accuracy with phylogeny,

particularly for multiple missing vital rates. Penone et al. (2014) linked the influence of phylogeny on trait estimates in carnivores both to phylogenetic signal and to how much traits covaried with body size. We found that imputation accuracy deteriorated for multiple missing vital rates, suggesting that covariance patterns among the vital rates were important.

Imputation tended to overestimate maturation rates (Appendices S9 and S13). In discrete time, stage-based population models, species that mature in a single time step have a maturation rate of 1, whereas for species with delayed onset of reproduction, maturation rate can be markedly <1. The resulting bimodal distribution is severely non-normal, even after transformation. The imputation model we used estimated covariance among normally distributed variables and did not compensate for this unusual distribution.

Our finding that body mass and life-history trait data improved the accuracy of imputed values contrasts with studies that showed relatively minor effects of species-level traits on the estimation of demographic rates. For example, body mass does not improve estimation of per capita population growth rate in mammals (Fagan et al. 2013), and size and growth form largely fail to improve predictability of demographic rates in plants (Che-Castaldo et al. 2018).

We found that accuracy of demographic metrics typically used for conservation assessment purposes, such as generation time (Mace et al. 2008), depended both on the accuracy of imputed values and on the sensitivity of the metric to the imputed vital rates. Moreover, the simplified life cycle underlying our approach may introduce bias in some demographic outputs (Fujiwara & Diaz-Lopez 2017). Many researchers advise caution in the interpretation of demographic model outputs due to parameter uncertainty (Beissinger & Westphal 1998; Ellner et al. 2002; Reed et al. 2002); similar care is necessary for models parameterized with imputed values.

Our results are limited by the availability and partiality of demographic data (Salguero-Gómez et al. 2015, 2016; Conde et al. 2019), which inform estimates of covariance among vital rates. Including data for more species may improve accuracy of imputed vital rates by strengthening patterns of covariance (e.g., Penone et al. 2014). However, vital-rate data may be missing not at random (MNAR) for species of conservation concern, and such biases in missing values can influence comparative analyses by skewing trait distributions (Nakagawa & Freckleton 2008; González-Suárez et al. 2012). Although geographical variation in demographic traits (e.g., differences in clutch size and survival across latitudes) could create different patterns of covariance among vital rates, including phylogeny, life-history traits, and latitude may be sufficient to control for such variation (Jetz et al 2008; Scholer et al 2020). Future studies could use a broader coverage of avian life history to investigate how biases in

the availability of demographic data affect imputation accuracy and could assess imputation of vital rates in other taxonomic groups.

Recommendations

The success of phylogenetic imputation rests on the validity of the data covariance structure. This structure is determined by the phylogeny and by the known values for vital rates and important covariates, such as body size. Thus, the quantity and accuracy of these data may strongly influence the reliability of imputed values. We suggest exploring the impact of uncertainty in the input data by, for example, varying the values within reasonable limits to determine the sensitivity of outputs. Uncertainty in the phylogeny could be explored in a similar way by sampling from a distribution of plausible trees.

We found that maturation rate was poorly handled by the distributional assumptions of the imputation method. We advise the use of an alternative approach, such as using a two-component mixture model to capture the bimodal distribution for maturation rate.

We have provided a qualitative assessment of how differences in the accuracy of imputed vital rates translate to accuracy of demographic metrics. A global sensitivity analysis could be used to quantify how uncertainty propagates from imputed vital rates to demographic metrics.

We used a novel approach to bridging gaps in demographic analysis with phylogenetic imputation. Although this method cannot replace demographic metric calculation when detailed age-specific life-history parameters are available, the ability to impute vital rates for species with sparse demographic data is valuable in a data-limited conservation context and avoids biases associated with assuming family- or genus-based mean values for underlying traits (Schafer & Graham 2002). Accurate demographic information is vital for indicators, such as the IUCN Red List, which informs conservation decision-making from species-level conservation to spatial prioritization (Rodrigues et al. 2006), and the IUCN Green List, a framework for assessing species recovery and conservation success (Akçakaya et al. 2018). In addition, data-driven assessments are essential in guiding business processes and supporting sustainable development goals (Brooks et al. 2015; Bennun et al. 2018).

Acknowledgments

Supporting Information

Data extraction procedure, species list, phylogenetic tree, and taxonomic bias (Appendices S1–S4); exploration of phylogenetic uncertainty (Appendix S5); comparison of imputation with and without phenotypic variation (Appendix S6); observed vs imputed vital rates for post-breeding census data under the null (Appendices S7–S10) and phylogenetic (Appendices S11–S14) models; observed vs imputed vital rates for pre-breeding census data under the null and phylogenetic models (Appendices S15–S16); and results for life history (Appendices S17–S19) and population growth (Appendices S20–S22) metrics are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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