

Population viability analysis using Bayesian networks

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ABSTRACT

Traditional population viability analysis (PVA) does not address the degree of measurement error or spatial and temporal variability of vital rate parameters, potentially leading to inappropriate conservation decision-making. We provide a methodology of applying Bayesian network (BN) modeling to PVA addressing these considerations, particularly for species with complex stage-class structures. We provide examples of three species from eastern Australia - hip pocket frog (*Assa darlingtoni*), squirrel glider (*Petaurus norfolcensis*) and giant burrowing frog (*Heleioporus australiacus*), comparing traditional matrix-based PVA with BN model analyses of mean stage abundance, quasi-extinction probability, and interval threshold extinction risk. Both approaches project similar population sizes, but BN PVA gave more clearly identifiable thresholds of population changes and extinction levels. The PVA BN uniquely represents complex stage-class structures and in a single network, including variation and uncertainty propagation of vital rates, to better inform conservation management decisions.

1. Introduction

A building block of conservation is ensuring the recovery and continued viability of species populations, particularly at-risk species (e.g. Schultz and Hammond 2003). Decision-makers often rely on demographic projection models to gauge the potential outcomes of management actions affecting the viability – size, trend, and probability of persistence – of populations (Saunders et al., 2018). These models are subject to the uncertainty in the input data. Failure to account for uncertainty can result in incorrect decisions with dire consequences for population conservation outcomes.

Population viability analysis (PVA) is a useful method for the quantitative projection of the size of a biological population under scenarios of specified survival and reproductive vital rates. The projection determines probabilities of decline or extinction over a specified time horizon (Shaffer 1990). PVAs have been central to population conservation for decades (Soule 1987; Gerber and González-Suárez 2010; Chirakkal and Gerber 2010; Saunders et al., 2018). PVAs can be conducted aspatially based on demographic vital rates with the use of a standard Leslie matrix life-table analysis and simulation projection models (Kajin et al., 2012), using programs such as Vortex and RAMAS (Lindenmayer et al., 2000; LaRue and Nielsen 2016). PVAs also can be spatialised with individual-based simulation models (Watkins and Rose 2017) such as HexSim (Schumaker and Brookes 2018) or through

spatially and temporally explicit population simulations (Visitin et al., 2020).

Results of PVAs are used in management (e.g., Schtickzelle et al., 2005) to help identify minimum viable population sizes to meet conservation objectives (Reed et al., 2003), to evaluate potential success of reintroductions (Licht et al., 2017), to determine potential impacts on populations from environmental disturbances and anthropogenic stressors (Tuma et al., 2016), and for informing other management objectives (e.g., Klavitter et al., 2003; Schultz and Hammond 2003). PVAs are also used to determine the probability of a population falling below a particular non-zero size, known as a quasi-extinction level (Ginzburg et al., 1982). Such probabilities are calculated as the proportion of replicate model runs with n below a specified quasi-extinction level, at a particular point in time or over a given duration of time. PVAs can also be used to project potential impacts of demographic and environmental stochasticity including random variation in vital rates of survivorship and reproduction due to environmental variation (Engen et al., 2005; Fox 2005).

A fundamental aspect of uncertainty to consider is the degree of measurement error and spatial and temporal variability of vital rate parameters (age- or stage-class survivorship and reproduction), which existing PVAs generally do not address. A construct that holds promise for addressing both types of uncertainty in an efficient manner is that of Bayesian network (BN) modeling. BNs are directed acyclic graphs that

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link variables with conditional probabilities (Koski and Noble, 2011). BNs have been used in a very wide array of environmental, ecological, and conservation problems (Pourret et al., 2008) including determining the IUCN (International Union for Conservation of Nature) red-list of threatened species categories (Newton 2010), and evaluating impacts of habitat conditions, disturbances, and stressors on populations of fish (Vilizzi et al., 2013), carnivores (Johnson et al., 2013), and marine mammals (Jay et al., 2011). BNs have been used to evaluate general population responses to habitat conditions, threats, and management considerations (e.g., Brown and Ferguson 2019; Zeigler et al., 2019). Although Bayesian statistical (non-network) approaches have been used with PVAs for some time (Goodman 2002; Saunders et al., 2018; Servanty et al., 2014; Maunder 2004; McCarthy et al., 2001), BNs have not yet been developed as PVAs per se, explicitly depicting age- or stage-class vital rates.

The structure of BNs is flexible and lends itself to modeling the event space of population stage classes to track cohort strength over time (e.g., Johnson et al., 2010) mimicking and extending traditional and non-network Bayesian PVA constructs. Traditional PVAs use repeat sampling within distributions among stage classes, such as with Markov chain Monte Carlo (MCMC) algorithms (Gross et al., 2002). BNs can propagate uncertainty throughout the model, as do Bayesian PVAs (Saunders et al., 2018). However, BNs are more flexible in their structure and can better depict complex life stages such as substages less than a single time step in the model, for example the egg and juvenile stage of most birds. This aspect of BNs allows for stage-specific management interactions to be tested across the life cycle of species. In turn, this would result in improved decision-making for conservation. Further, BNs can help solve the quandary posed by Fox and Kendall (2002) who suggested that systematic variation, rather than random variation, among individuals leads to overestimation of extinction risk in populations. That is, BNs can include probability distributions of many forms as explicit depictions of random variation in vital rates. Whereas traditional PVA modeling at best typically includes systematic variation in vital rates, although recent advances may include such considerations in non-network Bayesian implementations of PVA (Saunders et al., 2018).

Here, we provide a framework, methodology, and demonstration of applying BN modeling to PVA. The framework better accounts for variability and uncertainty in demographic vital rates and provides a more flexible framework than existing matrix or simulation approaches for species with complex stage-class structures. We first develop the concepts, then provide the computational modeling structure, explore three species examples, and conclude with a review of the value and limitations of the approach and future development needs.

2. Methods

2.1. Study species

Three species were used for modelling population viability in this study - the hip pocket frog (*Assa darlingtoni*; hereafter *Assa*), squirrel glider (*Petaurus norfolcensis*; hereafter *Petaurus*) and the giant burrowing frog (*Heleioporus australiacus*; hereafter *Heleioporus*). The three species were chosen due to the availability of population viability models (Keith et al., 2014; Penman et al., 2015; H. Kujala, N. Cadenhead, and L. O'Connor, University of Melbourne, Australia, pers. comm.) and the life-stages of the species. Both *Assa* and *Petaurus* have life histories that fit within the traditional PVA model, that is, they have life histories with annual life stages such as juvenile, young adult, mature adult.

The three species are found in forests and woodlands of south-eastern Australia (Fig. 1). *Assa* occurs in moist rainforests and eucalypt forests of the coastal escarpment, generally in areas about 600m elevation (Keith et al., 2014). It lays a small number of large eggs and has a relatively quick tadpole period (40 days) after which they emerge as sub-adults. *Petaurus* occurs throughout forests and woodlands of eastern Australia,

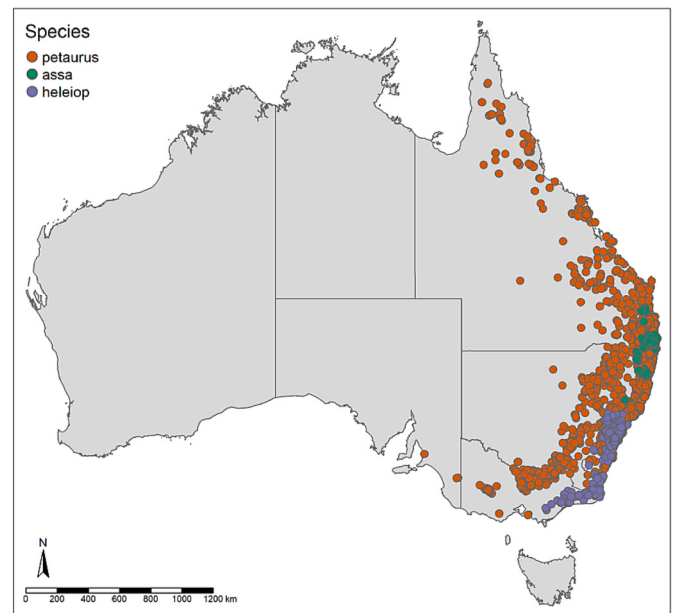


Fig. 1. Distribution records for the three species used in the study. *Petaurus* (orange), *Assa* (green), *Heleioporus* (purple). Source: Atlas of Living Australia (www.ala.org.au), accessed 5 August 2020.

although much of its habitat has been cleared for agriculture (van der Ree 2002). *Petaurus* is a hollow-dependent marsupial species, and its population ecology has been well studied (Quin 1995; van der Ree 2002; Smith 2003). *Heleioporus* is a ground-dwelling forest frog (Lemckert and Brassil 2003; Littlejohn and Martin 1967) with a complex life-cycle where adults move to breeding sites to lay eggs which hatch into tadpoles within two days to a week. These individuals can remain in the tadpole stage for three months to two years (Daly 1996; Penman et al., 2004); after transformation, the juveniles disperse into the forest before returning to the breeding population site up to several years later (Penman et al., 2008). *Heleioporus* has greater complexity in its life history than the other two example species explored here that results in a traditional PVA needing to combine individual stages into composite stages. Within a single year, an individual can advance from egg to tadpole and finally to juvenile frog stages. All of these stages are subject to different survival rates, variations, and risks. Previous studies have combined these stages into a single stage in the Leslie matrix, thereby making it difficult to disentangle the effects of management on the individual stages (Penman et al., 2015).

2.2. Population viability modelling approach

Two approaches to PVA were considered in this study, each being an aspatial representation of a single population. The first was the traditional Leslie matrix approach implemented in the RAMAS GIS® program (Version 5 Akçakaya and Root 2005). The Leslie matrix approach divides the population into groups based on age classes. Using estimates of survival and fecundity, matrix multiplication is used to model the changes in each age class of a population over time in discrete time steps. This approach is the foundation for PVA in a range of software packages (Lindemayer and Burgman (2005)). Although RAMAS GIS links spatial distribution data with PVA to estimate population extinction risk, only the basic RAMAS functions are used in this study for comparison. The second approach was to develop non-parametric continuous Bayesian networks (BNs) (Hanea et al., 2015) using Uninet software v2.97.16 (<https://lighttwist-software.com/uninet>, accessed August 2020) operated via R version 3.4.4 (R-Development Core Tea 2007) with the RDCOM-Client package version 0.93-0 (www.omegahat.net/RDCOMClient/). Discrete BNs are more commonly used in environmental decision

making (Aguilera et al. 2010, 2011; Johnson et al., 2010; Marcot et al., 2001; Newton 2010; Penman et al., 2020). In discrete BN models, the nodes represent discrete random variables where the model specifies marginal distributions for nodes with no parents (that is, that lack direct antecedents), and conditional probability tables for all child nodes (that is, with direct antecedents). Because all variables in our study were continuous, we chose to use the relatively new approach of non-parametric continuous BNs which associates nodes with random variables for which no parametric marginal distribution assumption is made (Hanea et al., 2015) and arcs (links between nodes) are parameterized by conditional rank correlations using normal copulas (Nelsen, 2007). It is well beyond the scope of this paper to describe non-parametric continuous BNs in detail, but we refer readers to Hanea et al. (2015) who provide extensive details of the method. Our two PVA approaches are described more fully below.

RAMAS matrix models were developed based on available model data (Keith et al., 2014; Penman et al., 2015). All matrix models are female-only. The Leslie matrix structures, including vital rate mean and standard deviation values, and initial abundances used in the RAMAS models of each species, are presented in Supplementary A. The life stages, vital rates, and their standard deviations are the same for the matrix model and the BN models. Vital rates as implemented in the RAMAS and BN models varied between life stages and also varied annually because of demographic stochasticity. Each RAMAS model was run for up to 100 years. The time period was chosen to replicate studies using two of the study species (Keith et al., 2014; Penman et al., 2015). To examine the effects of variations in vital rates, we ran both 100 and 1000 replicates for each species. Density dependence was represented by a ceiling model (Akçakaya and Root 2005) for *Assa* based on Keith et al. (2014), and by a ceiling model for *Heleioporus* based on Penman et al. (2015). There was no density dependence provided for *Petaurus* and this was not relevant as the population shrank to extinction and is therefore not expected to be influenced by density. For simplicity, we only modeled a single population for all species and therefore did not include dispersal or patch recolonization.

BN models were designed to represent stage transition dynamics for a single year. Nodes in the BN models represent vital rates and numbers of individuals of each life stage, and arcs represent the directional influence of each source or affector node (termed "parent node") to their immediate outcomes (or "child nodes") (Nyberg et al., 2006). In BN models, distributions in the child nodes are determined through equations relating conditional influences of the parent nodes. For simplicity, we used Gaussian distributions requiring only empirically-based mean values of numbers and vital rates, and their standard deviations to represent demographic stochasticity. We elected to use Gaussian distributions for a direct comparison with the RAMAS model, but noted that Uninet also allows for a diverse range of parametric, non-parametric and empirical distributions which could significantly expand the application of our approach. The BN models represent the full life stage structure of each species. When run, the models are looped so that the output distribution becomes the input distribution in the following year, thereby carrying the uncertainty forward.

The BN model for *Assa* is presented in Fig. 2. This model works for a single year and is iterated over 100 years to get outputs comparable with RAMAS. Nodes are included to represent the number of individuals (prefix 'N') per stage for either the start of the year 'Y0' or at the end of the year 'Y1'. For example, N1Y0 represents the number of individuals in stage 1 at the start of the year, whereas N1Y1 represents the number of individuals in stage 1 at the end of the year. Transition rates represent both survival and fecundity. Transition rates are represented by nodes prefixed with 'T' and the numbers representing the rates from stage x to stage y. For example, T.1.2 represents the transition rate for stage 1 to stage 2. Numbers for each stage at the end of the year are the product of the number at the start of the year and the transition rate. In the case where multiple stages breed or contribute to a life stage, these values are then added to determine the total number for that stage for the following year. At the end of each year, distributions for all Y1 nodes are used as Y0 nodes for the following year. If values are calculated to fall below 0, they are truncated to 0. These calculations were undertaken in R and the resultant distribution returned to the Uninet model. Returned

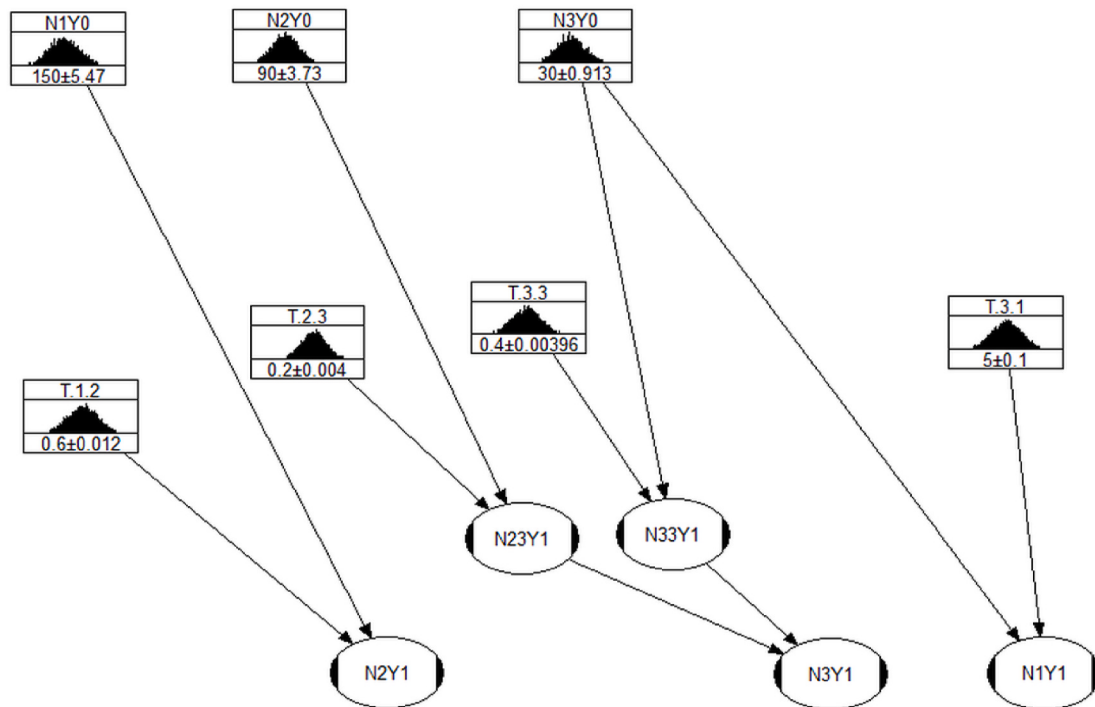


Fig. 2. UNINET Bayesian Network for *Assa*. Nomenclature for the nodes: 'NAYB' is the number of individuals in Stage A in Year B; and T.C.D is the transition rate from stage C to stage D. Nodes presented as histograms are inputs, and those as ellipses are the equations. Equations all take the form of $N_{(x+1)Y1} = N_{xY0} * T_{x,(x+1)}$. The exception is N3Y1 which simply sums N23Y1 and N33Y1.

distributions are then no longer considered Gaussian distributions; rather, they are considered empirical distributions derived from the model.

A more complex model was developed for *Heleioporus* to demonstrate the capacity of the BN modelling approach (Fig. 3). Traditional matrix model PVAs require each stage to be of a similar time step, often annual. In the BN approach for *Heleioporus*, we can include transition rates across multiple stages within a single modeling cycle, as well as the annual transitions. *Heleioporus* lays eggs which hatch within a week (Penman et al., 2004); this was included in nodes prefixed with 'NEg'. The tadpole phase can last six weeks to two years (Daly 1996) and therefore we included two stages of tadpoles – those that metamorphosed in a single season prefixed with 'T1' and those that took two seasons 'T2'. The species then remains in the transformed, juvenile phase for approximately three years, represented by nodes prefixed with 'NJ'. Juveniles then become sub-adults with lower breeding rates (nodes prefixed with 'NSA') and then move to larger adults with higher breeding rates – nodes prefixed with 'NLA'. Individuals were assumed to survive a maximum of 11 years (Penman et al., 2015). We do not vary survival rates within each stage as there is no evidence to support such an approach (Penman et al. 2004, 2015).

2.3. Analysis

We used three metrics to compare the two modelling approaches: mean stage abundance, quasi-extinction probability and interval threshold extinction probability. *Mean stage abundance* is the abundance of each stage per year, as calculated from the RAMAS 100- and 1000-replicate results, and from the Uninet BN results (hereafter Uninet). *Quasi-extinction probability* is the probability that the population will fall below a threshold population size. We scaled populations to a threshold of 1.0 to allow for simple comparisons within and between species. The Uninet model uses a distribution of values to derive the extinction probability as the proportion of values below 1. The *interval threshold*

extinction risk gives the probability that population size will fall below a threshold of abundance at least once during the simulation. In the Uninet model, we calculated this using the proportion of the distribution that fell below the range of abundances during the simulation.

We assessed the three modeling constructs – RAMAS with 100 replicates, RAMAS with 1000 replicates, and Uninet – based on graphical comparisons. Mean and uncertainty values were examined with non-overlapping 95% confidence intervals (RAMAS), and with 95% credible intervals (Uninet) that are equivalent to significance at the $p = 0.05$ level for a two-sample t -test (Walshe et al., 2007). Here we make the assumption that the confidence and credible intervals are approximately equivalent. Plots are presented for the mean values in the results for clarity.

3. Results

There was strong agreement with the stage-class abundances of *Assa* and *Petaurus* across the Uninet and RAMAS 1000 replicate models (Fig. 4), with the RAMAS 100 replicate model suggesting a decline over the 100 years. The other two models predicted that all three stages of the *Assa* model plateaued around 15 years from the start of the analysis at abundance values of 150, 90 and 30 individuals in stages 1, 2 and 3 respectively. After this point, there was little variation over time with any of the three models. The models for *Petaurus* all predicted extinction of the species between 30 and 35 years after the simulation began (Fig. 4). There was very little difference in the abundances for each stage between the modelling approaches.

Differences were seen in the *Heleioporus* model with RAMAS predicting higher abundance values of stage 1 (juveniles) compared to Uninet (Fig. 4). In contrast, RAMAS predicted similar abundance values of stage 2 (small adults); and Uninet and RAMAS predicted significantly lower abundance values of stage 3 (large adults). The Uninet models resulted in far narrower variations (SD) in average total population sizes for *Assa* and *Petaurus* but wider variations in the more complex life

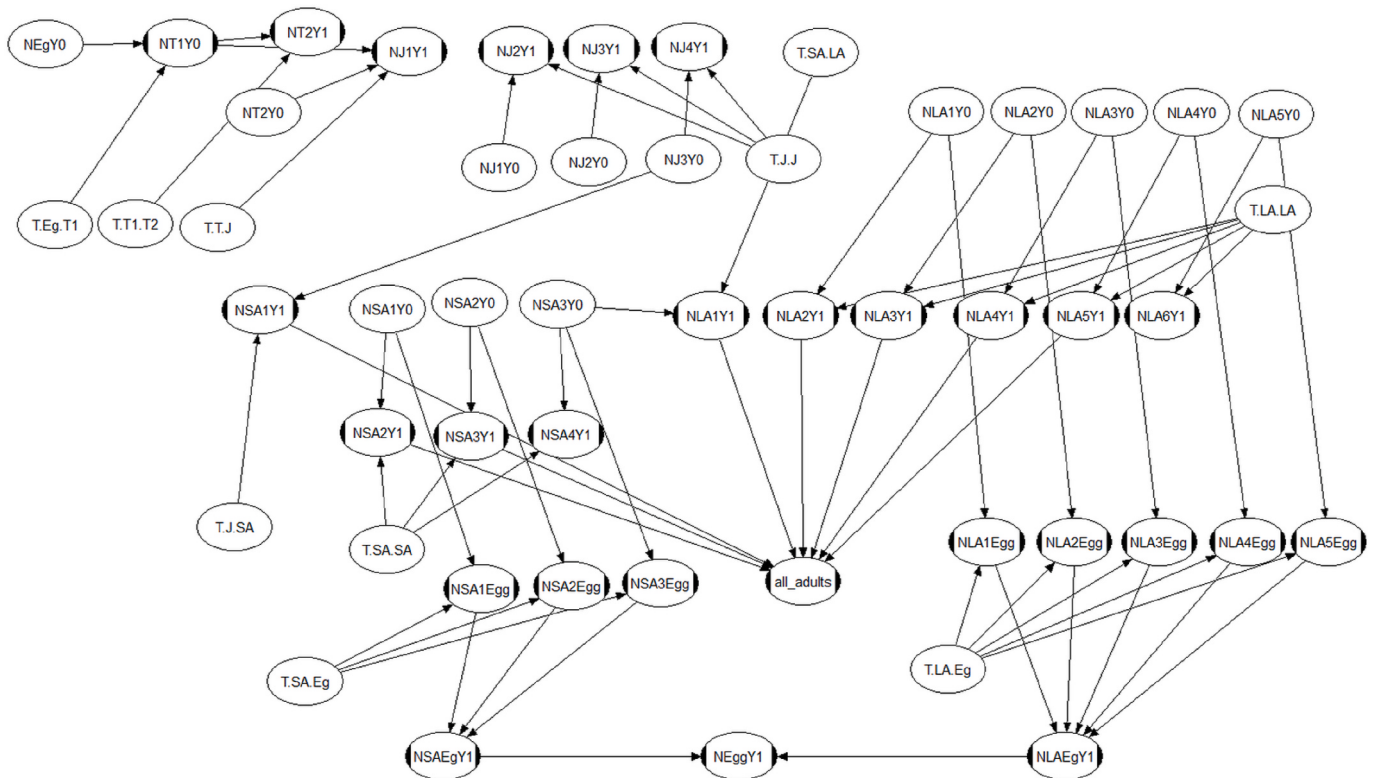


Fig. 3. UNINET Bayesian network for *Heleioporus australaicus*. Terminology is as per Fig. 2 with the exception that the stages are Eg = egg, T = tadpole, J = juvenile, SA = small adult, LA = large adult.

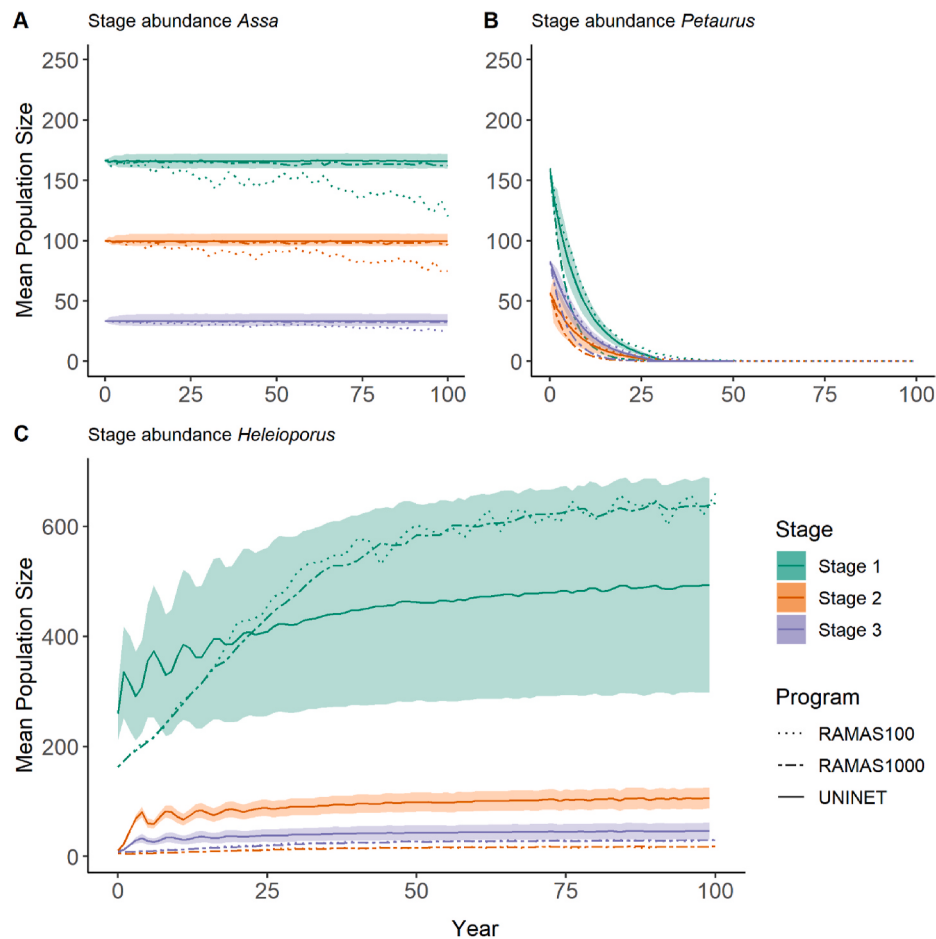


Fig. 4. Comparison of stage abundance levels between RAMAS with 100 and 1000 replicates and UNINET Bayesian network models of a) *Assa*, b) *Petaurus*, and c) *Heleioporus*. In the case of *Heleioporus*, tadpoles are not included in the population size estimates. Note that RAMAS did not provide stage specific variance values.

history structure of *Heleioporus* (Supplementary Material Fig. S1).

Differences among the quasi-extinction probability estimates occurred between the modeling approaches (Fig. 5). All three modeling approaches predicted no or very low extinction probabilities for *Assa* over the 100 years, with a maximum value of 0.2% from the RAMAS

1000 Model. Patterns for *Petaurus* were similar between the two RAMAS approaches but differed with the Uninet approach (Fig. 5). Both RAMAS models predicted the quasi-extinction probability to rise from around 10 to 20 years after the model started, to eventually reaching values of approximately 0.9 by 60 years. In contrast, the Uninet model predicted a

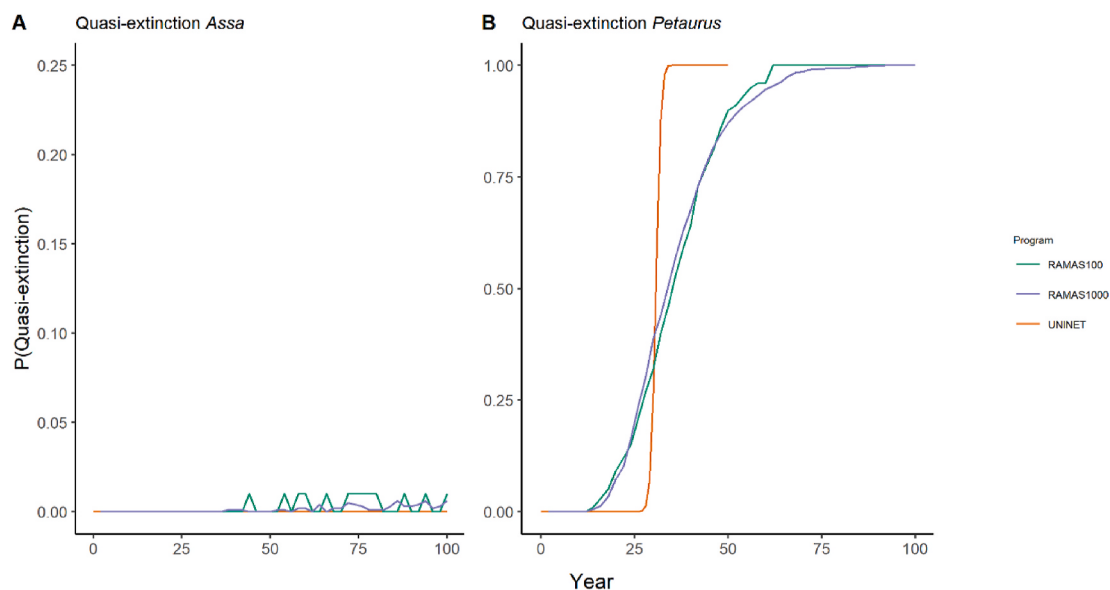


Fig. 5. Comparison of quasi-extinction levels between RAMAS with 100 and 1000 replicates and UNINET Bayesian network models for a) *Assa* and b) *Petaurus*.

zero probability until around 30 years when it switched to a quasi-extinction probability of close to 1. No model predicted a quasi-extinction probability greater than zero for *Heleioporus* (thus, not included in Fig. 5).

There were differences among the modelling approaches in the results for the interval threshold extinction risk. RAMAS models of *Assa* populations predicted a rise from a probability value of 0.1 for small populations up to 1, at an extinction threshold level of around 300. In contrast, the Uninet model predicted a steep threshold between 260 and 280 where the extinction risk rises from 0 to 1 (Fig. 6). All three approaches for *Petaurus* predicted interval threshold risk to be 1 for all population sizes (Fig. 6).

Both RAMAS and Uninet resulted in logistic-shaped responses for *Heleioporus*, although the modeling approaches differed in the resulting absolute values of population abundance thresholds extinction probabilities. RAMAS predicted threshold-extinction risk values starting from 0.1 and rising to 0.75 at population sizes of approximately 150. Uninet predicted extinction risk values of 0 up to population sizes of approximately 30 and rising to an extinction risk of 1 at a population size of approximately 100.

4. Discussion

We have demonstrated that the PVA BN approach results in essentially the same projected overall population sizes resulting from more traditional Leslie matrix analysis such as used in RAMAS for the three case studies investigated. However, projected sizes of specific life stages

of some species, e.g., stage 1 of *Heleioporus* (Fig. 4), may differ between the two approaches. The PVA BN approach results in more prominent thresholds of population changes and extinction levels, which could better determine specific quasi-extinction brinks or minimum viable population sizes (Brook et al., 2000; Reed et al., 2003).

A major difference between the two models was the estimation of the extinction risk values. In most cases, the BN approach predicted a threshold value where risk switched from 0 to 1, whereas the Leslie matrix approach generally predicted a more continuous transition. The exception to this was the *Heleioporus* model where similar shaped responses were found, but with the BN predicting extinction at smaller population sizes. There are a number of reasons these differences could occur. One of the main reasons would be the methods used to calculate the values. The Leslie matrix approach selects values randomly from distributions and then makes multiple traces, finally averaging across the traces to determine values and uncertainties. In contrast, the BN approach multiplies distributions to determine the values. Only a single “replicate” of the BN is required and therefore it is less subject to stochasticity and is more data driven. Greater uncertainty in population estimates can also represent demographic stochasticity which can lead to a greater probability of extinction under low population sizes (Jeppsson and Forslund 2012). The choice of model used and the method for dealing with uncertainty (distributions vs replicates) clearly influence estimates of population size, extinction and quasi-extinction risks and therefore have implications for conservation decision making.

The BN PVA approach explicitly accounts for variation and uncertainty in population vital rates of births and deaths, and for propagation

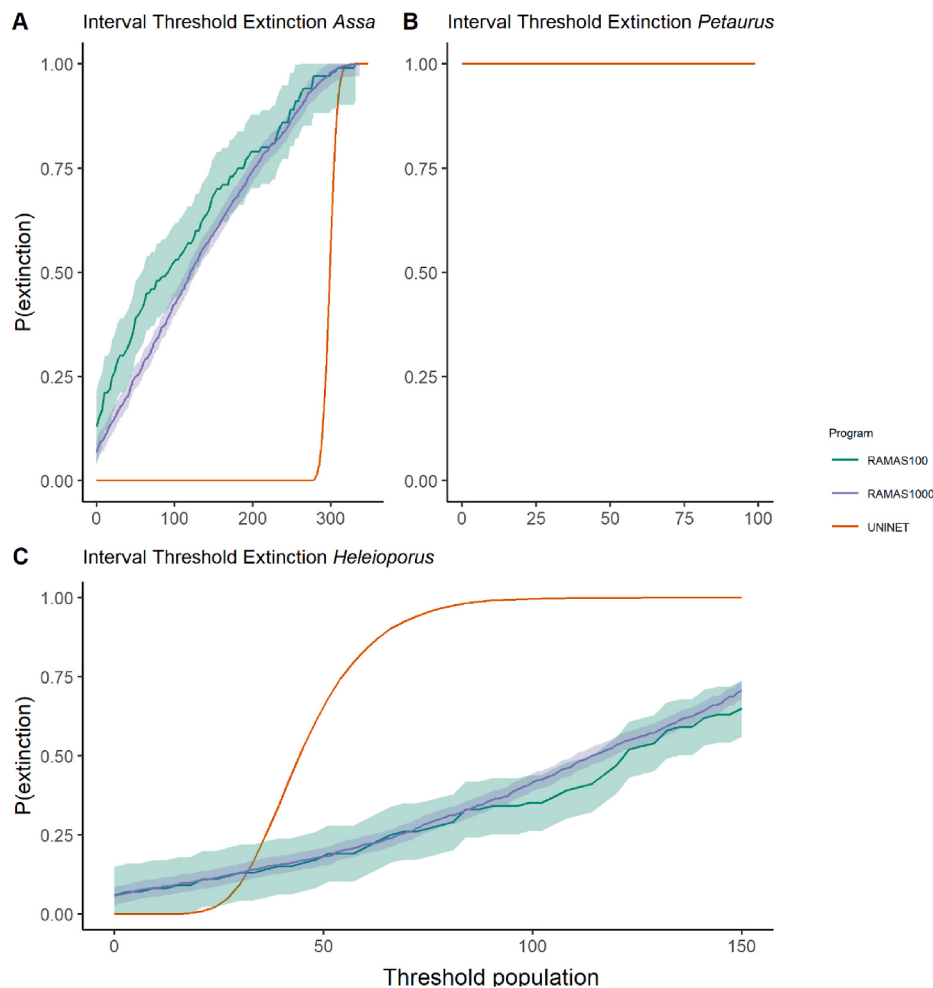


Fig. 6. The probability of extinction (y axis) as a function of the minimum threshold population size (x-axis) between RAMAS with 100 and 1000 replicates and UNINET Bayesian network models for a) *Assa*, b) *Petaurus*, and c) *Heleioporus*.

of that uncertainty across life stages and time periods. This is evident through the cycling of empirical distributions between years. As such, it can explicitly account for demographic and environmental stochasticity and can track relative cohort strengths over time. Bayesian PVA can include random deviates of any distributional pattern in defining the probability distributions of vital rate values with specified levels of uncertainty and variation (Saunders et al., 2018). Whereas the Leslie matrix includes only frequentist statistical parameters of variability such as standard deviation. Additionally, the influence of external disturbance events on those probability distributions can be added easily and explicitly into a BN PVA model through additional nodes or probabilistic sub-models.

Our approach can also account for complex or overlapping life stages in stage-structured populations, i.e. multiple stages occurring within one age class as defined by a Leslie matrix. This was demonstrated with our *Heleioporus* example potentially having both an egg stage and more than one tadpole stage. Other examples include analysis by Aubry et al. (2010) for a toad species that can pulse-breed with several successive cohorts of eggs and tadpoles within the same season. However, rather than the complex set of multiple population matrices resulting from their analysis, our BN PVA approach can more simply represent overlapping life stages and population outcomes in a single network. The BN PVA model can also be extended to various time frames representing specified numbers of generations. To represent real-world cases, the PVA BN can be initialized with empirical abundances of each life stage class. Also, the BN PVA approach can be used to combine otherwise disparate information sources on population structure and vital rates, such as from multiple studies and expert knowledge elicitation, much as used in integrated population models (Saunders et al., 2019) but with explicit calculations of the sequential propagation of value uncertainties in population projections.

Our PVA BN approach is in the early stages of development and does not utilize the full capacity of BNs. In this study, we sought to demonstrate the method rather than definitively summarize the strength of BNs. The BN could be expanded beyond the PVA approach here to quantify the influence and stochasticity of environmental factors on survival and reproduction (Enright et al., 2014), the role of disturbances such as fire that result in increases in population size through germination of soil stored seed banks (Swab et al., 2012) or complex interactions with other species by combining two PVA BNs. Furthermore, we initialized our model with simple Gaussian distributions however any parametric, non-parametric or empirical distribution could be used. We do note that it is likely that these steps could potentially be programmed into statistical packages such as R or MATLAB and our approach presented is not necessarily limited to BNs. However, the BN approach has an existing structure, available software, and a well-established literature supporting its use for such approaches.

We offer several caveats of the PVA BN approach. First, it may be difficult in this framework to incorporate density-dependency limitations and Allee effects that represent biological constraints to unlimited population growth, that can be modeled with time-dynamic logistic equations (Cross and Beissinger 2001) or other analytic approaches (Carlos and Braumann 2017). Second, our PVA BN modeling framework is essentially insensitive to population structures because (1) it remains aspatial and (2) is structured for evaluating viability of single populations rather than multiple populations (Leasure et al., 2019), although other non-network Bayesian methods have been used to evaluate population structures (Harrison et al., 2011; O'Hara et al., 2002). Third, our framework does not account for variations in life histories among individuals within a population, for example as found in some species of Pacific salmonid fishes (Fujiwara 2007). And finally, although results of PVA BN projections could be mapped, the structure currently is essentially aspatial, but may be a useful complement to spatially-explicit individual movement models. The major advantages of the PVA BN approach lie in efficiently representing entire stage-class structures in a single network and displaying the effect of variation

and propagation of uncertainty in those classes, representing demographic and environmental stochasticity, on projected population size and trend.

Next steps in development of the PVA BN framework could include making it spatially explicit (Swab et al., 2012; Penman et al., 2015; Schtickzelle and Baguette 2004). Traditional Leslie matrix PVAs tend not to be spatially-referenced although packages such as RAMAS seek to address this issue. BNs also have that capability whereby results can be mapped showing resulting probabilities, uncertainties, and their empirical basis or sample sizes (Havron et al., 2017; Wiest et al., 2019). Life stages within the PVA BN could be assigned individual spatial occurrences by modeling them as objects in object-oriented and agent-based Bayesian networks (Marcot and Penman 2019), with results applied to geographic information systems to map outcomes denoting projected population size, trend, and uncertainties.

5. Conclusions

Modeling population viability with probability networks provides a means of representing age- or stage-class structures and effects of random uncertainties in vital rates on population outcomes in a single, parsimonious, and efficient network structure rather than, at best, a complex set of population matrices.

Specifically, our PVA BN approach, as implemented here in the BN modeling shell Uninet as continuous-variable networks, compares well with traditional results calculated with Leslie matrices with the RAMAS program. Moreover, the PVA BN approach provides a far more flexible structure for explicitly and clearly representing complex life history stage classes and the role and influence of disturbances. The PVA BN model structure provides probability distributions of the size of each stage class and of total population size at each time interval analyzed. Such distributions can be used to quickly calculate Bayesian credible intervals of stage class, cohort, and population size, including probabilities of quasi-extinction rates.

Our method allows for population modelling for a greater diversity of species, particularly those with complex and overlapping life stages. Conservation managers can use model outputs to make informed decisions over a greater array of species and explicitly accounting for environmental and demographic stochasticity and data-driven uncertainty.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envsoft.2021.105242>.

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