Novel Challenges and Opportunities in the Theory and Practice of Matrix Population Modelling

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"Theory and Practice in Matrix Population Modelling"

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Abstract

Demography is at the core of ecology, evolution, and conservation biology. The simple recognition that individuals in a given population contribute to its dynamics in different ways revolutionised the ways in which demographers approach data collection, analyses, and interpretation of their study populations, from bacteria to humans. Matrix population models, discrete-time, discrete-state (*i.e.* individuals are categorised into discrete categories based on traits such as age or stage), were first introduced to the scientific community by Patrick Leslie 75 years ago. Since then, the applications of matrix population models to ecology, evolution, and conservation biology have strongly been running strong and in parallel with its robust mathematical development. This special feature contains 14 novel contributions that represent some the cutting-edge mathematical formulations and applications of this powerful demographic tool. In addition to highlighting the key contributions of this manuscripts, we provide suggestions to some of the challenges that researchers using matrix population models must overcome in the coming decades to truly unlock the potential of this analytical demographic tool.

Keywords

Comparative biology; Data gaps; Matrix averaging; Population ecology; Potential-growth indicators; Population viability; Stochastic growth rate.

1. Introduction

The 1945 publication ‘On the use of matrices in certain population mathematics’ by Patrick H. Leslie has revolutionised mathematical demography and population ecology. This manuscript, together with many others produced throughout Leslie’s prolific career (1948; Caswell, 2001, and refs therein), marked the inception of the vastly rich world of *Matrix Population Models* (*MPM*s, hereafter). Now, at the 75th anniversary of the publication of this seminal contribution, MPMs have moved from being an exclusively useful exercise ‘in certain population mathematics’ to a powerful, frequently used tool across numerous disciplines, including ecology (e.g., Crone et al., 2011), evolution (e.g., van Tienderen, 1995), and conservation biology (e.g., Morris and Doak, 2002). MPMs have been applied to a wide range of taxonomic groups, from humans (Nicol-Harper, 2018), to whales (Chiquet et al. 2013), penguins (Jenouvrier et al., 2012), plants (Salguero-Gómez et al., 2016), bacteria (Watwe et al., 2006) and even viruses (Wallace, 2004). Indeed, MPMs have become as equally popular among field ecologists as they continue to be among theoretical ecologists. Even now, Leslie’s pioneering work motivates new developments in the mathematical theory of nonnegative matrices (Li and Schneider, 2002; Tuljapurkar and Haridas, 2006; Protasov and Logofet, 2014; Logofet, 2018, 2019a; Razzhevaikin and Tyrtyshnikov, 2020), a single mathematical basis of diverse applications.

MPMs represent an elegant, relatively straightforward, powerful tool to describe the dynamics of a population in discrete time and discrete structure (Caswell, 2001). The population structure, whereby individuals are classified following a relevant set of criteria that separates them into discrete states (e.g., ages, size ranges, development, nationality, etc.), together with information regarding the species’ life cycle, allows researchers to draw direct links between transitions and per-capita contributions of different stages along the lifecycle (*i.e.*, the *Life Cycle Graph, LCG*), as well as the likelihood/intensity of those demographic events (*i.e.*, *vital rates*).

When calibrated with field or laboratory data, the *Population Projection Matrix* (PPM), the core of any MPM, serves as an indicator of the environment quality and biological properties of the species’ population under study (Caswell, 2001). This PPM provides a rich repertoire of quantitative characteristics that allow not only for the careful characterisation of the current and future state of that population (e.g., Jenouvrier et al., 2009), but also for comparative (e.g., Jones et al., 2013), empirical (e.g. Crone et al., 2011) and theoretical research (e.g., Haridas and Tuljapurkar, 2007).

Depending on the data source and organism under study, MPMs face interesting analytical challenges, but also provide unique research and methodological opportunities. The Special Issue “*Theory and Practice in Matrix Population Modelling*” in *Ecological Modelling* aims to reflect the current state-of-the-art in the *Theory and Practice of Matrix Population Modelling*. Together, the special feature includes 14 contributions (marked hereafter with ^{SI}) that address topics at the frontiers of MPM's development and applications. Our goal here is to outline some of the next frontiers in the theory and praxis of the MPM world, while highlighting how each of these publications makes a clear contribution to these areas.

2.1. Exploring taxonomic/ecoregion biases

Although the usage of MPM across a wide range of species and regions has become a reality, important biases remain in the demographic literature (Conde et al., 2019). These biases are preventing researchers from examining the validity of general rules (see next Section). For instance, even though most of the terrestrial biodiversity worldwide is found in tropical ecoregions (Tomašových, 2019; Wang et al., 2019; Loiseau et al., 2020), most of the studies that have used MPMs on terrestrial animals and plants have taken place in grasslands and temperate ecoregions (Salguero-Gómez et al., 2015a, b). From this angle, the following manuscripts in this special feature make contributions to expanding our demographic knowledge across the Tree of Life and the planet.

Pinto et al. (2020^{SI}) make an important contribution to our understanding of the demography of insects. Insects are the most specious animal groups, with an estimated >1 million species (Zhang, 2013), yet very little is known about their demography, particularly using MPMs. This dearth of insect data contrasts with their rather discrete life cycles, which renders them particularly amenable to modelling via MPMs (Caswell, 2001). These authors explore the demographic and performance effects of alternative host usage by a Neotropical treehopper *(Alchisme grossa*) to examine whether these effects exert a selective pressure sufficient for the evolution of species divergence. In the Bolivian Yungas forests, the subsocial treehopper (Hemiptera: Membracidae) utilises two sympatric hosts, *Brugmansia suaveolens* and *Solanum ursinum*. Adults use their natal host species, and females take care of nymphs (e.g., feeding facilitation, antidepredatory defense) during their development on both hosts. However, the duration of pre-imaginal development differs markedly between the host species, but two corresponding stage-structured MPMs have not revealed any statistical difference in their λ_1s, hence individuals of *A. grossa,* though hatching to different hosts, still belong to a single-species population. Thus, the contribution opens a new direction for resolving the eternal dialectics of population dynamics vs. evolution.

Another important contribution from the angle of ecoregion representativeness is that by Santostasi et al. (2020^{SI}), who developed and introduced a framework to examine the role of hybridisation for two case studies, with one of them being in marine species (below). This is particularly important, as most of our demographic understanding across the Tree of Lie is constrained to terrestrial ecosystems, despite our dependence on the resources and ecosystem services that aquatic ecosystems provide (Tallis and Kareiva, 2005).

2.2. Finding generality in ecology, evolution, and conservation biology using big data

Ecology, Evolution, and Conservation Biology are ideally positioned to tackle and provide solutions to the current biodiversity crisis of the Anthropocene (Proctor, 2013). However, most ecological, evolutionary, and conservation biology research that has been carried out to date with MPMs has been local in spatial extent and focus on single species. All species, from *Escherichia coli* to blue whales (*Balaenoptera musculus*), have in common the fact that individuals in their populations must invest to a certain degree in four key demographic (vital) rates: survival, development, reproduction, and recruitment. Notably, however, there is a great deal of variation in how individuals fine-tune the investment of the limited energy, via trade-offs, in each of these vital rates (Gaillard et al., 1989; Salguero-Gómez et al., 2016; Healy et al., 2019). However, despite the vast amount of life history strategy variation that emerges from this differential investment in vital rates, these vital rates ultimately allow species to persist and adapt to their local environments (Stearns, 1992).

The last decades have witnessed the utilisation of ever-growing volumes of published MPMs from open-access databases (Salguero-Gómez et al., 2015a, b) to tackle questions regarding the universality of the evolution of senescence (Jones et al., 2014; Salguero-Gómez, 2017), the link between functional traits and demographic performance (Adler et al., 2014), the predictive power of demographic schedules for species presence and absence (Csergő et al., 2017), the examination of main axes of variation in life history strategies (Salguero-Gomez et al., 2016; Healy et al., 2019), or responses of organisms to climate change (Herrando-Perez, S., 2013).

Decomposition analyses in demographic studies, such as Life Table Response Experiments (LTRE, Caswell, 2000) have become a common, powerful way to examine ways in which experimental treatments affect the overall dynamics of a population via its underlying vital rates. These solutions have now been developed both for deterministic (Caswell, 2000) as well as stochastic environments (Caswell, 2010, 2019; Davidson et al., 2010). Davison et al. (2019[SI]) apply stochastic LTRE (sLTRE) tools to a subset of 220 populations from 62 species archived in COMADRE and COMPADRE. They find that stochasticity drives 28% of fitness effects, exceeding the mean effects by 7.78%, and thus further evidencing the need to describe populations and their abiotic effects in stochastic rather than deterministic terms.

Together, these novel contributions accentuate the promise of using large volumes of demographic data to find generality in ecology, evolution, and conservation biology.

2.3. Eco-evolutionary dynamics

Classically, *evolution* (i.e., the change in phenotypes in populations linked to their heritability via natural selection) and *ecology* (i.e., the interactions of individuals with their own kind, other species, and their local environments) have been treated as self-contained disciplines acting in their separate silos. The main argument for their separation was a temporal one, under the assumption that evolution occurs at much longer time scales than ecology. However, research in the last decade has revealed that evolution can and oftentimes does shape individual performance and community dynamics at relatively short time scales (e.g., via rapid evolution; Hart et al., 2019). Similarly, ecological interactions can have long-lasting repercussions that place them right at the same temporal scale as classical evolutionary thinking (Hendry, 2017; Power et al., 2018). Demographic tools allow for the reconciliation of eco-evolutionary dynamics in a single, robust framework (Govaert et al., 2018; Takada and Shefferson, 2018; Shefferson and Salguero−Gómez, 2015). Santostasi et al. (2020[SI]) use a novel approach via matrix population models to examine the extinction of specific genomes in hybridizing populations. This approach is extremely relevant to our understanding of conservation biology, as hybridization is a main mechanism of biodiversity loss. In their paper, the authors model the breeding of two parental groups as separate components. They apply this model to two case studies regarding terrestrial (the wolf *Canis lupus* and its domestic counterpart *Canis lupus familiaris*) and marine species (the striped dolphin *Stenella coeruleoalba* and the common dolphin *Delphinus delphis*) facing hybridization. This article presents original utilisations of the matrix-based demographic machinery to advance our understanding of eco-evolutionary dynamics.

2.4. Testing and overcoming classical assumptions in demographic modelling

Since the rigid postulates of Leslie's demographic model, testing and overcoming classical assumptions have been representing the main course of the mathematical developments of MPMs (Lefkovitch, 1965; Cohen, 1979; Tuljapurkar, 1990, 2013; Logofet, 1993, 2018; Cushing and Yicang, 1994; Caswell, 2001, and refs therein; Li and Schneider, 2002; Logofet, 2013, 2018). The following contributions make important progress along this course: de Vries et al. (2020[SI]), Barraquand and Gimenez (2019[SI]), and Takada and Kawai (2020[SI]).

The contribution by de Vries et al. (2020[SI]) provides methods to overcome two classical assumptions in MPMs. First, motivated by application to pesticide resistance in the flour beetle (*Tribolium castaneum*), the authors add genotype as the second basis to classify individuals (a rarely considered, yet important trait; but see Coulson et al. 2011), thus expanding the classical formalism to a general framework for the *stage*- and *genotype*-structured population. Second, when the classical linearity of demography meets the classical nonlinearity of population genetics, the PPM becomes a nonlinear density-dependent operator governing selection in this kind of population. The Jacobian matrix of this operator enables obtaining the stability conditions of homozygous equilibria, in particular, those of pesticide resistance domination. These results are useful for the pest management theory and they open a novel dimension in studying eco-evolutionary dynamic.

Barraquand and Gimenez (2019[SI]) have overcome the classical MPM paradigm of single-species population dynamics by introducing a stage-structured model for a predator–prey community in which the populations are represented by juveniles and adults, predation is stage-specific, and the juvenile prey density positively affects predator fecundity. Estimating the parameters of species interaction in this framework requires a combination of traditional and novel ways to integrate data for single-species demography, thus leading to Integrated Community Models (ICMs). In a sense, this returns to the second birth of population dynamic models, i.e., the classical Lotka–Volterra prey–predator equations (Lotka, 1925; Volterra, 1931). Our authors assessed the value of different data sources using simulations of ICMs under different scenarios contrasting data availability and the presence/absence of intraspecific density-dependent effects. Combining all the data types (capture-recapture, counts, and reproduction surveys) allows the estimation of both demographic and interaction parameters, unlike count-only data which typically generate high bias and low precision in the interaction parameter estimates for short time series. As an accurate representation of stage structure in community dynamics, the ICMs open a wide spectrum of research perspectives, from the development of efficient observational study designs for monitoring communities in the field to the analysis of more sophisticated stage-structured MPMs.

Takada and Kawai (2020[SI]) avail from the large volume of MPMs stored in the COMPADRE Plant Matrix Database (Salguero-Gómez, 2015a) to examine the most optimal way to analyse and depict elasticities of population growth rate with respect to vital rates in a comparative framework. *Elasticities*, i.e., the relative impacts of different demographic processes on the overall dynamics of a population (De Kroon et al., 1986, 2000) remain one of the most widely ways to quantify demographic processes’ impacts on the viability of species (Morris and Doak, 2002). However, the ways in which they have been quantified and visualised (e.g., Enright et al., 1995; Franco and Silvertown, 2004) has not been free of criticism (e.g, Shea et al., 1994; Franco and Silvertown, 1994). Specifically, Takada and Kawai use 68 MPMs from semelparous plant species in COMPADRE to examine the biologically meaningful patterns that should emerged from their elasticity vectors when presented in a ternary plot. Then they contrast these results to those of randomly generated MPMs with the same life history strategy. Their analyses help explain why, when the elasticities to survival, growth, and reproduction of plant species are plotted on a ternary plot, the overall pattern shows a strong curvature, with a "gap" in the ternary plot that is not "invadable".

2.5. Novel contributions to stochastic demography

Examining stochastic demographic properties by means of MPMs is typically done when more than one (a time series of) PPMs ("annual" PPMs) exist for a single population. This approach has become popular in ecology as most ecological systems are characterised by oscillatory environmental conditions (Salguero-Gómez and de Kroon, 2010), and climate change projects are likely to make natural systems suffer from a high frequency of climatic anomalies (IPCC, 2020). In this approach, the *stochastic growth rate*, λ_S, is typically defined via an infinite sequence of annual PPMs chosen at random from the given (finite) set of annual PPMs, and it is generally used as a proxy to population viability in the stochastic environment. In the special case of permanent non-stochastic environment, λ_S coincides with λ_1, the asymptotic growth rate. On the one hand, theoretical approximations of λ_S exist that require certain additional assumptions regarding the given set of PPMs, such as the deviations from an average PPM with known temporal auto-covariances of the vital rates (Tuljapurkar, 1990; Caswell, 2001, Section 14.3.6.3). On the other hand, once a rule for the random choice of matrices, such as the *i.i.d.* (*independent, identically distributed* matrices, *ibid.*), the simplest and most popular rule (e.g. Cohen, 1979; Caswell, 2001; Buckley et al., 2010) has been accepted (but see Paniw et al., 2018), the λ_S can be estimated from a series of Monte Carlo simulations of the long enough random sequence. Unfortunately, the assumptions of both theoretical estimates of λ_S and Monte Carlo simulations may often not be accepted in practice. The challenge is therefore to attenuate those assumptions in response to theoretical and practical needs.

A key paper in this regard is by Sanz (2019[SI]). In it, the author considers minimal and maximal vital rates among the given PPMs and obtains four new lower and upper bounds for the stochastic growth rate. These bounds enable calculating the sufficient conditions for population growth or population extinction. The author illustrates those conditions with a hypothetical random environment toggling between "poor" and "rich" situations.

Practical needs dictate rejecting the assumption of modelling stochastic dynamics of a natural population according to i.i.d. Instead, a more realistic approximation is to arrange the simulations in a way that reflect ways in which the natural environment oscillates through time (IPCC, 2020). Since the i.i.d. assumption represents a particular degenerate case of the time-homogeneous Markov chain (Logofet et al., 2020c), an important challenge for future research is to construct a governing Markov chain whose states would correspond to different types of environmental conditions and to calibrate its transition matrix from real data on those conditions.

The metapopulation environments may change randomly as well as that of a single population. In this special issue, Sanz and Bravo de la Parra (2019[SI]) analyse the situation where the migrations between patches and demographic processes proceed at different time scales, the former being k times faster than the latter. Common formalisms for discrete-structured populations suggest that these two kinds of event occur sequentially one after the other, so that the combined effect of both processes can be described by the product of the slow-process matrix times the k^{th} power of the fast-process matrix. In nature, however, the processes may act simultaneously. The authors alternatively included survival into the fast process and approximated its effect during the fast time unit, referring to such an approach as the *re-scaling* of survival to the fast time scale. They adapt their original method of re-scaling to the proposed stochastic models and compared the asymptotic behaviour of the model populations with and without re-scaled survival. The outcome of principal importance is that the corresponding stochastic growth rates may appear qualitatively different for the same vital rate values: while the former predicts exponential growth, the latter indicates extinction. So, the order of events does matter in the MPM formalism for metapopulation dynamics in the stochastic environment; the both versions are ready in theory, and now it is the turn of real migrating populations to "migrate" right here.

Van Daalen and Caswell (2020[SI]) introduce a framework to simultaneously quantify the variance components in demographic vs. environmental stochasticity in life history outcomes using matrix population models. The introduced mathematical machinery allows for the calculation of such effects in a general manner. The authors further illustrate the power of their approach using frailty analyses of fruit flies and explicitly quantifying survival–reproduction trade-offs in a plant study. This approach has the great potential to understand the extent to which demographic stochasticity vs. environmental stochasticity shape population outcomes worldwide.

As regards climate change, Romanov and Masterov (2020[SI]) compare the effects of adult survival and productivity on the persistence of the Steller's sea eagle (*Haliaeetus pelagicus*) populations. The authors simulated the corresponding MPM under several scenarios in a stochastic environment and found that the fecundity alone, varying within broad limits, can lead to population decline in this charismatic species. Although the population growth is less sensitive to the fecundity than to adult survival, the authors argue that the former is more appropriate as a target of conservation management.

2.6. Averaging the PPMs.

An alternative way to assess population viability in stochastic environments from a given set of annual PPMs is to calculate $\lambda_1(\boldsymbol{G})$, the dominant eigenvalue of the average matrix $\boldsymbol{G}$. However, in contrast to nonnegative numbers, it is not trivial to average several given nonnegative matrices unless the average is arithmetic or weighted arithmetic (due to the linearity of matrices as operators in the vector space). Arithmetic average might make sense when the matrices to be averaged represent a *metapopulation* distributed among several habitats at the same moment of time, but it does not make sense when we have a time series of $m \geq 2$ PPMs, from the initial moment of observation ($\boldsymbol{L}_1$) to the final one ($\boldsymbol{L}_m$). If we want the average matrix, $\boldsymbol{G}$, to project population vectors in the exactly same manner as the annual PPMs do, then it has to be their *multiplicative* (or *geometric* by the analogy with numbers) average (Logofet, 2018; Logofet et al., 2018a,b), which suggests extracting the m-th root of the matrix product.

To find a unique nonnegative matrix root is a matter of nontrivial calculations with a serious theory behind (Polity, Popolizio, 2014, 2015). A practical sufficient condition for the unique *principal root*, $\boldsymbol{A}^{1/m}$, to exist for a given matrix $\boldsymbol{A}$ is the lack of negative/zero eigenvalues in the spectrum of $\boldsymbol{A}$ (*ibid.*), and the routine can really succeed in this case. However, what the routine returns will hardly have the same matrix pattern as the PPMs to be averaged – it will rather be positive-valued at best or complex-valued in general, the both cases making no sense as an average PPM that should correspond to the same LCG as the given PPMs to be averaged.

This requirement motivated a new concept of matrix average, namely, the *pattern-geometric* average (Logofet, 2018), or *pattern-multiplicative* average to be pedantic, meaning the same matrix pattern of the average matrix $\boldsymbol{G}$ as of those to be averaged. It is also logical that each element of $\boldsymbol{G}$ lies within the bounds of this element known from the set of given PPMs. Mathematically, finding the pattern-multiplicative average of a given set of annual PPMs reduces to a kind of constrained optimization problem, and this problem was efficiently solved for some practical cases (Logofet, 2018; Logofet et al., 2018a,b), but theoretical issues are still to be investigated in what concerns the uniqueness and accuracy of the optimal solution.

The λ_S and $\lambda_1(\boldsymbol{G})$, these two measures of viability assessment, generate the question of how they correlate quantitatively when applied in real cases, and Dmitrii Logofet has tried to give an answer (2019b[SI]). Two former case studies of alpine Red-Book perennials (*Eritrichium caucasicum* and *Androsace albana*) resulted in respectively two sets of 8 annual PPMs, based on which both λ_S estimates and $\boldsymbol{\lambda}_1(\boldsymbol{G})$ values are reported. These both measures of population viability turn out fairly close each other in both case studies, but *E. caucasicum* λ_S estimates are unambiguously less than $\lambda_1(\boldsymbol{G})$, whereas those *for A. albana* are certainly greater than $\lambda_1(\boldsymbol{G})$. The reason for this difference is not yet known, which gives one more incentive to further developing both the λ_S and $\boldsymbol{\lambda}_1(\boldsymbol{G})$ methods.

2.7. Uses and abuses

As with any research tool that is both highly technical and popular, matrix population models are not free of accidental mis-usage. We are not the first ones to call for caution in the construction, analysis, and interpretation of MPMs (e.g., Caswell 2001). Our hope here is to be the last ones. In this special feature, Nguyen et al. (2019[SI]) and Kendall et al. (2019[SI])-provide invaluable advices on how to use this tool as well as the vast amount of demographic data available in the format of an MPM.

Nguyen et al. (2019[SI]) highlight once again (Doak et al., 2002) the importance of getting the basic life cycle right before parameterising the pertinent matrix population model. There is a wealth of MPMs for species across the Tree of Life (Werner and Caswell, 1977; Caswell 2001; Salguero-Gómez, 2015a,b). However, some of the models, particularly in plants, may not contain all, or the most, key life cycle stages. In the case of some plant species, permanent seed banks do occur, but are often not included due to logistical practicalities of the fieldwork. Nguyen et al.'s work show that their inclusion/exclusion can have very important repercussions for the ways we assess the deterministic and stochastic dynamics of the populations under study. Importantly, the emerging message therein is that the ways in which ignoring cryptic life stages affects our estimates of population performance are not systematically biased in a specific way, rendering generalisations with these key data rather limiting.

Kendall et al. (2019[SI]) present a summary of a subset of published MPMs in animal species. The authors highlight three errors commonly encountered in published MPMs: (1) failing to include survival in the fertility coefficient; (2) introducing a one-year delay in the age at first reproduction; and (3) incorrectly calculating the growth rate out of a stage class. The first two errors are found in 34% and 62%, respectively, of the published studies collected in COMADRE; of the studies where stages may last longer than one time step, 53% constructed the growth rate using inappropriate formulas for estimating the asymptotic population growth rate or its sensitivity to demographic parameters. Kendall et al. review the sources of such errors and reveal their impact on model predictions, using lionfish and American alligator models as examples. These results suggest that further efforts are required to educate biologists on the construction of MPMs, and many studies that are based on MPMs may need to be re-examined; synthetic studies using the COMADRE Database need to be accompanied by careful examination of the underlying knowledge and data. Luckily, the researchers curating large demographic datasets are well aware of these issues, and are expediently working together with the demographic community to help the users of big data overcome these challenges. The solutions are already discussed in the response to Kendall et al.'s paper in a complementary response by Che-Castaldo et al. (2020).

2.8. How many bases to classify individuals?

What is mentioned above concerns mostly what to do with ready MPMs. But to get them ready, given some knowledge of/data on a particular population is not a self-evident, nor a simple task. Historically, the ‘certain population mathematics’ adopted highly rigid postulates about the population *age* structure and proposed a highly specific pattern of the *Leslie* matrix (Leslie, 1945). Then, the postulates were attenuated and the pattern expanded to the *stage* structure (Lefkovitch, 1965) and to the *generalised stage* structure that suggested a classification of individuals by any observable/measurable trait such as size, weight, etc. (Caswell, 2001). Soon, a single trait became insufficient to practical demands where data on two traits, such as *age* and developmental *stage* (Logofet et al., 2006, 2014, 2016; Caswell, Salguero-Gómez, 2013), *stage* and *space* (Hunter, Caswell, 2005), or *stage* and *genotype* (de Vries et al., 2019[SI]), were available, and the model formalism was expanded to block-structured PPMs (*ibid.*; Caswell, 2012; more samples of pairs in Roth and Caswell, 2016). The block-structured PPMs appear also in the single-trait metapopulation model with migrations among the local habitats (Sanz, Bravo de la Parra, 2019[SI]); here the issue of time scale difference between demographic and migration processes needs further investigation.

Today, we witness an attempt to formalise an MPM for multi-trait population data, a 3-trait case in Coste and Pavard (2020[SI]). The PPM transforms now to a 3D array of vital rates, which is called a *tensor* in mathematics. Authors have not yet dared to launch this term to the field of MPMs, but it will perhaps become common for the future generations of matrix modellers. Note however that a *hyperstate* matrix model, a competing term, has already been launched by Roth and Caswell (2016), with a general formalism for many bases.

3. Concluding remarks

The diversity of topics presented above are sufficient to recognize the MPM as a powerful “multi-tool” for modeling the population and community dynamics. However, the range of topics covered in this editorial does not represent the wide spectrum of MPM applications in ecology, evolution, and conservation science. Below we discuss two (of many potential) areas of further enquiry where MPMs have much to offer to researchers.

3.1. Potential-growth indicators

Among the current challenges of MPMs, studying their mathematical foundations is a key one. In particular, the most commonly used outcome of an MPM is $\lambda_1(\boldsymbol{L})$, the dominant eigenvalue of $\boldsymbol{L}$, its PPM, i.e., the asymptotic population growth rate, which is interpreted as a measure of population adaptation that is local in space and time (McGraw and Caswell, 1996). Matrix modellers are so focused on λ_1 that they frequently forget its subscript 1 in the notation and what the subscript means itself. In fact, the subscript originated from the standard of nonnegative matrix theory to order all the eigenvalues of a given $\boldsymbol{L}$ by their decreasing absolute values, so that the dominant eigenvalue (which is always positive by the Perron–Frobenius theorem) becomes λ_1. However, recent findings have revealed $\lambda_2(\boldsymbol{L})$ to be important, too. Specifically, if λ_2 is positive and less than 1, then a simple function of matrix elements, $R_1(\boldsymbol{L}) = 1 - \det(\boldsymbol{I} - \boldsymbol{L})$, can serve as a *potential-growth indicator* (hereafter PGI). In other words, under these conditions, the PGI always locates at the same side of $\lambda = 1$ as $\lambda_1(\boldsymbol{L})$ does (Protasov, Logofet, 2014; Logofet, 2019a). There are certain merits of *indication* prior to the calculation of λ_1; in particular, $R_1(\boldsymbol{L})$ has turned out useful in solving calibration problems under data uncertainty (Logofet, 2013).

Another, more senior, PGI instance is the well-known *net reproductive rate* $R_0(\boldsymbol{L}) = \rho(\boldsymbol{F}[\boldsymbol{I} - \boldsymbol{T}]^{-1})$, where $\rho(\ldots)$ denotes the *spectral radius* (the largest absolute value of matrix eigenvalues) and $\boldsymbol{L} = \boldsymbol{T} + \boldsymbol{F}$, the sum of its transition and fertility parts (Cushing, Yicang, 1994; Caswell, 2001). However, calculating the spectral radius is, in general, much more difficult than the determinant in $R_1(\boldsymbol{L})$. The problem with $R_1(\boldsymbol{L})$ is that its PGI property is proved for a less general class of PPM patterns than $R_0(\boldsymbol{L})$ is valid for.

A recent expansion of the classical Perron–Frobenius theory, namely, the theory of *rank-1 corrections* of nonnegative matrices (Protasov, Logofet, 2014), has enabled proving the PGI property of $R_1(\boldsymbol{L})$ when the rank of fertility part $\boldsymbol{F}$ equals 1. For instance, when $\boldsymbol{F}$ has only one nonzero row or column of fertility rates meaning a single recruiting or a single generative stage in the LCG, respectively. Can this wide, yet not universal, class of PPMs be expanded? Some particular examples give a positive answer, but theoretical justification is still a target for future efforts.

3.2. Integer-valued formalism

The ‘identified individuals’, a standard for stage-structured demographic models (Caswell, 2001, p. 134), can often provide the calibration of PPMs in a unique way. Since all the events of transitions along the LCG links are inherent in the data, the transition rates are just the frequencies of the corresponding events, hence the rates are certain *rational* numbers according to the arithmetic way of calculation. Naturally, the number of recruited individuals is always integer. However, the tradition is to treat the basic calibration equation of the MPM as an equation in *real* numbers in spite the rational-valued PPM does project $\boldsymbol{x}(t)$, an integer-valued population vector, into the integer-valued $\boldsymbol{x}(t + 1)$.

The tradition to deal with real numbers did make certain sense in the last century, when computers had only been dealing with binary representations of all numbers including the machine approximations of the irrational roots of the characteristic polynomials. However, modern systems of mathematical software, such as R or MatLab, with its Symbolic Algebra Toolbox (Mathworks, 2020), enable algebraic manipulations with the rational-/integer-valued numbers as symbols, thus avoiding the machine round-off errors and providing for the absolute (logical) accuracy of calculations. Also, the existence of strong computational support enables us to validate each step of the calibration or manipulation in other related problems, e.g., backward prediction (Clutton-Brock and Sheldon, 2010; Ehrlén et al., 2016; Nater et al., 2018; Logofet et al., 2020a) or uncertainties in the dynamics of cryptic stages (Paniw et al., 2017; Nguyen et al., 2019[SI]; Logofet et al., 2020b[SI]). The calibration equation or other pertinent expressions hold true, with the absolute accuracy, for the integer- or rational-valued parameters, unlike the approximate real values to be found from the classical least-squares procedures of curve fitting. This approach helps solve at least some of the 'persistent problems in the construction of matrix population models' and we encourage matrix modellers to incorporate them in their demographic enterprises.

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