



Trait level analysis of multitrait population projection matrices



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HIGHLIGHTS

- A novel method for building multitrait population projection matrices is proposed.
- Asymptotic properties of multitrait matrices are explored.
- A new evolutionary demography tool, the trait level analysis, is proposed.
- Trait level analysis sheds light on effect of traits on multitrait dynamics.
- A parity–fertility–fecundity model reveals the potential of trait level analysis.

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ABSTRACT

In most matrix population projection models, individuals are characterized according to, usually, one or two traits such as age, stage, size or location. A broad theory of multitrait population projection matrices (MPPMs) incorporating larger number of traits was long held back by time and space computational complexity issues. As a consequence, no study has yet focused on the influence of the structure of traits describing a life-cycle on population dynamics and life-history evolution.

We present here a novel vector-based MPPM building methodology that allows to computationally-efficiently model populations characterized by numerous traits with large distributions, and extend sensitivity analyses for these models. We then present a new method, the *trait level analysis* consisting in *folding* an MPPM on any of its traits to create a matrix with alternative trait structure (the number of traits and their characteristics) but similar asymptotic properties. Adding or removing one or several traits to/from the MPPM and analyzing the resulting changes in spectral properties, allows investigating the influence of the trait structure on the evolution of traits.

We illustrate this by modeling a 3-trait (age, parity and fecundity) population designed to investigate the implications of parity–fertility trade-offs in a context of fecundity heterogeneity in humans. The *trait level analysis*, comparing models of the same population differing in trait structures, demonstrates that fertility selection gradients differ between cases with or without parity–fertility trade-offs. Moreover it shows that age-specific fertility has seemingly very different evolutionary significance depending on whether heterogeneity is accounted for. This is because trade-offs can vary strongly in strength and even direction depending on the trait structure used to model the population.

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1. Introduction

In early population projection models – those mathematical models used for the study of the dynamics and structure of populations projected over time – individuals were grouped according to one single trait (or *i*-state). This single trait was generally the age of the individuals (Euler, 1760; Lambert, 1772; Sharpe and Lotka, 1911). This was also the case for the original matrix models

developed by Lewis (1942) and Leslie (1945). As ecologists started borrowing this powerful tool from classical demographers for species conservation and life-history evolution, one-trait models incorporating other traits than age, such as size or developmental stage were considered (Lefkovich, 1965; Usher, 1969). Just as ecologists' interest in matrix population models prompted their development, evolutionary demographers' growing focus provided tools to understand the evolutionary processes at play. Demographic sensitivity analysis instruments (e.g., first and second level parameter sensitivities, life history graph and loop analysis) were early made available for one-trait models (see Caswell, 1978; de Kroon et al., 1986; Goodman, 1971).

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However, additional traits are often required in order to accurately study the dynamics of a population. In the literature so far, most multitrait population projection matrices (MPPM¹), sometimes called metapopulation (Hanski, 1999), multidimensional (Van Imhoff, 1992), multistate (Rogers, 1980), multi-regional (Rogers, 1966) or multisite (Lebreton, 1996) models, actually incorporate two traits. Rogers (1966) was the first to add a second dimension (location) to a one-trait (stage) matrix model and many important articles on stage-and-location modeling followed (e.g., Le Bras, 1970; Rogers, 1980, 1974). In a seminal paper, Goodman (1969) then introduced matrix models for both age-and-sex and age-and-parity structured populations. Such templates were later extended to model populations characterized by age and stage (e.g., Law, 1983). In parallel, perturbation and sensitivity analysis tools were extended from one-trait to multitrait models (Caswell, 2012; Willekens, 1977). Those instruments provide information on the impact on population dynamics of vital rates and other parameters. Other tools are however needed to investigate the behavior and properties of MPPMs. A one-trait model and a two-trait model of the same population indeed do not merely differ in level of scrutiny; they will also exhibit different population dynamics. The addition of a trait into a model therefore raises new questions, as for example, the extent to which this addition modifies the sensitivities of fitness to other traits. An analysis at the trait level is therefore required, and has yet to be developed.

Generalization to any number of trait was for a long time reined in by a lack of generalized building methodology – such models were mostly built, transition by transition, as concatenations of *ad-hoc* block matrices (e.g., Goodman, 1969; Le Bras, 1970; Lebreton, 2005; Rogers, 1966) – and by their space/time computational complexity (MPPMs increase in size and complexity with the number of traits). In 1969, Goodman hints at a three-trait model but does not build it (1969). And it would actually take another forty years before n -trait models (with $n > 2$) make their appearance. This emergence was due to efforts, first, from ecologists targeting a particular question (e.g., the mother hypothesis for Pavard and Branger, 2012; their made-to-measure model preventing over-size by only using biologically realistic combinations of traits as matrix entries). Second, from theorists: very recently, Roth and Caswell (2016) extended to any number of traits, the construction of MPPMs, which they denote as “hyperstate” matrices, via the vec-permutation approach previously developed for 2-trait models (Caswell and Salguero-Gómez, 2013; Caswell and Shyu, 2012; Hunter and Caswell, 2005). This approach formalizes the construction of an MPPM via the product of intermediary matrices, each representing the transitions between values taken by one of the traits when all others are fixed (thus decomposing an MPPM into a succession of independent processes).

Progress in the field of multitrait matrices is therefore at two levels. First, the growing focus on methodologies for building multitrait matrices has to be pursued. Computationally efficient methods are especially required to relax the compromise between number of traits and ability to build, analyze and perform perturbation analyses. Second, a theory of multitrait projection models is required to understand the impact of the traits themselves on population dynamics and life-history traits evolution. These developments are crucial for addressing emerging questions in evolutionary demography.

A recent developing field, for example, is that of *memory* models. Classical projection matrices – behaving like Markov chains – infer the entire future behavior of organisms from their current state. The fate of most natural organisms depends, however, on their whole life history trajectory (e.g., later life survival may be influenced by reproduction trajectories (Bell, 1980), or early

life factors (Lemaître et al., 2015)). Adding traits is a solution to keep track of individual past events. This is the case, for instance, for models incorporating family structures where an individual's survival and reproduction depend on cooperation and/or competition relationships with its surviving kin. In such models, kin survival status and reproduction has to be recorded over time. For example, in order to understand the impact of maternal care on population dynamics, Pavard and Branger (2012) developed a one-sex projection model in which maternal and grand maternal survival status (along with age) impact juveniles survival rates. A woman's survival depends on her age and on the aliveness of her own mother, itself a function of the mother's age. This implies the use of three traits: age of individual, orphanhood, age of mother. Another example is the parity–fertility trade-off (also called cost of reproduction in ecology) whereby an individual fecundity or survival at a given age is compromised by its past reproductive effort (e.g., Boonekamp et al., 2014). As they develop, *memory* models will be increasingly demanding with regards to the number of traits.

In this context, individual heterogeneity, “*the variation observed in a trait among individuals*” (Plard et al., 2012) is more and more considered in population models (Vindenes, 2010). This heterogeneity can be split into dynamic observable heterogeneity and constant heterogeneity that is fixed-at-birth and cannot be observed directly, but can potentially be deduced from its impact on vital rates. The latter component was first called frailty in the context of survival models developed by Vaupel (1979) and collaborators. Models have been developed that implement both parts of heterogeneity (see the continuous time vitality-frailty model by Li and Anderson (2009)) and the dynamics of each component can be studied and its relative contribution to total heterogeneity analyzed (Caswell and Kluge, 2015; Tuljapurkar and Steiner, 2010). Multitrait models would allow for the incorporation of individual heterogeneity: accounting for observable dynamic heterogeneity component via the addition of (stage, spatial, social, etc.) traits and accounting for constant unobservable heterogeneity via the addition of fixed heterogeneity classes.

In this article, we first present an MPPM building methodology which is computational-efficiency-driven and alternative to the transition by transition building method and to the vec-permutation method of Roth and Caswell (2016). As in any MPPM, in our model, individuals are classified by multiple traits. There is no real limitation with respect to the nature of these traits: they can be categorical, discrete or discretized, observable (a measurable parameter) or unobservable (e.g., hidden heterogeneity). Those traits can be constant for an individual (inherited or acquired at birth) or varying throughout its life. In order to manage MPPMs increasing sizes and complexities with the number of traits, the matrix building methodology we develop here is vector-based and relies on sparse matrices (matrices in which most of the elements are zero). Because no loop is involved in the matrix building process – by contrast with the two alternative methods: the transition-by-transition and the vec-permutation approaches – the time computational cost associated with such an object is contained. The use of sparse matrices, for its part, drastically reduces space and thus time complexities. Through a sequential process, the method generates, in turns, (1) vital rates for each combination of traits, (2) output combinations of traits and corresponding distributions for each vital rate, and finally (3) all transitions between every pair of states. After a brief discussion of the existence and unicity of ergodic growth rates for MPPMs, we extend the computation methods of classical demographic measures, and most importantly, sensitivity analyses to our vector-based MPPM construction methodology.

We then develop a new type of evolutionary demography analysis, the *trait level analysis*, allowing the evaluation of the impact

¹ MPPM = multitrait population projection matrix.

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