

## Editorial

## Fifty years of Theoretical Population Biology

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## ABSTRACT

The year 2020 marks the 50th anniversary of *Theoretical Population Biology*. This special issue examines the past and continuing contributions of the journal. We identify some of the most important developments that have taken place in the pages of *TPB*, connecting them to current research and to the numerous forms of significance achieved by theory in population biology.

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## 1. Introduction

When *TPB* published its first articles in 1970, it created a new venue for mathematical papers contributing to demography, ecology, epidemiology, evolution, and genetics. The founding of the journal coincided with increasing interest in mathematical contributions to biology during the 1960s; the same era saw the beginnings of other journals at this intersection (*Journal of Theoretical Biology*, 1961; *Mathematical Biosciences*, 1967; *Journal of Mathematical Biology*, 1974).

The creation of *TPB* was also a reaction to the challenge of reporting theory contributions in the main journals of its constituent biological fields (Feldman, 2013). The period leading up to the journal's founding had seen significant tension between maturing mathematical perspectives in multiple subfields of population biology and non-mathematical traditions that, then and now, produce most of the research in the relevant subfields. Mathematicians such as Sam Karlin and Pat Moran were interested in contributing to discourse among biologists, but the mathematical emphasis in their work exceeded that of the more intuitive style of theory emerging within biology itself (Felsenstein, 1989; Grodwohl, 2017); even leading theoretical researchers anchored in the biological disciplines had difficulty convincing reviewers of the interest of their theory work (Fretwell, 1975). By the late 1960s, the mathematical traditions in population biology had grown strong enough to support their own forum for publication.

As evidenced by the founding editorial board, which included many leading figures of the time (Fig. 1), *TPB* was centrally relevant in its subfields from the beginning. The journal immediately attracted fundamental and significant contributions. The first issue (Fig. 2) contained an influential study by Robert MacArthur of “species packing,” the question of how many competing species can be “packed” into an environment (MacArthur, 1970; Chesson,

2020), and an analysis by Karlin and Marc Feldman of surprising dynamics in a relatively simple population-genetic dynamical system with two loci (Karlin and Feldman, 1970; Bürger, 2020).

A key insight in the new journal's scope was a recognition that despite a focus on substantially different domains, across the journal's core areas of demography, ecology, epidemiology, evolution, and genetics, mathematical theory occupies a similar position in relation to the biology. The theory is motivated by the biological problems, and the goal of the mathematics is ultimately to contribute to biological advances. Thus, although contributions in the different subfields follow different directions, the role of the mathematics is shared among them. This sharing extends to the methods used in the modeling: ideas such as identification and analysis of equilibria (Bürger, 2020; Pacala, 2020), investigation of mechanistic dynamics (Andreasen and Gog, 2020; Kisdi, 2020), inversions of perspective (Schreiber and Křivan, 2020; Steel, 2020; Wakeley, 2020), network and spatial methods (Degnan, 2020; Pacala, 2020), optimality arguments (Mangel, 2020; Van Cleve, 2020), and conversions of heterogeneous scenarios into “effectively” homogeneous ones (Lutscher, 2020; Steiner, 2020; Wakeley, 2020) are often shared among subfields. The mathematical techniques themselves are borrowed from one area to another, such as in the use of Fisher's wave of advance from genetics (Feldman, 2020) to examine ecological invasions (Lutscher, 2020), and research questions often sit between subfields, such as in studies of kinship structures and their demographic and genetic consequences (Edge and Coop, 2020; Pavard and Coste, 2020). The journal provides a home for these interactions and hybridizations among different areas of theory in population biology.

Since the early years of the journal, technological changes have occurred both with the development of new forms of data (Wakeley, 2020) and with advancing computational capabilities enabling analyses of themes such as spatially explicit models (Pacala, 2020) and algorithmic techniques such as dynamic programming (Mangel, 2020). In the last two decades, the journal has reported special issues on emerging and mature branches of

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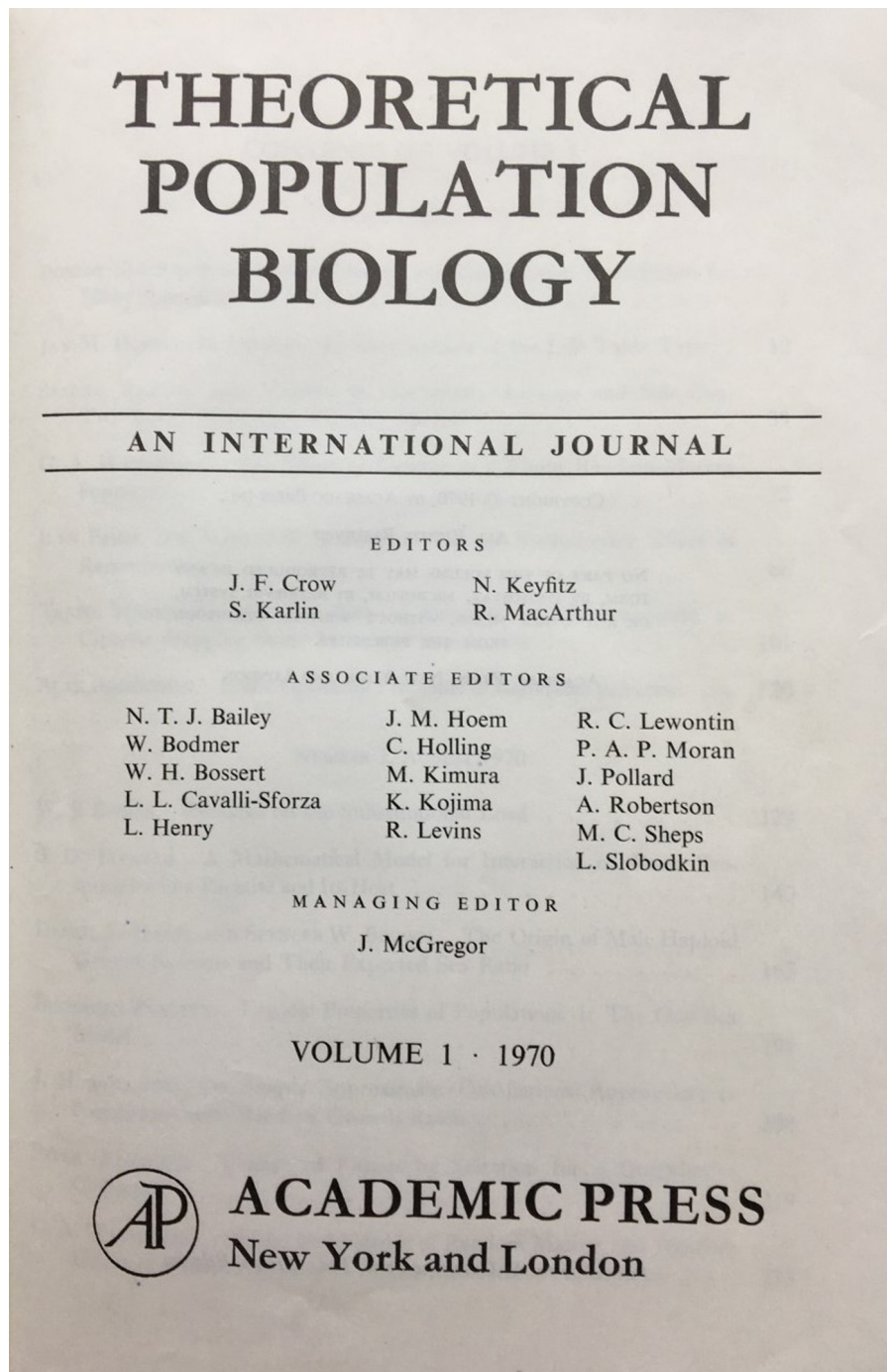


Fig. 1. Editorial board from the first volume of *TPB*.

theory, some in areas only lightly represented in *TPB* outside the special issue (Table 1). Nevertheless, the core approach of using population models, and many of the phenomena of most frequent interest – competition, natural selection, population dynamics, population growth, and variable environments, to name a few – have persisted as long-term central themes of the journal's scope (Rosenberg, 2013).

The decades since the founding of *TPB* have seen increased integration of theory into the journal's subfields (Scheiner, 2013; Marquet et al., 2014; Servedio et al., 2014). The forum provided by the journal for sustaining a dedicated community of theorists has surely contributed to this development. In this special issue, members of the editorial board and other leading theorists

comment on research areas advanced largely in the pages of *TPB* and on major papers in the history of *TPB* that have continuing salience. The special issue also features research contributions on topics that showcase both connections to long-standing topics of interest for the journal and new directions. Together, the commentaries and research articles highlight the contributions of the journal and the achievements of theory in population biology more generally.

## 2. Two iconic papers

In assessing the key contributions of the journal over the past five decades, two papers stand out for having reached an

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Fig. 2. Table of contents of the first two issues of *TPB*.

iconic status: [Ewens \(1972\)](#) and [Charnov \(1976\)](#). These two early studies, representing quite different research areas, highlight the impact that emerged for the journal quickly after its founding. Both studies produced a central easily-stated mathematical result. In both cases, that result, based on a relatively minimal set of assumptions, became a baseline for testing for the importance of various additional factors in data, and catalyzed theory of deepening complexity. Both papers have contributed to significant bodies of work, with meaning well beyond the subfields of population biology in which the results originated. And both, as we will see, are “ubiquitous” ([Crane, 2016a](#)), making unexpected appearances in the life of a theoretical population biologist.

### 2.1. [Charnov \(1976\)](#): the Marginal Value Theorem

In a seminal study in foraging theory, [Charnov \(1976\)](#) examined the behavior of a predator foraging in a patchy habitat. For a predator optimizing energy intake in a habitat containing a heterogeneous distribution of prey across patches, what rules are predicted to guide the path of the predator through the habitat? A predator in a patch with abundant prey decreases the abundance in that patch; yet moving to a different patch does not necessarily promise similar prey abundance. In a simple model, Charnov's Marginal Value Theorem states that an optimally foraging predator is expected to leave a patch when the capture rate for the patch decreases to the mean capture rate across the entire habitat.

**Table 1**  
TPB special issues.

Topic	Date
William Hamilton: evolution of social and behavioral traits	February 2001
Linkage and association analysis	November 2001
Evolution of genome structures	June 2002
Use of DNA and genetic markers for forensics and population studies	May 2003
Understanding the role of environmental variation in population and community dynamics	November 2003
Demography in the 21st century	June 2004
John Maynard Smith	July 2005
Evolutionarily-stable-strategy theory	May 2006
Sam Karlin	June 2009
Structured population models: construction, analysis, inference	December 2012
Coalescent theory	August 2013
Evolution of learning	February 2014
New developments in relatedness and relationship estimation	February 2016
Paul Joyce	July 2018
Marc Feldman's 75th birthday	October 2019
50th anniversary of TPB	June 2020

In a reflection on his paper that appeared in the Citation Classics series, Charnov (1989) cited as major influences on its development the work of Emlen (1966) and MacArthur and Pianka (1966) that promoted the treatment of foraging behavior with an optimality perspective from economics. These earlier works had considered food preferences rather than a spatial perspective, and the achievement of a simple result in the work of Charnov (1976) emerged from a focus only on the spatial distribution of the total energy gained from the prey, ignoring preferences for specific prey species.

Charnov's work gives a straightforward theorem that has been foundational in optimal foraging theory (Mangel, 2020), one of the largest recognizably distinct branches of theory in ecology (Marquet et al., 2014). The simplicity of the theorem has enabled numerous empirical tests to determine if predators follow it. Because the model that gives rise to the theorem is minimal in the sense that it does not incorporate other factors affecting movement of the predator – such as predation risk for the predator itself, potential for mating opportunities, or dependence on the predator's current internal state – it provided a sort of fundamental theorem of foraging, a baseline from which it becomes possible to examine the effects of other factors on foraging behavior (Nonacs, 2001).

Beyond its influence in ecology, the analogy of foraging with other behaviors of searching in uncertain conditions has generated connections between the Marginal Value Theorem and scenarios in cognitive science, computer science, economics, and information science that involve tradeoffs between exploring a “habitat” and exploiting the resource of a patch (Pirolli, 2007; Hills et al., 2015). Such tradeoff scenarios arise with remarkable frequency. For example, I found myself thinking about the Marginal Value Theorem during a recent episode of repeated laptop thefts from motor vehicles on the Stanford University campus. The campus police reported that most thefts had taken place in a single “patch” of parking lots over a period of several months. I followed the story, as I often parked in the targeted region. The situation was puzzling: with a high correlation in parking locations for individual university employees from day to day, one would expect that thieves would quickly predate enough laptops in the targeted patch that employees would be vigilant about not leaving them in their cars. The “capture rate” would drop lower than elsewhere on campus, and the Marginal Value Theorem would predict that the thieves would shift to other patches. While walking from the parking lot to my lab, each time I noticed a parked police car, I wondered why, even with the increased “predation risk” thieves would experience from the police presence, thefts continued to occur in this rather than another patch.

The solution revealed itself when the campus police provided a more precise description of the theft locations. This report clarified that the affected patch had a high concentration of visitor parking—a region with continual refreshment of the prey supply to a level evidently above the campus mean. Hence, the behavior did indeed make sense in the framework of the Marginal Value Theorem. It was little surprise to then discover in the literature that the Marginal Value Theorem had also been used in analyzing the spatial distribution of crime (Johnson, 2014).

## 2.2. Ewens (1972): the Ewens Sampling Formula

The paper of Ewens (1972) was a response to the introduction of the neutral theory of molecular evolution, which proposed that most protein allelic variants were selectively neutral (Kimura, 1968; King and Jukes, 1969). Assuming that alleles were neutral, what distribution of allele frequencies would be expected in a population? Ewens, in his own Citation Classics reflection (Ewens, 1989), wrote that one expectation was that allele frequencies would be generally similar due to the lack of selection preference for any of them (also see the Supplementary Text). However, this claim disregarded the fact that alleles arose at different times, so that frequencies would likely differ due to these different times of origin.

Kimura & Crow had developed the infinitely-many-alleles model, in which each mutation generates a novel allele (Kimura and Crow, 1964), providing a basis for examining the question: under the infinitely-many-alleles model, what predictions did an assumption of neutral evolution make about the properties of the allele frequency distribution of a sample? Using the model, Ewens (1972), and the accompanying formal addendum by Karlin and McGregor (1972), derived the joint distribution for the allelic counts in a sample of size  $n$ . Consider the set of all possible vectors for the allelic counts  $(C_1, C_2, \dots, C_n)$ , with  $C_1, C_2, \dots, C_n \geq 0$  and  $C_1 + 2C_2 + \dots + nC_n = n$ . Each vector tabulates the number of alleles of frequency  $i$  for each  $i$  from 1 to  $n$ , so that  $C_i$  gives the number of alleles of frequency  $i$ . The probability is found, as a function of a single composite parameter  $\theta$  incorporating mutation rate and population size, that the allele frequency distribution equals  $(c_1, c_2, \dots, c_n)$ . An interesting feature of the resulting distribution – the Ewens Sampling Formula – is that conditional on the total number of alleles  $K = C_1 + C_2 + \dots + C_n$ , the probability distribution of the vector of counts is independent of the parameter  $\theta$ .

The formula has had diverse applications in population genetics well beyond its motivation in the original neutral theory – as the cornerstone of one of the classic models for predicting properties of population-genetic samples, the infinitely-many-alleles model; in characterizing and testing neutrality from allele

frequency distributions (Watterson, 1977; Slatkin, 1994); and in its use of genealogical arguments that contributed to the development of coalescent theory (Wakeley, 2020). It finds applications in efforts to examine sampling distributions of species in the neutral theory of biodiversity that are analogous to the theories of neutral variation in population genetics (Hubbell, 2001). It also represents a leading example of a case in which a contribution to theory in biology has generated contributions to mathematics that are entirely separate from the biological context (Cohen, 2004). A recent review, entitled “The ubiquitous Ewens Sampling Formula,” described connections in many areas of mathematics and statistics, including algebra, Bayesian statistics, combinatorics, number theory, and stochastic processes (Crane, 2016a).

I had my own experience with this pervasive appearance of the Ewens Sampling Formula during a group retreat of 50 or so members of the Stanford University ecology and evolution community. Early one weekend morning at the field station of the university’s biological preserve, the graduate students running the event conducted an icebreaker game, in which each participant wrote a personal fact on a card, in most cases related to their work in population biology. The cards were collected, shuffled, and redistributed, and each person was tasked with finding the person whose card they had received. Once everyone had located their target, the organizer reconvened the group, reading the card he had drawn and naming its writer, who in turn named the writer of the card she had drawn, and so on.

Evidently expecting that the game would proceed through all 50 cards in a single chain back to the card contributed by the organizer, the group was surprised when after a few cards, someone named the organizer, and it was unclear whose turn would be next. As the organizer restarted the game with a random person who had not yet read their card, I wondered how many such terminations would be expected in a random assignment of the cards. Because the procedure for assigning cards to their authors amounted to drawing a random permutation of numbers 1 through 50, it was quickly clear that the number of terminations would equal the number of cycles in a random permutation of  $n$  objects.

With a quick search, I found that the joint distribution of the numbers of cycles of length  $(1, 2, \dots, n)$  that partition a random permutation follows the Ewens Sampling Formula with  $\theta = 1$  (Arratia et al., 2003, p. 3): the joint distribution of the numbers of distinct alleles of frequencies  $(1, 2, \dots, n)$  under the infinitely-many-alleles model with  $\theta = 1$ . The total number of cycles has the same distribution as the number of distinct alleles under the Ewens sampling theory (Arratia et al., 2003, p. 10), and the mean number of cycles follows the harmonic number  $1 + 1/2 + 1/3 + \dots + 1/n$  that gives the mean number of distinct alleles under the infinitely-many-alleles model with  $\theta = 1$  (approximately 4.5 for  $n = 50$ ). According to Crane (2016b), “Wherever random partitions appear, with few exceptions, so does Ewens’s sampling formula.”

Two years after listening to a variety of ecology students’ personal facts about mishaps in remote field sites, and one theory student’s social media success after dressing up as a model – a statistical model – this unexpected example of the ubiquitous appearance of the Ewens Sampling Formula remains the most memorable fact from the icebreaker game. The trajectory of an activity among population biologists followed a mathematical formula ultimately derived from population biology itself.

### 3. Highlighted articles from 50 years of the journal

Including the papers of Ewens (1972) and Charnov (1976), and treating one group of three papers as a unit, 15 significant papers from the five decades of *TPB* are covered in this special

issue in retrospective commentaries (Table 2), as are five research areas. For some of the papers and research areas, suggestions were received from the editorial board, often accompanied by an interest from a board member in writing the commentary. For others, matches were sought between lists of candidate papers and research areas and lists of potential contributors.

With a large number of papers from which to choose, the specific choice of papers that we have selected seeks to represent a diversity of time periods, ranging from the very first paper in the journal, volume 1 page 1 by Robert MacArthur, to a study as recent as 2013. The papers also represent a diversity of techniques and research subfields. Together, the commentaries are revealing not only about their associated subfields, but about the way in which theory is often prescient or underappreciated, and about the various ways in which theory research can generate significant impact.

#### 3.1. Prescience

Several of the commentators describe papers as being ahead of their time, in that the theory represented a major jump, sometimes far preceding any relevant work with data, or even far predating notable additional works of theory. For example, Mangel (2020) reports on Iwasa et al. (1984) that their stochastic dynamic programming approach to incorporating physiological state while foraging opened a new direction in foraging theory. Whereas work such as that of Charnov (1976) did not consider states such as hunger or fear that affect foraging, Iwasa et al. (1984) devised a way of doing so, using a parasitoid system that Mangel (2020) describes as a brilliant choice. Andreasen and Gog (2020) comment that the change in perspective introduced by Pease (1987) for modeling effects of evolution of the influenza pathogen and not only turnover in the host population has become so embedded in the subfield of influenza epidemiology that modern authors have no need to refer to the origin of the idea.

Another example of prescience and *TPB* is provided by early efforts on the stepwise mutation model discussed by Wakeley (2020). Ohta and Kimura (1973) had developed a model for mutation in which discrete allelic classes are ordered and mutations change the allele by one step up or down. In this model, introduced during a time at which protein alleles were assayed by the extent of their movement through a gel, it was assumed that movement in the gel was connected to electric charge of the protein. Mutations represented quantized discrete changes in electric charge for protein molecules, so that over time, alleles would mutate by units of  $+1$  or  $-1$  in charge. The model found some of its most complete expression in the *TPB* work of Moran (1975), with results such as the expectation under the model of the variance of the size distribution of alleles.

By the end of the 1970s, the stepwise mutation model, despite its elegance, was abandoned as not relevant to protein variants, which did not appear to mutate in the manner it assumed. After a decade or more of dormancy, with the discovery of widespread short-tandem-repeat loci in the 1990s, however, the model reappeared as ideally suited for a new form of genetic variation in which alleles mutate by an increase or decrease in their numbers of copies of a repeated DNA segment. Though the significance of this development does not approach the importance of the rediscovery of Mendel in 1900, the episode has the same flavor of giving lost work its due. The rediscovered stepwise mutation model of the 1970s has remained a central model for theoretical studies of DNA repeats, including in several papers in *TPB* (Kimmel and Chakraborty, 1996; Pritchard and Feldman, 1996; Wiehe, 1998; Campbell, 2007; Szpiech and Rosenberg, 2011).

One of the best examples of a prescient paper featured in this anniversary issue is described by Edge and Coop (2020). The

**Table 2**Fifteen significant articles from 50 years of *TPB*, including one group of three articles treated as a unit.

Article
R MacArthur (1:1-11, 1970) Species packing and competitive equilibrium for many species.
WJ Ewens (3:87-112, 1972) The sampling theory of selectively neutral alleles.
LA Goodman, N Keyfitz, TW Pullum (5:1-27, 1974) Family formation and the frequency of various kinship relationships.
EL Charnov (9:129-136, 1976) Optimal foraging, the marginal value theorem.
RD Holt (12:197-229, 1977) Predation, apparent competition, and the structure of prey communities.
J Haigh (14:251-267, 1978) The accumulation of deleterious genes in a population—Muller's ratchet.
SD Tuljapurkar, SH Orzack (18:314-342, 1980) Population dynamics in variable environments I. Long-run growth rates and extinction; SD Tuljapurkar (21:114-140, 1982) Population dynamics in variable environments II. Correlated environments, sensitivity analysis and dynamics; SD Tuljapurkar (21:141-165, 1982) Population dynamics in variable environments. III. Evolutionary dynamics of <i>r</i> -selection.
KP Donnelly (23:34-63, 1983) The probability that related individuals share some section of genome identical by descent.
Y Iwasa, Y Suzuki, H Matsuda (26:205-227, 1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number.
N Shigesada, K Kawasaki, E Teramoto (30:143-160, 1986) Traveling periodic waves in heterogeneous environments.
CM Pease (31:422-452, 1987) An evolutionary epidemiological mechanism, with applications to type A influenza.
R Durrett, S Levin (46:363-394, 1994) The importance of being discrete (and spatial).
LW Ance (58:307-319, 2000) Undermining the Baldwin expediting effect: does phenotypic plasticity accelerate evolution?
C Meng, LS Kubatko (75:35-45, 2009) Detecting hybrid speciation in the presence of incomplete lineage sorting using gene tree incongruence: a model.
A Lambert, T Stadler (90:113-128, 2013) Birth-death models and coalescent point processes: the shape and probability of reconstructed phylogenies.

approach of [Donnelly \(1983\)](#) to evaluate the probability that two genomes share segments identically by descent as a function of their level of relatedness was developed decades before it became possible to regularly perform such calculations with data. So far ahead of its time was this work that no significant steps were taken toward the kind of empirical identity-by-descent calculations it presaged until well into the 1990s, and only in the last decade have such calculations become a regular feature of the landscape of the study of relatedness.

An example from an addendum to the commentary of [Edge and Coop \(2020\)](#) written by Kevin Donnelly sharpens the most recent dramatic consequence of his work. Donnelly, of Scottish ancestry, comments on the use of literary figures in his 1983 paper to illustrate the computations. The threshold number of generations for likely genomic sharing between a pair of relatives lies between 10 and 20 generations. He relates the anecdote that his Ph.D. advisor, the English geneticist Elizabeth Thompson, advised him to include “the Scottish poet” in reference to Robert Burns, a shockingly unnecessary addendum to a Scot; thus, the 1983 paper comments on the possibility that modern descendants of “the Scottish poet Robert Burns” or “the English playwright William Shakespeare” share segments of genome with their celebrated ancestors. This comparison informs the striking success of long-range forensic search, in which triangulation of a genome among distant relatives by identity-by-descent sharing is used to identify the source of a crime-scene DNA sample. Whereas Shakespeare lived too far back in time to have a high probability of sharing genetic material with one of his living descendants chosen at random, many of the distant relatives used in high-profile criminal cases have been related to the suspects at a level comparable to that of the relationship of living descendants to their famed Scottish poet ancestor.

### 3.2. Underappreciation

Accompanying prescience is frequent underappreciation of the work, at least initially. The tortuous path to publication for [Charnov \(1976\)](#) illustrates the problem. The Marginal Value Theorem first appeared in an unpublished book manuscript of [Charnov and Orians \(1973\)](#), based on Charnov's Ph.D. dissertation work at the University of Washington ([Charnov, 1973](#)). According to Eric Charnov (pers. comm.), the book was commissioned by Robert MacArthur, who served as editor of the Monographs in Population Biology series for Princeton University Press, a week before his untimely death from cancer in 1972. During this period of tension in integrating theoretical approaches into ecology, pre-publication reviews of the book were unfavorable, and Charnov & Orians withdrew it from Princeton University Press, distributing it only as an unpublished manuscript in 1979. The 1976 paper reporting the Marginal Value Theorem itself received negative reviews from *TPB* as mathematically uninteresting; it was accepted over their objections by the handling editor, Tom Schoener ([Schoener, 1987](#)).

While the publication difficulty of [Charnov \(1976\)](#) reflected not that the work was too mathematical, but that the theory was not mathematical enough, a more typical trajectory is that heavily mathematical *TPB* work only achieves wide notice when presented in a less mathematical and more broadly palatable form. A pattern emerges among some of the commentaries in which outstanding works of theory have appeared in *TPB*, and only later, when the ideas have been rewritten in other venues, for less theoretical audiences, have they achieved wide significance. Some of the commentators report a sense that the recognition never arrived, and that foundational work is not as well-known as it should be.

Mangel (2020) laments that the paper of Iwasa et al. (1984) introducing dynamic programming and physiological state to the optimal foraging problem is underappreciated compared to later work presenting similar ideas. Mangel speculates that the relative neglect is due in part to the choice by Iwasa et al. (1984) of an insect parasitoid study system well-suited to the problem but not widely interesting to researchers who focused on other taxonomic groups. An additional claim is that its early use of the dynamic programming technique might have been difficult for non-theorists.

Similarly, in discussing the work of MacArthur (1970) on competitive coexistence, Chesson (2020) comments that the paper is not as well-known as a more “user-friendly” treatment in a later book (MacArthur, 1972). Amarasekare (2020) comments on this same phenomenon in the work of Chesson himself, reporting that many of the more difficult ideas of the TPB paper of Chesson (1994) describing mechanisms of coexistence achieved widespread significance only with a later review paper of Chesson (2000) in the *Annual Review of Ecology and Systematics*.

Are groundbreaking mathematical contributions destined to be underrecognized in the broader field? Some TPB authors appear to be reconciled to this fate; as one reviewer put it in describing a manuscript that recently appeared in TPB: “There is no question that this is an important contribution to the literature. But like the later Beethoven string quartets, this is clearly aimed at future generations of scholars rather than a broad readership.”<sup>1</sup>

Such a fate is not inevitable, however. In many of the commentaries – Pavard and Coste (2020) on Goodman et al. (1974), Desai (2020) on Haigh (1978), Steiner (2020) on Tuljapurkar and Orzack (1980) and Tuljapurkar (1982a,b), Andreasen and Gog (2020) on Pease (1987), Plotkin (2020) on Ancel (2000), and Degnan (2020) on Meng and Kubatko (2009), for example – the influence of the source TPB paper emerged without repackaging. The same is true of the iconic and heavily mathematical Ewens (1972).

In characterizing the different fates of theory articles, one well-known study of citation patterns by Fawcett and Higginson (2012) hypothesized that equation density – the number of equations per journal page – limits dissemination of theoretical work. However, the study did not examine theory journals, and in TPB, counterexamples to the claim are abundant. A favorite is Fu (1995), a significant paper in coalescent theory that predicts patterns in allele frequencies under the coalescent model—and in which some of the pages consist only of equations with no more than a few words of intervening text. Fawcett and Higginson (2012) focused on dissemination of theory to empirical researchers, whereas dissemination among theoretically oriented researchers follows a different dynamic.

Noting that Iwasa et al. (1984) wrote only one paper on their new approach to optimal foraging in insect parasitoids, Mangel (2020) commented that single papers on topics in population biology sometimes do not on their own achieve significance. The hypothesis is that the influence of the work emerges from longer treatments or continued contributions over several studies, as in Chesson’s coexistence work described by Amarasekare (2020), or Tuljapurkar’s work on population growth in variable environments, as described by Steiner (2020).

Those who find that their carefully constructed theory papers accumulate no broader notice in the field might think of

the words of a Scottish poet, “*The best-laid schemes o’ mice an’ men/Gang aft a’gley,/An’ lea’e us nought but grief an’ pain,/For promis’d joy!*”<sup>2</sup> However, works of theory often have a different fate: initial underappreciation followed by a building influence owing to sustained effort. Or, according to an English playwright, “*To climb steep hills/Requires slow pace at first.*”<sup>3</sup>

### 3.3. Forms of significance

In describing some of the journal’s most influential work, the 15 highlighted papers provide a source of information for the question: in what ways does theory, at its best, influence population biology? The papers illustrate multiple forms of significance, as discussed in their associated commentaries.

Works of theory typically adopt one or more of the following objectives (Rosenberg, 2014): (1) to understand the effect of one or more biological phenomena on other phenomena; (2) to understand the determinants of a biological phenomenon observed in a specific organism; (3) to determine if an empirically observed phenomenon can be explained under natural assumptions; (4) to add a new phenomenon to an existing theoretical framework; (5) to generalize a framework to encompass a broader range of scenarios; or (6) to compare two or more models. The mathematics is placed in service of the biology, with the connection of the mathematics to the biology typically demonstrated by one or more of the following approaches: (1) illustration of the theory in interpreting a specific data set; (2) insertion of parameter values from empirical studies into simulations or computations; (3) construction of the theory with a goal of answering a specific empirical problem; or (4) broad discussion of the relevance of the theory across a range of biological problems.

Adding to these objectives and methods of converting mathematics into theory, we can use the 15 highlighted papers to introduce a classification of the ways in which the significance of the theory can be understood (Table 3). Some of these forms of significance map neatly onto the list of possible objectives, but some do not.

First, the significance of a paper can lie in the importance of the new biological concept that it introduces, as described for example by Schreiber and Krivan (2020) with the introduction of the idea of apparent competition by Holt (1977). This form of influence is also seen in Edge and Coop (2020), with the recognition of the distinction between genealogical and genetic sharing introduced by Donnelly (1983) as a key concept of pedigree analysis.

For empirical phenomena that are already known but that have not been studied theoretically, the significance can lie in providing convincing theoretical frameworks for explaining their occurrence, as described by Andreasen and Gog (2020) for the modeling of empirically observed recurrent epidemics of influenza by Pease (1987). A variant on this form of significance occurs when a paper provides the foundational framework for characterizing a theoretical phenomenon, as described by Desai (2020) for the work of Haigh (1978) to understand effects of Muller’s ratchet. Yet a third variant involves significance that comes from providing the theoretical evaluation of verbal arguments about a theoretical phenomenon, as Plotkin (2020) describes for the use of a model by Ancel (2000) to assess the claim that “plasticity accelerates evolution.”

The significance can lie in being an early model to incorporate important additional features into existing frameworks, as described by Lutscher (2020) for the introduction by Shigesada et al.

<sup>1</sup> The reviewer refers to a well-known anecdote. Violinist Felix Radicati is reported to have commented regarding Beethoven’s opus 59 (Forbes, 1992, p. 409): “I said to [Beethoven] that he surely did not consider these works to be music?—to which he replied ‘Oh, they are not for you, but for a later age!’” Wallace (2018, p. 183) quotes a review of the first concert of Beethoven’s opus 133: “Perhaps the time is yet to come when that which at first glance appeared to us dismal and confused will be recognized as clear and pleasing in form.” See also Dusinberre (2016).

<sup>2</sup> Robert Burns, *To a Mouse*.

<sup>3</sup> William Shakespeare, *Henry VIII*, Act I, Scene I.

**Table 3**

Some forms of significance for theoretical contributions. Each of the highlighted articles is associated with its most salient form of significance.

Form of significance	Examples
Introduce a new concept or phenomenon	Holt (1977), Donnelly (1983)
Explain existence of an empirical phenomenon	Pease (1987)
Characterize the determinants of a theoretical phenomenon	Haigh (1978)
Formalize a verbal model	AnceI (2000)
Add a new feature to a theoretical framework	Shigesada et al. (1986), Meng and Kubatko (2009)
Change the perspective on a known phenomenon	MacArthur (1970), Lambert and Stadler (2013)
Simplify the understanding of a theoretical effect	Durrett and Levin (1994)
Introduce a new mathematical technique to biology	Iwasa et al. (1984)
Solve a mathematical problem arising in the theory	Goodman et al. (1974), Tuljapurkar and Orzack (1980) and Tuljapurkar (1982a,b)
Introduce new mathematics	Ewens (1972)
Set an agenda for empirical studies	Charnov (1976)

(1986) of spatial heterogeneity into models of the spatial propagation of a population, and by Degnan (2020) on the introduction of hybridization into models of gene tree evolution in Meng and Kubatko (2009). A common form of significance occurs when a study devises an influential change in perspective on an existing phenomenon, as described by Chesson (2020) for the interspecific competition model of MacArthur (1970), and by Steel (2020) for the coalescent-point-process formulation of Lambert and Stadler (2013) for evolutionary trees.

One particular form such a change can take is to organize a complex literature by finding simple ways of understanding a phenomenon. For example, the significance of the Marginal Value Theorem of Charnov (1976) likely traces in part to the simplicity of its memorable result. Pacala (2020) describes how the contribution of Durrett and Levin (1994) lies in its finding a simple scenario for understanding the effects of two modeling assumptions—the distinction between spatially explicit and non-spatial models, and the distinction between modeling populations as having a continuously varying size and as consisting of a discrete number of individuals.

The significance of theory can be methodological, in introducing a fruitful mathematical technique that is new to the field, as Mangel (2020) describes for the dynamic programming method of Iwasa et al. (1984). It can be in providing solutions to well-characterized mathematical problems, as described by Pavard and Coste (2020) for the mathematical description of kinship structures by Goodman et al. (1974), or Steiner (2020) for the work of Tuljapurkar and Orzack (1980) and Tuljapurkar (1982a,b) to predict population sizes in changing environments. Alternatively, the key contribution of the theory work can be in its contribution to mathematics itself, as seen with Ewens (1972).

In most cases of significant contributions to theory covered in this special issue, the primary contribution of the paper has been in its influence on theoretical rather than empirical understanding. One notable exception is that the Marginal Value Theorem of Charnov (1976) can be understood as providing a testable theoretical prediction about patch occupancy behavior that launched an empirical agenda to test it. Ewens (1972) also generated theoretical predictions about allele frequency distributions, inspiring early methods of testing the fit of population-genetic data to theoretical models. Thus, the significance of the two iconic papers might relate partly to the way in which they helped to set the direction of empirical research.

Of course, many of the papers possess significance in multiple dimensions, and their significance is not always neatly classified among these various categories. Reflections on the value of theory in population biology have sometimes drawn attention to some of the specific forms of significance that theory can achieve, such as developing conceptual frameworks for achieving understanding (Marquet et al., 2014), providing tests of verbal reasoning (Servedio et al., 2014), and using theory to guide empirical research (Scheiner, 2013; Fitzpatrick et al., 2018). It is hoped that the 15 highlighted papers can be regarded as an informal field

study of theory examples with demonstrable influence in the research community, generating a set of “principal components” of the space describing forms of significance achievable for theory contributions.

#### 4. Highlighted research areas and new research papers

In addition to commentaries on specific papers, the special issue includes longer commentaries on five research areas that have developed largely in the pages of *TPB*. As discussed by Bürger (2020), multilocus theory in population genetics has been with *TPB* since the very beginning, with several major papers in the first volume and a continuing regular presence in the journal. Coexistence theory in *TPB* traces to the first issue (Chesson, 2020), continuing through the influential papers of Peter Chesson (Amarasekare, 2020).

The areas of coalescent theory and adaptive dynamics are two subfields whose origins and development have been woven into *TPB* through its entire existence. Eva Kisdi provides the analogy that once an astronomical object is known, astronomers comb through past observations and often find sightings that predate the “discovery” of the object (Kisdi, 2020). Both in the area of adaptive dynamics that she describes and in coalescent theory (Wakeley, 2020), one sees the early work, the influence, and the “sightings” such as Ewens (1972) that predate the initial discovery. Van Cleve (2020) traces the integration of evolutionary game theory and kin selection, which emerged in the 1960s, with dynamical models of population genetics, connecting the areas of game theory and kin selection with multilocus theory, adaptive dynamics, and coalescent theory.

The nine research articles in the special issue advance areas of long-standing interest in the journal. Soares and Lessard (2020) continue the tradition described by Van Cleve (2020) of linking evolutionary game theory with dynamical population-genetic models. Their title “First-order effect of frequency-dependent selection on fixation probability in an age-structured population with application to a public goods game” concisely packs an exceptionally large number of frequent *TPB* key words. François (2020) contributes a study in the modeling of phylogenetic diversification, the subfield in which the highlighted paper of Lambert and Stadler (2013) also lies. Nakamura et al. (2020) examine models in cultural evolution, an area that has its roots in early papers in *TPB*, as described by Feldman (2020).

Several of the articles are inspired directly by specific studies from theory pioneers. The paper of Arbisser and Rosenberg (2020) explores an observation of Sewall Wright that the  $F_{ST}$  measure of genetic “distance” need not satisfy the triangle inequality (Wright, 1978). The study of Uyenoyama et al. (2020) is tightly connected to the foundational *TPB* work of Ewens (1972) and Karlin and McGregor (1972), extending the neutral sampling theory in the case of a structured population. The work of Schreiber (2020) traces to a *TPB* model of Gillespie (1978) on a classic



*TPB* topic: the way in which variable environments facilitate the maintenance of genetic diversity.

The study of diversity also appears in several of the other papers. In an epidemiologic context, [Mulberry et al. \(2020\)](#) introduce a measure of the level of coinfection with multiple pathogenic strains. [Steiner and Tuljapurkar \(2020\)](#) present a study in life-history theory, considering the diversification of individual life histories and the relationship of that diversification to life stages that influence population growth rate. [Khan and Wahl \(2020\)](#) examine the bimodal size distribution of bacterial prophages, explaining this bimodality as the result of multiple interacting forces. This shared interest illustrates the centrality of factors that promote maintenance of diversity, also discussed in the commentary by [Bürger \(2020\)](#), as a focus of interest in all subfields of *TPB*.

## 5. *TPB* people

A trainee of mine once reported that while interviewing for a faculty position, a member of the hiring department had been particularly excited to meet him. This interviewer's enthusiasm derived from his perusal of my trainee's CV, from which he discovered to his delight that the trainee was "a *TPB* person."

Who are *TPB* people? The journal has been fortunate to be sustained by the efforts of dedicated and rigorous reviewers, many of whom have contributed reliably and continuously to serving the journal's community over many years. [Fig. 3](#) depicts the tenure of all of the scientists who have served on the editorial board, from the initial group of 21 founding board members in 1970 to the board of today. The list illustrates both the long involvement of many members and the frequent renewal of the board.

Furthermore, in addition to serving prominent researchers, the concentrated body of theory in *TPB* has contributed to a basis of training for aspiring theoreticians. Indeed, leading researchers report papers from *TPB* to have been influential in developing their interest in the field ([Bürger, 2020](#); [Schreiber and Krivan, 2020](#)). During my own Ph.D. training in the lab of long-time *TPB* editor Marc Feldman, close reading of *TPB* papers and an aspiration to produce work worthy of publication in *TPB* were hallmarks of the training experience in the group. As noted in some of the commentaries ([Edge and Coop, 2020](#); [Plotkin, 2020](#)), the highlighted articles include several that represent single-author contributions of researchers who were trainees at the time that the work was conducted—Lauren Ancel Meyers, Eric Charnov, Kevin Donnelly, Robert Holt, and Craig Pease.

The question of "who are *TPB* people" has recently been raised by [Dung et al. \(2019\)](#), who conducted a study of the early years of *TPB*, identifying programmers cited in acknowledgments but not on author lists. Inspired by the film *Hidden Figures*, depicting the underrecognized work of African American women who contributed as "human computers" for the United States space program in the 1960s, [Dung et al. \(2019\)](#) studied the contributions of programmers cited in the acknowledgments of *TPB* papers from the 1970s and 1980s. They found that the proportion of women among the programmers was substantially higher than the low percentage of women authors ("Computers don't author reports," one of the women is chastised in the film, when she types her name alongside that of her supervisor). In their article, [Dung et al. \(2019\)](#) noted that many of the contributions described in these acknowledgments would result in authorship under the differing standards of today, so that perusal of the most prominent and visible "*TPB* people" appearing in [Fig. 3](#) provides an incomplete perspective on *TPB* contributors. A further analysis examined the changes in authorship 1991–2018, documenting increases in women authors that appear to follow trends seen in data from related fields ([Severson et al., 2019](#)).

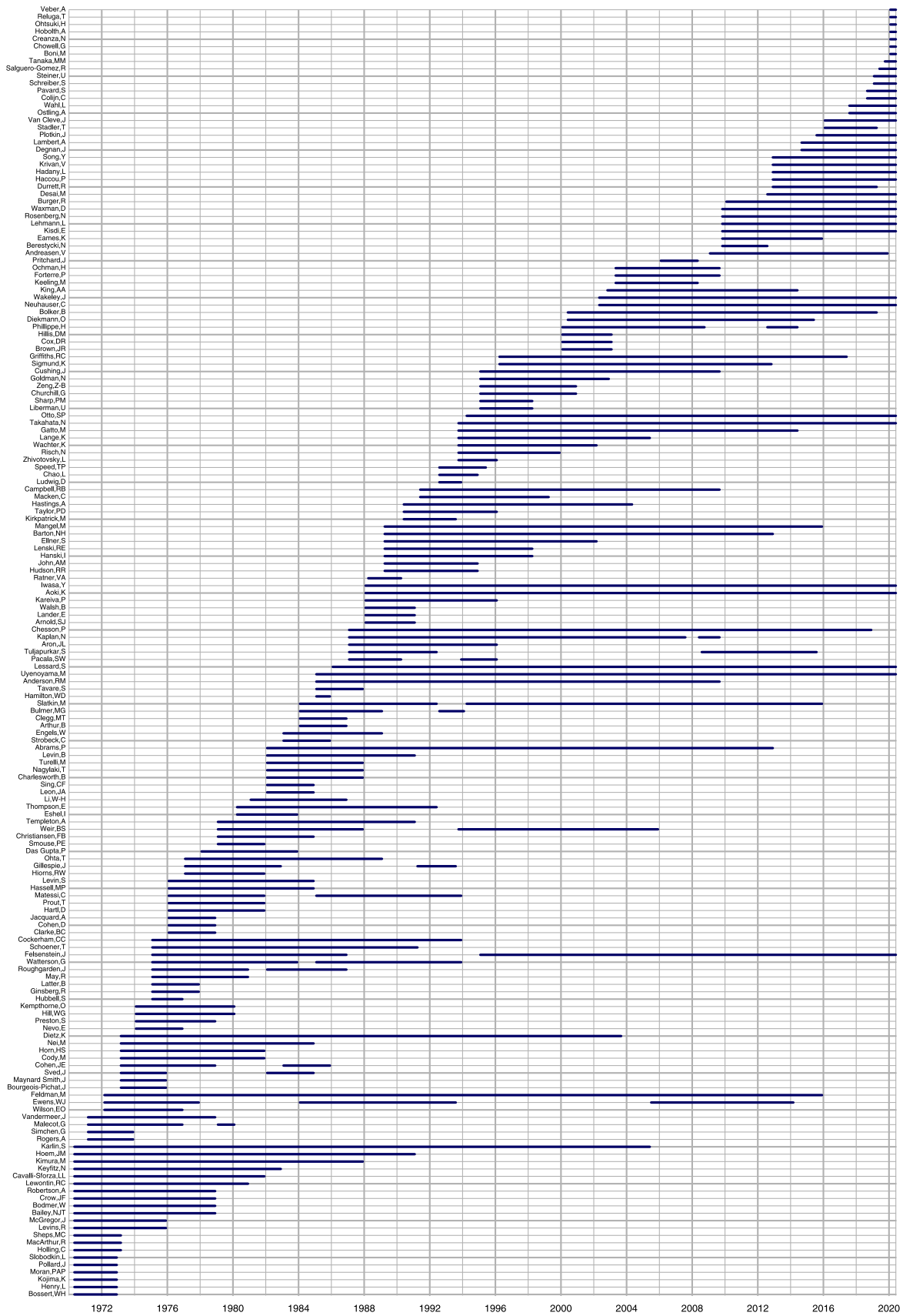
In this special issue, we include two biographical commentaries. As described by [Menken \(2020\)](#), mathematical demographer Mindel C. Sheps contributed groundbreaking work on fertility and family size, examining the effect of birth control on fertility and using renewal processes to study the sequences of reproductive events that contribute to a woman's fertility. She was the only woman on the founding *TPB* editorial board in 1970. After her death in 1973, the Population Association of America named an award for outstanding contributions to mathematical demography in her honor, a prize that has been awarded to many distinguished contributors to *TPB*, including Prof. Menken herself.

[Feldman \(2020\)](#) writes about Luigi Luca Cavalli-Sforza, best known for his empirical contributions in human evolutionary genetics, but whose prolific work on theoretical modeling in evolution and genetics stands as trailblazing in its own right. Cavalli-Sforza also served on the founding editorial board. His career in theoretical population biology spanned from his early training with R. A. Fisher in the 1940s through foundational studies of cultural evolution published in *TPB* in the 1970s well into the 2000s, with influential later Fisher-inspired work on waves of advance for the spread of alleles in spatially expanding populations.

The commentaries of [Menken \(2020\)](#) and [Feldman \(2020\)](#) highlight a number of similarities in the careers of Luca Cavalli-Sforza and Mindel Sheps. Both began their careers as physicians, arriving at topics of population biology only later, Sheps after a period of government service and health care activism, Cavalli-Sforza after conducting foundational work in bacterial genetics. Much of their work has a humanistic quality, as both were motivated by concerns about some of the great societal challenges connected to population biology—human population growth, racism, and women's decisions about their fertility and family size. In the words of Mindel Sheps, quoted by [Menken \(2020\)](#): "It would be well to approach all human problems with humility, with a strong sense of the limitations of our knowledge and of the existence of large areas of ignorance, and with readiness to admit the errors we may make... The only hope of solving the problems of this planet lies in the application of scientific understanding and skills in the service of human dignity, freedom and welfare. Neither science nor high ideals can do the job alone." We hope the careers of these two remarkable pioneers, and the commentaries and papers highlighted in the special issue, will inspire the next 50 years of theoretical population biology research.

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**Fig. 3.** The 175 past and current members of the editorial board of *TPB*, May 1970 to June 2020. For the plot, service on the board is regarded as starting at time  $y_1 + (m_1 - 1)/12$ , where  $(y_1, m_1)$  represent the first year and month when the name of an individual appears on the board, and ending at  $y_2 + (m_2 - 1)/12$ , where  $(y_2, m_2)$  represent the last year and month when the individual appears.

## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.tpb.2020.04.001>.

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