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Editorial

Theory in population biology, or biologically inspired mathematics?

TPB welcomes submissions from authors new to the journal, whom we hope to aid in preparing high-quality manuscripts that will succeed in our editorial process. Previous editorials described the topics of emphasis over the course of the journal's history (Rosenberg, 2013) and commented on three features expected in *TPB* papers: motivation from a biological perspective, significant mathematical contribution, and interpretation aimed toward advancing biology (Rosenberg, 2014). Long-time readers will recognize a distinction between (1) research contributions to mathematics inspired by progress in theoretical population biology, which are not the focus of the journal, and (2) contributions to theoretical population biology itself, the core interest of *TPB*. To provide further guidance to authors, this editorial elaborates on the difference between biologically inspired contributions to mathematics and theoretical advances in population biology.

Because theory in biology links mathematical and biological topics, theoretical population biology has often led to new advances in mathematics. A differential equation or stochastic process developed for a specific biological problem might open new research areas in the mathematical theory of differential equations or stochastic processes, as has happened many times in the history of theoretical biology (Cohen, 2004). More generally, a complex biological problem might generate a new mathematical entity whose utility in the mathematical sciences is subsequently recognized. The Ewens Sampling Formula first reported in *TPB* (Ewens, 1972), with its broad impact in probability and statistics (Tavaré and Ewens, 1997), is a celebrated example of this phenomenon.

In mature cases, the impact of a significant result in theoretical population biology can have a clear bifurcation into its contributions to biology and its contributions to mathematics. Thus, for instance, the Yule birth process, originally developed for understanding the distribution of the number of species across genera (Yule, 1925), is the starting point for a thriving intellectual tradition in biology that is still motivated in large part by an interest in exploring macroevolutionary phenomena (e.g. Aldous, 2001; Nee, 2006; Stadler, 2013), and that makes regular appearances in *TPB* (e.g. Wilkinson and Tavaré, 2009; Zhu et al., 2011; Heled, 2012; Lambert and Stadler, 2013). At the same time, however, the Yule birth process has also become a basic object underlying a substantial body of work in stochastic processes, where it often appears as a textbook example stripped entirely of the macroevolutionary context of the problem in which it originated (e.g. Karlin and Taylor, 1975; Grimmett and Stirzaker, 2001).

TPB manuscripts center on contributions to biology—empirical, theoretical, or both. Thus, whereas introducing new terms to equations from theoretical population biology and proving theorems about the resulting dynamical systems might generate advances in mathematics, such research might be termed "mathematics inspired by theoretical population biology". For all its potential significance mathematically, it does not on its own further biology. Mathematical studies of modifications or little-explored features of such population biology staples as the Lotka–Volterra equation or the SIR model, for example, have bifurcated away from the biological tradition of such models; they are not themselves "theoretical population biology" without a specific biological setting for the mathematical research.

Any of a number of recent articles from *TPB* can illustrate the nature of theory in population biology as distinct from biologically inspired mathematics. For example, concerned with the way in which human behaviors affect population dynamics of avian influenza in poultry populations, Boni et al. (2013) constructed susceptible–infected models of avian influenza transmission, in which epidemiological parameter values arise from choices that farmers make in order to maximize their profits from poultry sales. Boni et al. justified the components of their model equations with their understanding of the relevant populations, namely poultry populations on small farms in Asia. Their mathematical analysis identified parameter regions with qualitatively different behavior, in the form of different recommended government policies to minimize the societal cost of avian influenza. The study is mathematical, but each step, from the motivating background information through the analysis and its interpretation, is focused on the biological problem. The model and the mathematics are of interest to the extent that they assist in understanding the biology.

With its introduction of an empirical problem, justification of models relevant for solving the problem, analysis of the models, and interpretation for the biological scenario of interest, the study of Boni et al. (2013) exemplifies a classic structure for a population biology modeling paper. *TPB* articles whose contribution is primarily to a body of theory, and that make a stronger claim of mathematical interest in the results – separating them as stated theorems, for example – also place the mathematics in the service of biology. Csűrös (2014) proves new results about nonidentifiability from biallelic genetic markers of certain identity coefficients describing pairwise relatedness; the results are interpreted for their potential consequences in estimating the coefficients from data. Spouge (2014) derives new properties of the coalescent theory of subsamples, discussing their implications in understanding Neanderthal gene genealogies and the origin of disease mutations. Cohen (2014) proves results about limiting behavior of the relationship between the mean and variance of

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population size over independent realizations of a Markov chain; the work is presented not as an abstract treatment of Markov chains, but as a way to explain empirical observations of Taylor's law describing the relationship between the mean and variance of population densities over spatial regions.

When a result in theoretical population biology does give rise to progress in mathematics, it is often an indication of the significance and depth of the theoretical work, and the mathematical impact is a development sure to be appreciated by the theoretical population biologist. Without the motivating biological setting, however, the mathematics is not theory. It is only in association with their placement in the context of biological problems and interpretations that mathematical results generate contributions to theoretical population biology.

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References

Aldous, D.J., 2001. Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. Statist. Sci. 16, 23–34.
Boni, M.F., Galvani, A.P., Wickelgren, A.L., Malani, A., 2013. Economic epidemiology of avian influenza on smallholder poultry farms. Theor. Popul. Biol. 90, 135–144.
Cohen, J.E., 2004. Mathematics is biology's next microscope, only better; biology is mathematics' next physics, only better. PLoS Biol. 2, e439.
Cohen, J.E., 2014. Stochastic population dynamics in a Markovian environment implies Taylor's power law of fluctuation scaling. Theor. Popul. Biol. 93, 30–37.
Csűrös, M., 2014. Non-identifiability of identity coefficients at biallelic loci. Theor. Popul. Biol. 92, 22–29.
Ewens, W., 1972. The sampling theory of selectively neutral alleles. Theor. Popul. Biol. 3, 87–112.
Grimmett, G., Stirzaker, D., 2001. Probability and Random Processes, third ed. Oxford University Press, New York.
Heled, J., 2012. Sequence diversity under the multispecies coalescent with Yule process and constant population size. Theor. Popul. Biol. 81, 97–101.
Karlin, S., Taylor, H.M., 1975. A First Course in Stochastic Processes, second ed. Academic Press, San Diego.
Lambert, A., Stadler, T., 2013. Birth–death models and coalescent point processes: the shape and probability of reconstructed phylogenies. Theor. Popul. Biol. 90, 113–128.
Nee, S., 2006. Birth–death models in macroevolution. Annu. Rev. Ecol. Evol. Syst. 37, 1–17.
Rosenberg, N.A., 2013. Editorial. Theor. Popul. Biol. 83, A2–A3.
Rosenberg, N.A., 2014. Core elements of a *TPB* paper. Theor. Popul. Biol. 92, 118–119.
Spouge, J.L., 2014. Within a sample from a population, the distribution of the number of descendants of a subsample's most recent common ancestor. Theor. Popul. Biol. 92, 51–54.
Stadler, T., 2013. Recovering speciation and extinction dynamics based on phylogenies. J. Evol. Biol. 26, 1203–1219.
Tavaré, S., Ewens, W.J., 1997. Multivariate Ewens distribution. In: Johnson, N.S., Kotz, S., Balakrishnan, N. (Eds.), Discrete Multivariate Distributions. Wiley, New York, pp. 232–246.
Wilkinson, R.D., Tavaré, S., 2009. Estimating primate divergence times by using conditioned birth-and-death processes. Theor. Popul. Biol. 75, 278–285.
Yule, G.U., 1925. A mathematical theory of evolution based on the conclusions of Dr. J.C. Willis. F.R.S. Phil. Trans. R. Soc. Lond. B 213, 21–87.
Zhu, S., Degnan, J.H., Steel, M., 2011. Clades, clans, and reciprocal monophyly under neutral evolutionary models. Theor. Popul. Biol. 79, 220–227.

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