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TrendsTalk

The new society for modeling and theory in population biology

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The scope of population biology is wide, encompassing topics in ecology, evolution, genetics, epidemiology, and more. The unifying element of the field is not a particular set of phenomena to be studied, but instead a shared approach to thinking about the fundamental principles governing dynamics of biological populations. The development and conceptualization of this shared approach has been fostered, over many decades, by a scientific community dedicated to theory and modeling. To bring this community together, facilitate collaborations, and discuss the new frontiers for population biology, a new society is forming – The Society for Modeling and Theory in Population Biology (SMTPB). Following a series of online talks and discussions, the society convened for the first time at the Banff International Research Station for Mathematical Innovation and Discovery (BIRS) in May 2024, a meeting that included 40 theoreticians and modelers from across the disciplines of ecology and evolution.

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The role of modeling and theory in population biology

It is hard to think of topics in ecology and evolution that have not been substantially influenced by mathematical models and the development of theory. For over a century, modeling has shaped the way we think about natural populations, and ecologists and evolutionary biologists across many domains can recognize the contributions that both modeling and theory have made to their specific subject areas. The meeting in Banff laid out a conceptual mapping of the theoretical frameworks and advances in population biology, highlighting where the boundaries of our knowledge are currently drawn and what open questions lie ahead. Many of the talks discussed the topic of modeling utility: what exactly it is that we use models for, and what makes for a useful, interpretable model? For example, both Caroline Colijn (Simon Fraser University) and Mark Broom (City University of London) discussed the value and complexity of mathematical modeling of natural biological systems. They described the different flavors of models in population biology and how mathematical modeling has played a crucial role in helping us understand, predict, and modify natural systems. Mathematical models can also suggest new mechanisms, explore possible interplay of factors that cannot be separated easily experimentally, and conceptualize and illuminate 'hidden entities', many years before we are able to experimentally see and understand them in the laboratory (e.g., Mendel's work on genetics, Fisher's work on polygenic traits, Maynard Smith's work on evolutionary stable strategies, and Lewontin's and Kojima's work on linkage disequilibrium [1–5]).

Historically, the field of population biology has pioneered the introduction and assimilation of models and mathematics to describe biological processes and phenomena. For example, to study population dynamics, the Lotka–Volterra model was introduced a century ago, and versions of this model are still useful today, across many disciplines. In her talk, Lindi Wahl (University of Western Ontario) postulated that extinction rates in bacteria are shaped by eco-evolutionary predator–prey dynamics involving phages, a process described by mathematical formulations similar to those in the Lotka–Volterra model. Similarly, the Kermack–McKendrick epidemic model, developed in the same period as Lotka–Volterra model, which describes the spread of a disease in a population by a set of differential equations, is still in use today, and has been mentioned in several talks in the context of the COVID-19 pandemic. Another important contribution of mathematical biology has been the description of the relationship between species, lineages, or individuals using phylogenetic trees, which can be traced back to sketches in Darwin's 1837 notebooks, and has become a core conceptual tool in evolutionary biology. This line of research was highlighted in the meeting with talks by Noah Rosenberg (Stanford University), Chloe Shiff (Stanford University), Julia Palacios (Stanford University), and Carolin Kosiol (University of St. Andrews), who presented new research on the combinatorics and statistics of phylogenetic trees.

Tension between tractability and realism in modeling

When mathematically representing a biological system, a tension arises between model parsimony (preserving only essential features) and model complexity (better reflecting the different features of the natural phenomenon). How the balance between these is incorporated in model design shapes the explanatory power of the model and this issue was a reoccurring topic of discussion in the meeting. In her talk, Ailene MacPherson (Simon Fraser University) discussed how practitioners often add enough 'spice' to models to make them interesting by starting with simple models and adding features needed to adequately describe a phenomenon. Brute-force incorporation of the details of a system might be able to more realistically represent a system, but this approach would often entail keeping track of hundreds of parameters, with little hope of analytical tractability or heuristic understanding of the underlying process. In contrast, the best models offer abstract maps of reality and preserve only the essential features and structures of a system; this, in fact, increases their utility. Any modeling approach, therefore, must carefully consider which features of the system should be incorporated and which should be left out, and what would the consequence be of adding or removing a biological feature from a model.

One thread of discussion along these lines was on the amount of spatial or population structure to consider when studying evolutionary dynamics. For example, a talk by Daniel Weissman (Emory University) challenged some classic results on the genomic signatures of selective sweeps, which have been traditionally derived at the limit of well-mixed populations. By incorporating an additional spatial parameter into existing models, he demonstrated how the expected time scale for the effect of sweeps on genetic diversity may be substantially longer than previously considered. Similarly, recent work described by Oana Carja (Carnegie Mellon University) aims to understand how the effects of population structure on evolutionary dynamics depend on the topological properties of the structure considered. By using the versatile mathematical proxy of networks, she discussed the graph properties relevant for shaping evolutionary dynamics, from probabilities and times to fixation, to clonal interference and rates of evolution. Developing an intuition for when and why the well-mixed approximations might not apply is requisite for forming sensible null expectations about experimental, observational, and genomic data. One clear message from the meeting was that the tension between model realism and analytical tractability is an inherent part of the art of modeling, in many fields of study, and acquiring the skills to properly address it should be a focus in thinking about the training of the next generation of population biology modelers.

Models at the interface of disciplines: the interplay between ecology and evolution

One interesting topic discussed was the way in which evolution and ecology interact to shape the fate of biological systems. Rohan Mehta (Elmhurst University), for example, used a game-theory approach to ask how the evolution of autotomy (self-amputation as a self-defense mechanism) is shaped by interactions between predators and prey. In one session, which was focused on demography and stage structure, Maria Orive (University of Kansas) talked about demography and evolutionary rescue when species reproduce both clonally and sexually (so that both total and additive genetic variances contribute to the response to selection), and Amy Forsythe (University of British Columbia) discussed how heterogeneity in vital rates in different life stages can be incorporated to understand selection using Leslie matrices. The eco-evolutionary interplay clearly generates intriguing explanations for biological phenomena, and well-designed models can reveal many fundamental properties of such processes.

An issue that was raised in several talks was the importance of noticing the relative time-scale differences between ecological and evolutionary processes. Ulrich Steiner (Freie Universität Berlin) discussed this in the context of stochastic molecular and demographic processes, and how this has consequences for intracellular damage. It is interesting to note that the importance of timescale was revisited in different contexts of organization, such as the scale of genomic signatures under recurrent mutation by Daniel Weissmann and Oana Carja, the scale of the spread dynamics of gene drives by Gili Greenbaum, and trajectories of bacterial evolution by Lindi Wahl. The discussions in the meeting made it clear that eco-evolutionary feedbacks are of particular interest to the community, and future studies should consider the relationship between the ecological and evolutionary time scales of the system under study.

Examples of applications of models and theory in population biology

While the SMTPB community is primarily interested in theoretical aspects of population biology, many of the models and methods presented have important and direct applications. For example, Ben Peter (Rochester University) discussed the mathematics of principal component analysis, and how it can be used to interpret results from ancient DNA studies. Emilia Huerta-Sanchez (Brown University) presented a statistical method for ancient genomic data that can be used to infer past introgression events, and Matt Osmond (University of Toronto) presented a method for tracking geographic locations of ancestors using gene trees. Oren Kolodny (Hebrew University of Jerusalem) discussed applications of demographic models to conservation of threatened species, and Maike Morrison (Stanford University) talked about a new way to measure differences in microbiome compositions that can detect perturbations caused by antibiotic treatments. Highlighting the applicability of models throughout systems and fields of study, and the shared ideas across different applications, will likely be an important goal of the new society.

Gili Greenbaum (Hebrew University of Jerusalem) highlighted that there are systems and applications where the gap between theory and models to policy applications and decision making, often wide and involving many intermediaries, can narrow significantly under some circumstances. These cases require theoreticians to pay particular attention to how models are implemented and understood by the regulators and the public. To this point, he discussed the field of gene drives, a genetic control technology that, due to the risks involved in running field experiments, currently relies primarily on modeling. Another clear and recent example for a narrow gap between theory and application is represented by models of pathogen spread during the COVID-19 pandemic. Brandon Ogbunu (Yale University) and Viggo Andreasen (Roskilde University) discussed how models informed the understanding of the progression of the pandemic and the evolution of SARS-CoV-2, and how existing theory and models were adapted, modified, and developed as the pandemic unfolded. Identifying cases where the theory–application gap is narrow, and directly addressing it through model design and audience-aware dissemination of results, can help improve how models are adopted by those that need to use them in the field.

Open questions and longstanding debates

Overall, the meeting served as yet another reminder that the foundational mathematical formalism of population biology is an expanding body of knowledge. Even though we have theoretically formalized biological processes for over a century, the structure of our theory itself keeps evolving, with new questions emerging alongside revisiting of longstanding debates. For example, Joanna Masel (University of Arizona) discussed currently lacking mathematical formalism around the widely used concept of fitness, which can depend on the timescale considered and is better framed by explicit modelling of birth-death processes. Similarly, Yoav Ram (Tel Aviv University) highlighted the need for models and methods to determine when new evolutionary innovations are true stepping stones towards adaptation, versus merely evolutionary diversions. Many open questions still exist when it comes to the role of genetic and epigenetic variability in shaping rates of evolution and response to environments undergoing perpetual fluctuations. Daniel Weinreich (Brown University) discussed approaches that aim to understand evolutionary strategies to survive and adapt to ever-changing fluctuating selection pressure and the use of 'modifier models' for the study of how biological systems evolve. There was also a session on open questions in cultural evolution, with talks by Nicole Creanza (Vanderbilt University), Egor Lappo (Stanford University), and Kaleda Denton (Stanford University) focused on identifying the processes by which cultural traits are transmitted and accumulated across human or animal cultures.

Since the early days of Yule, Fisher, Wright, Lotka, and Voltera, population biology has always been a field spearheading the development and application of sophisticated abstract models and methods to understand the natural world. These mathematical efforts have also provided important theoretical new concepts and underpinnings for a wide range of areas of research and fields far beyond population biology, and led to significant mathematical advances in network theory, statistical theory, diffusion theory, and economics. The new SMTPB will surely strive to continue this important tradition.

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