Let's train more theoretical ecologists - here is why

Axel G. Rossberg[1†*], György Barabás[2,3†], Hugh P. Possingham[4,5], Mercedes Pascual[6,7], Pablo A. Marquet[8], Cang Hui[9,10], Matthew R. Evans[11], and Géza Meszéna[12,3†]

[1]School of Biological and Chemical Sciences, Queen Mary University of London, London, UK
[2]Division of Theoretical Biology, Dept. IFM, Linköping University, Linköping, Sweden
[3]ELTE-MTA Theoretical Biology and Evolutionary Ecology Research Group, Budapest, Hungary
[4]The Nature Conservancy, Arlington, VA, 22203, USA
[5]The University of Queensland, Brisbane, 4072, Australia
[6]Department of Ecology and Evolution, University of Chicago, 1101 E 57th Street, Chicago, IL, 60637, USA
[7]Santa Fe Institute, Santa Fe, NM, 87501, USA
[8]Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
[9]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Matieland, South Africa
[10]African Institute for Mathematical Sciences, Muizenberg, South Africa
[11]School of Biological Sciences, Kadoorie Biological Sciences Building, The University of Hong Kong, Pok Fu Lam Road, Hong Kong, SAR, China
[12]Department of Biological Physics, Eötvös Loránd University, Budapest, Hungary
[†]International Initiative for Theoretical Ecology, `http://iite.info`
[*]Corresponding author: contact@iite.info

Accepted for publication in *Trends in Ecology and Evolution*, June 5, 2019

Abstract

A tangled web of vicious circles, driven by cultural issues, has prevented ecology from growing strong theoretical roots. Now this hinders development of effective conservation policies. To overcome these barriers in view of urgent societal needs, we propose a global network of postgraduate theoretical training programs.

Keywords: Theoretical ecology, ecological modelling, mathematical biology, biodiversity crisis, capacity building

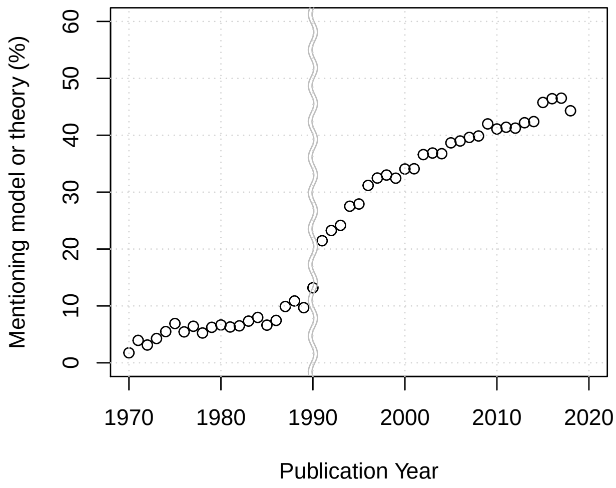

Figure 1: Interest in theory and models is increasing in ecological research. Points represent the proportion, amongst those scientific articles that mention 'ecology' (or grammatical variants) in title, abstract or keywords, that also mention 'theory' or 'model' (or variants), in articles listed in March 2019 in the database Science Citation Index Expanded (Clarivate Analytics). The discontinuity around 1990 is an artefact due to subsequent inclusion of abstracts in records. However, the degree to which the trend represents changes in methodology rather than a linguistic shift [7] is difficult to assess. Of the 50 most recent ecological publication in the database referencing 'theory' or 'model' (on 5 March 2019), only eight actually invoke process-based models or mathematical theory.

Why theoretical ecology

As for all natural sciences, identification of regularities in observations is the foundation of ecological research. Ecology has been highly successful in this respect, despite the challenges our complex research subject poses. However, any understanding *that* certain regularities occur [1, 2] also raises questions of *why* and *how* they arise in terms of basic principles and driving mechanisms (`https://iite.info/2018/12/10/understanding-that-why-or-how-in-ecology/`)—the principal concern of theory. While ecologists are becoming increasingly interested in theory and models (Fig. 1), answers to most fundamental questions have remained open or controversial. This limits our ability to extrapolate with confidence from known situations to the unknown [1], thus restricting the utility of the science of ecology to dynamically changing societies.

These limitations matter. An assessment of scientific tools available for policy support by the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES, an organisation under the auspices of the United Nations) drily concludes that "The scientific community may want to give priority to addressing gaps in methods for modelling impacts of drivers and policy interventions on biodiversity and ecosystem services." [3] The knowledge gaps identified by IPBES reach deeply into areas studied in theoretical ecology [3, Ch. 8]: species interactions and community dynamics, ecology on large spatio-temporal scales, responsiveness of ecosystems to external drivers, projection models for indicators and ecosystem services, inclusion of social decision making, methods for combining models, etc. Insufficiency of theoretical ecology has thus become a major hindrance to the effective management of biodiversity on a global scale.

Causes and remedies for this insufficiency have often been debated over the years [1, 2, 4–11]. The issues are so diverse that we provide an overview over the symptoms first before proposing a diagnosis and a possible cure.

Symptoms

At the purely technical level, we often see examples of problematic mathematical notation [12] and technical errors in the literature [13]—certainly more so than in disciplines with more mature theoretical traditions. In verbal arguments, theoretical concepts are often invoked inconsistently [4, 10].

A deeper running issue is that, despite building on a core canon of established understanding [14], Theoretical Ecology does not give the impression of an intellectually coherent field of study. Onlookers see a frighteningly diverse conglomerate of various particular models and ideas [1], which are at best unrelated and at worst contradictory. The problem of competitive exclusion and limiting similarity, reverberating in the literature to the present day, is a good example. Original models [15] asserted the existence of a definite lower limit to the similarity of coexisting species. But later it was found that this conclusion depended on particular assumptions, which, when relaxed, revealed that there is no hard-set limit to species similarity. It is even possible to construct models where a *continuum* of species coexist. This diversity of results must give the impression that all cases are different and no general conclusions can be drawn [16]. In fact, careful analysis connects these different findings, yielding a unified picture—the idea is to shift focus from whether the coexistence of a number of phenotypes is *stable* to whether it is *robust*; i.e., whether coexistence is maintained for a sufficiently large range of parameters [17]. It then turns out that instances where very similar species are able to stably coexist require aggressive fine-tuning of model parameters. In this altered sense, the limiting similarity principle still holds: very similar species can only coexist only in a very narrow parameter range. However, such analyses tend to dig deep into the mathematical toolbox and rarely percolate down to the canon of ecology textbooks. From our experience in teaching, young ecologists can be left with the impression that the theoretical literature forms a fractured, confused, and heterogeneous landscape. There is little guidance for what to learn and what to ignore, and which ideas and methods are most reliable and useful.

A wealth of theoretical concepts, ideas, and methods are regularly invoked in ecosystem management (e.g., stage-structured population models for fisheries or invasive species, epidemiological models, species distribution models, metapopulation models) [9, 11]. Practitioners find however their reliability uncertain [18]. This is partly why, rather than vindicating theoretical approaches and encouraging their development, these applications can be seen as justifying scepticism about theory. While theorists have found avenues to understand and deal with the inherent limits to predictability of ecosystems (e.g. Workshop on *Uncertainty, Sensitivity and Predictability in Ecology* on 26-30 October at the Mathematical Biosciences Institute in Columbus, Ohio), these remain underutilised [9, 18].

Remarkably many theoretical ecologists enter the community from the "outside": field ecology, chemistry, mathematics, physics, statistics, etc [2, 5]. Each of these disciplines has its own way of thinking, terminology, and notation. This can obscure strong connections between similar ideas which appear unrelated at first glance, so that important, well-established insights are easily missed. For example, the theory of population dynamical processes is treated in apparently different ways in ecology, population genetics, and the replicator dynamics used in evolutionary game theory. Rarely, if ever, is it emphasised that the different formulations of these sub-disciplines are really about one and the same thing—the various, seemingly different perspectives turn out to differ mostly in notation [19].

Scepticism about mathematical methods [2, 5–7, 16] (also `https://dynamicecology.wordpress.com/2014/11/03/a-hypothesis-about-why-some-ecologists-dont-like-pure-theory`) coupled with the mixed backgrounds of theorists also means that peer review of theoretical research does not necessarily operate as efficiently as it could. Journal editors tell us that they often have difficulty finding reliable reviewers for advanced theoretical manuscripts. There is a strong incentive to either drop detailed theoretical arguments entirely or else to hide them in supplements [8], which may not get as thoroughly reviewed as the main article. Consequences of this de-emphasis of formal reasoning are that errors creep in more easily, relationships between new and established results are harder to pinpoint, and the generality of new results is easily over- or underestimated [8].

Diagnosis

None of the symptoms we considered above suggests that the reasons for the insufficient development of theoretical ecology are inherent to the nature of the field itself. Rather, we believe that the main limiting factors are of a cultural nature.

In the tradition of natural history, many people enter ecology because they love being in nature (`https://teamshrub.com/2017/03/24/theory-meta-analyses-and-stylised-facts-in-ecology/`) [5, 8]. And when ecologists harbour uneasy feelings towards theory, they have a point: theoretical ecology,

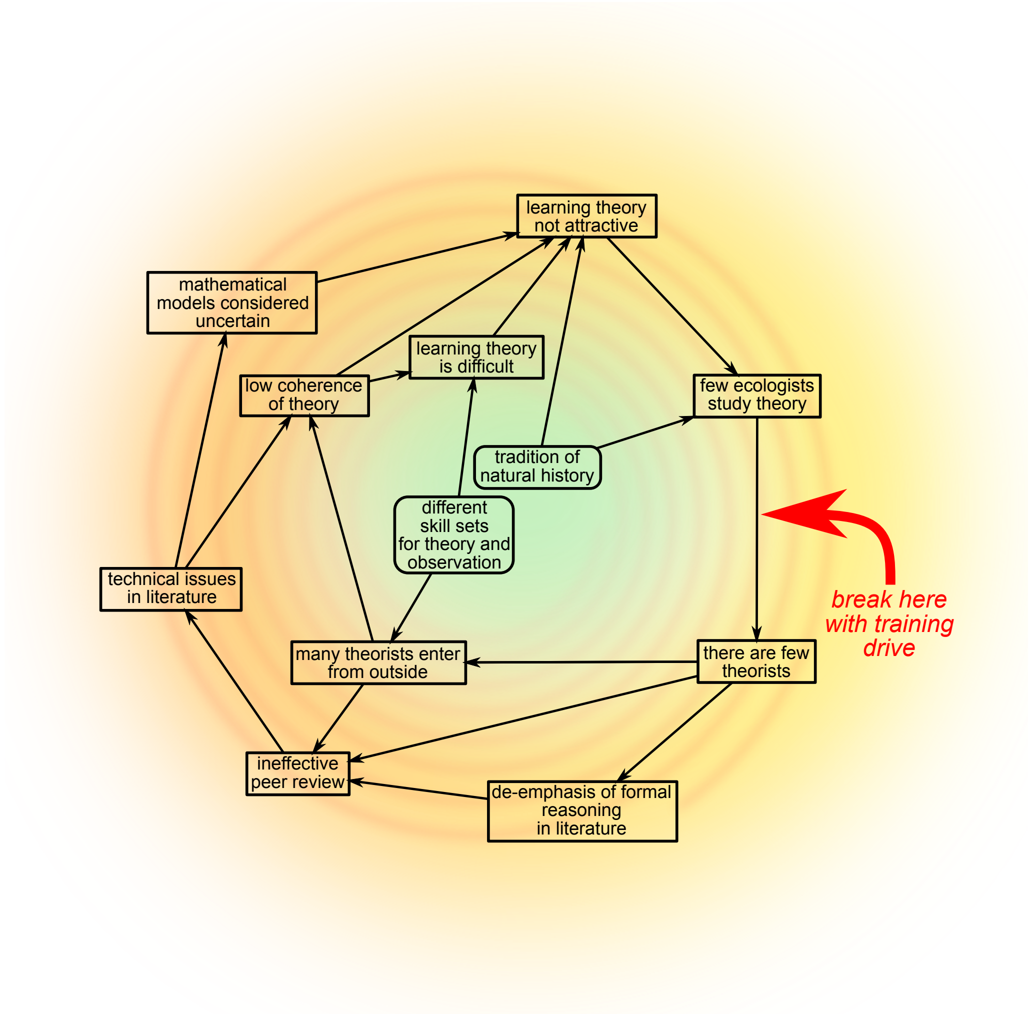

Figure 2: The tangle of vicious circles impeding development of theoretical ecology. Black arrows indicate causation. Boxes with round corners represent extrinsic drivers, the other boxes form part of the vicious circles. We proposed to train more theoretical ecologists as a way to break these circles. This will benefit the field as a whole by reversing observed symptoms along the indicated causal chains.

as they see it, does not motivate them to learn it, for the reasons discussed above. Theoretical methodology asking which limited sets of model elements ("assumptions") lead to which high-level phenomena [6] might strike ecologists as incessant rediscovery of empirically known phenomena using unrealistic models [2]. All this creates an undesirable positive feedback [5], whereby preexisting attitudes towards theory entice fewer ecologists to do theoretical research, which in turn erodes the amount and quality of theoretical research—reinforcing the impression that learning theory is not worthwhile.

Finally, ecology is a science where the required skill sets of empiricists and theorists can be very different [13]. As in other biological sciences, good empirical work requires mastery of a wide range of techniques and a detailed knowledge of the study system. However, contrary to genes, cells, and organisms, ecosystems and ecological communities do not replicate, are therefore not subjected to evolution by mutation and selection, and have not become living 'clockworks' that are best understood by studying the role and working of their individual parts. Instead, strong nonlinearity and a fair dose of randomness give rise to emergent phenomena (ecological patterns [1]) which theorists aim to explain using mathematical models, formulated in sufficient generality to accommodate the idiosyncrasies of living systems. The skills and techniques required for this are very different from those required for empirical work. Communication barriers easily arise, even when all participants acknowledge that good science ultimately means integration of theory and observation.

Theoretical ecology is thus held back by a tangle of vicious circles, reinforced by cultural biases that work against the organic development of the field (Fig. 2).

Treatment

To cut through these vicious circles, appeals for changes in attitude towards theory [1, 5, 11] and funding [11] are important, but insufficient. As a powerful remedy, we propose an intensive drive to train theoretical ecologists in a global network of postgraduate training centres (Fig. 2). This would scale up and build on experiences such as courses on modelling and theory in applied areas including infectious diseases and resource management that were initiated at the International Centre for Theoretical Physics (Trieste) by T. Hallam, S. Levin and L. Gross, aiming at participants from developing countries. We advocate for a mature state of ecology with regards to theory training, while also recognising the differences in skill sets underlying empirical and theoretical work. This is why we propose to target ecology graduates with theoretical interest [13], while also welcoming students from other backgrounds or disciplines. The training network will not only support efficient transmission of coherent theoretical knowledge to the next generation of researchers. It will also facilitate: a better coverage of the field by putting it in on a broader base; networking within the community at the level of both students and teachers; joint efforts to organise and consolidate advanced ecological theory in textbooks; applications of the science, by bringing the training closer to the places where societal change and planning needs are highest; and establishment of the profession of the Theoretical Ecologist as a recognised brand.

Prognosis

Our vision for ecology is to eventually become a science that explains the major observed patterns by a coherent set of theories; where these theories tell us not only what the dominant mechanisms are controlling predictable patterns but also what limits predictability and controllability elsewhere; where this understanding informs identification of management objectives and construction of problem-specific management models; where these models are calibrated—wherever they are needed—using cutting-edge methods of data collection and statistical inference; where society has confidence in what ecology predicts; and where curiosity-driven empirical and theoretical research discovers ever new possibilities for understanding and managing ecological systems.

Ecological research will always form a spectrum from purely empirical work through data-driven modelling to theoretical analysis of fundamental principles [1, 2, 5, 9]. It is essential however that all participants have a basic understanding and a joint sense of ownership of the entire spectrum [5, 20]. Only then can knowledge and understanding flow effectively in both directions, bringing to full fruition the unity and utility of our science.

Acknowledgements

G.B. acknowledges funding by the Swedish Research Council (grant VR 2017-05245), G.M. by the Hungarian National Research, Development and Innovation Office (grant K123796).

References

[1] Marquet, P.A. *et al.* (2014) On Theory in Ecology. *BioScience* 64, 701–710

[2] Keddy, P. (2005) Putting the Plants Back into Plant Ecology: Six Pragmatic Models for Understanding and Conserving Plant Diversity. *Ann Bot* 96, 177–189

[3] Ferrier, S. *et al.* (2016) *The Methodological Assessment Report on Scenarios and Models of Biodiversity and Ecosystem Services.* Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany

[4] Levin, S.A. (1975) On the Care and Use of Mathematical Models. *Am. Nat.* 109, 785–786

[5] Łomnicki, A. (1988) The Place of Modelling in Ecology. *Oikos* 52, 139–142

[6] Caswell, H. (1988) Theory and models in ecology: A different perspective. *Ecological Modelling* 43, 33–44

[7] Scheiner, S.M. and Willig, M.R. (2008) A general theory of ecology. *Theor Ecol* 1, 21–28

[8] Fawcett, T.W. and Higginson, A.D. (2012) Heavy use of equations impedes communication among biologists. *Proc. Natl. Acad. Sci. U. S. A.* 109, 11735–11739

[9] Evans, M.R. *et al.* (2013) Predictive systems ecology. *Proc Biol Sci* 280, 20131452–20131452

[10] Kendall, B.E. (2015) Some directions in ecological theory. *Ecology* 96, 3117–3125

[11] Courchamp, F. *et al.* (2015) Fundamental ecology is fundamental. *Trends in Ecology & Evolution* 30, 9–16

[12] Edwards, A.M. and Auger-Méthé, M. (2019) Some guidance on using mathematical notation in ecology. *Methods Ecol. Evol.* 10, 92–99

[13] Chiel, H.J. *et al.* (2010) From Biology to Mathematical Models and Back: Teaching Modeling to Biology Students, and Biology to Math and Engineering Students. *LSE* 9, 248–265

[14] Hastings, A. and Gross, L., eds. (2012) *Encyclopedia of Theoretical Ecology.* University of California Press, Berkeley

[15] MacArthur, R. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101, 377–385

[16] Simberloff, D. (1982) The status of competition theory in ecology. *Ann. Zool. Fenn.* 19, 241–253

[17] Barabás, G. *et al.* (2012) Continuous coexistence or discrete species? A new review of an old question. *Evol Ecol Res* 14, 523–554

[18] Milner-Gulland, E.J. and Shea, K. (2017) Embracing uncertainty in applied ecology. *J Appl Ecol* 54, 2063–2068

[19] Page, K.M. and Nowak, M.A. (2002) Unifying Evolutionary Dynamics. *Journal of Theoretical Biology* 219, 93–98

[20] Pásztor, L. *et al.* (2016) *Theory-Based Ecology: A Darwinian Approach.* Oxford University Press, Oxford, New York