Mathematical theory of biological diversity

Final report, NKFI grant 123796

Introduction

We promised in our grant application further development of a unifying mathematical theory of biological diversity that had been suggested earlier in several papers and in the textbook by Pásztor et al. (2016).

It is culturally difficult, because it is a general perception on ecology that all situations are different, and a general theory is neither possible, nor desirable (e.g., Lawton, 1999). Accordingly theoretical ecology is dominated by separately studied models. While the “strategic” models are supposedly wide in scope, but far from empirical details, the “tactical” ones may describe specific situations but fail to provide wider insight and predictive power. Neither of them builds a connection between general concepts and specific field situations. Instead, we propose top-level mathematical theory representing the commonalities of the ecological situations and describe the specific cases by models, which are consistent with that theory.

For the top-level theory we need a disciplined mathematical translation of existing, but vague and controversial, biological big pictures. A multitude of species can co-exist, because of the multitude of different possibilities for survival and reproduction, i.e., of the multitude of ecological niches. The emergence of a new species is an adaptation to an unoccupied niche. This seemingly simple and trivial picture was initiated by Darwin. However, it has become quite confused and controversial during the long history of development. According to our translation, the key issue is the mathematical structure of the feedback loops regulating species and ecosystems. Coexistence of species requires their differentiation with respect to the regulating environment. Emergence of new species is a consequence of the selection regime, which becomes frequency-dependent by very same regulating feedbacks.

Our work grew out from the involvement of the principal investigator of the current project (PI) in development of adaptive dynamics (Geritz et al.; 1988, Meszéna et al., 2005), which is essentially the fixed-point analysis of frequency-dependent selection. During the current project, we made progress on adaptive speciation theory on this basis. Going deeper, we worked on general mathematical development of niche theory, i.e., the theory of coexistence of different species. We worked on principal unification issues and contributed to specific debates in literature.

During the Covid epidemic, then by health issues of the PI in the last year publication of our results slowed down. By the time of reporting, we have published 4 papers with cumulative impact 34. An additional 4 papers are in different stages of preparation; we hope to publish them also in top journals of the field. Several of our research projects, including student projects, have not reached yet the publication stage. During the timespan of the current grant 5 BSc thesis work, supervised by the PI, has been defended successfully. An MSc project is under development. Three students (Anna Rédl, Krisztián Dobos, Fanni Adina Fébert) were financially supported from the project.

Below we describe the details of our progress centered around our published and work-in-progress papers and the student projects. We enlisted these outputs numbered at the end of our report. We provide non-public links for the manuscripts under preparation.

Adaptive speciation

Background

The essence of adaptive dynamics theory is that the fitness function is not something fixed. Instead, the fitness-driven evolutionary process feeds back to the fitness function. The main result of the fixed-point analysis of the combined “adaptive” dynamics for clonal (asexual) inheritance is branching evolution. That is, we found that adaptive evolution is not simply a hill-climbing optimum-seeking process, which stops at the first local maximum. Instead, branching evolution, which is able to occupy a multitude of fitness peaks, is a natural feature of the process of adaptation. From parsimony we posited from the very beginning, that speciation is essentially this process, which we refer to, as adaptive speciation.

Suggestion of adaptive speciation was in contrast with the then mainstream theory of allopatric speciation suggested by, Mayr (1942). Contrary to Darwin's hypothesis, he posited that speciation is initiated by an external factor dividing the population into two subpopulations, between which gene flow is eliminated by a geographical barrier. The resulting subpopulations may then adapt to different habitats or ecological roles. In this picture, speciation, i.e., the genetic division of the population, and adaptation are two unrelated processes. However, a large number of empirical studies have established by now that speciation (at least in many cases) is driven by ecological adaptation in presence of gene flow. This type of speciation is referred to as ecological. While theoretical and empirical research seem to be converging, it is not generally recognized that adaptive and ecological speciation are essentially the same thing.

One of the limiting factors of the emerging synthesis is the lack of a widely accepted detailed theory of adaptive speciation. The theory of evolutionary branching is simple and general in the case of clonal inheritance, but it must be complemented by studying emergence of reproductive isolation for sexuals. As evolutionary branching happens in the vicinity of a (frequency-dependent) fitness minimum, we can generically expect selection against the hybrids with intermediate phenotypes. Depending on the details, it may translate to selection for avoiding hybridization. Naturally, modelling emergence of a specific mechanism of reproductive isolation has a lover level of generality than of adaptive dynamics. Modelling adaptive speciation is hard even on the specific level because one has to follow two, mutually dependent, sub-processes: ecological diversification and genetic isolation. By this reason the suggested models rely often on an oversimplified representation of the underlying genetics.

Our contributions

The PI has been cooperating with Ulf Dieckmann (International Institute of Applied Systems Analysis, Austria and Okinawa Institute of Science and Technology, Japan) in developing better understanding adaptive speciation based on the model suggested by Diecmann & Doebeli (1999).

This model stands out from the rest, as it considers the evolving traits as determined by many loci – which is the generally accepted picture on quantitative traits. In the model there are two such traits, controlling the ecology and the mating behavior. During speciation we expect diversification in the first trait and evolution towards assortativity (preferred mating between similars) in the second one. Unfortunately, the very feature making this model realistic is also its disadvantage: analytic treatment of a population genetics model with 10 loci for each trait is not feasible.

The individual-based simulation by Diecmann & Doebeli (1999) supported the adaptive speciation expectations: clear speciation events were observed in a wide range of parameter space. However, this conclusion surprised the population geneticist community, because a multilocus trait tends to be

Gaussian distributed by the central limit theorem. Transition of a multilocus character from a unimodal Gaussian distribution to a bimodal one had never been observed before in any model of multilocus genetics. This community expected a different and more familiar outcome: a widely distributed, but still monomorphic population (Polechová & Barton, 2005). Colleagues doubted the genericity of the numerical results because lack of analytic grasp on the process limited the insight considerably.

The goal of cooperation between the PI and Ulf Dieckmann was the reinvestigation of this model with significantly larger locus number and population size to getting a clearer picture of what is happening during the speciation transition. Because of the complexity of the phenomenon, the unavoidably large number of parameters and the slowness of the individual-based simulations, it took many years until we started to see the light at the end of the tunnel.

Now we feel that we have a full understanding of the phenomenon.

Our basic observation is that the speciation process has three different phases in a wide range of parameter space. The first phase is fast and ends up with a widely distributed population and an intermediate level of assortativity. Then the genic level of variance of the ecological trait erodes away slowly during a long second phase, resulting in an increasingly bimodal trait distribution. The process is terminated by a fast transition into two, almost completely separated, populations.

The key point is that emergence of reproductive isolation requires both evolution of assortative mating and reduction of genic variance. The latter one is the new and non-trivial understanding. Genic variance evolves slowly for high locus number. This is why bimodality emerges gradually during the second phase. The fast third phase is driven by self-accelerating sexual selection.

The process is significantly more complicated than the situations usually discussed in the population genetics literature. Models with many loci are intractable by the combinatorically large number of variables. The limit theory assuming infinitely many loci (infinitesimal model, Barton et al., 2017) is simple again, but the genic variance cannot evolve in this limit. The hypergeometrical approximation used e.g., by Polechová & Barton is also invalid in our circumstance.

Our theoretical invention is the analytical treatment of large, but not infinite number of loci. In this case genic variance can evolve in a calculable manner under proper selection regimes. The process slows down for increasing locus number and becomes arrested in the infinite loci limit. Therefore, the “near infinitesimal” regime implements a time-scale separation between the slow genic variance and the rest of the variables. On the short time-scale evolution of the phenotype distribution of the population can be described by the infinitesimal model, leading to an integro-differential equation. Dynamical equations for the genic variance and the mating trait (both can be approximated by a single value) complete our analytical descriptions. The behavior of this approximation is intuitively very transparent and fully explains our hard-earned numerical results.

A manuscript on the numerical results and their verbal interpretation was submitted to American Naturalist [5]. The editorial decision was “Decline Without Prejudice”, but the extremely long (cc. 7600 words) decision letter by very interested eminent scientists strongly suggested resubmission. Their main objection was that they did not find our explanation of the observed phenomenon clear enough and asked for more formal treatment. We replied to all the comments and questions (cc. 8400 words), considered all the Referee’s suggestions and wrote a new Appendix detailing the analytic framework. Still, the numerical results remain the main topic of this paper. We will resubmit it soon.

The PI attended the Gordon Research Conference on Speciation in February 2023 and presented a poster (also linked) on the results. The Conference, on the one hand, represented full acceptance of ecological speciation; esp. if compared to earlier similar events. On the other hand, however, recognition of theoretical connection to frequency dependence and adaptive dynamics was lost completely. Our paper will be very timely, when appears.

Meanwhile Anna Rédl [11] and Krisztián Dobos [12] have been studying different versions of the analytic model via numerical integration. Based on their work a further publication on the stand-alone analytic model is envisaged later.

We hope that our work establishes convincingly that speciation is a natural consequence of adaptive evolution and requires neither chance intervention by external factors, nor unlikely coincidences.

Coexistence-niche theory

Background

The useful generality of adaptive dynamics motivated us to seek analogous generality in the underlying ecological theory. While adaptive dynamics is based on the general mathematical notion of fitness, understanding diversity on the ecological level needs additionally a sufficiently precise notion of the ecological niche.

Competitive exclusion *versus* coexistence has been one of the deepest controversies of ecology since very early on. The principle of competitive exclusion states that “complete competitors cannot coexist” (Hardin, 1960), because one of them wins the competition and ousts the rest. The related concept of limiting similarity claims that species should differ sufficiently for coexistence. Hutchinson’s “niche space” concept envisions an abstract space that species have to partition among them to coexist. All these suggestions were (admittedly) vague from the very beginning and initiated endless controversies converging nowhere.

Resource competition is the most discussed specific case: species can coexist if consume different resources. More exactly, no more species can coexist than the number of resources. In sharp contrast to the previous ones, this statement is exact and easy to prove. However, its validity is restricted to the case of equilibrium resource competition.

Levin (1970) argued that the proof can be generalized beyond resource competition by counting all variables in the regulating feedback loop (we call them regulating variables), instead of just the resources. This generalization has not become widely recognized, probably because it is on a more abstract level. One cannot count the regulating variables without studying the inner working on the ecosystem of interest.

Historically, fluctuations were cited as one of the most important objections against the validity of the competitive exclusion principle (see e.g., Huston 1994). After decades of debates, theory by Peter Chesson (2000) represents the current mainstream: fluctuations do not invalidate competitive exclusion. Instead, they provide additional ways for species coexistence. He argued that fluctuation could be averaged out in a linear model. Chesson distinguished between two different fluctuation-dependent coexistence-maintaining effects: the “effect of relative nonlinearity” and the “storage effect”. These represented two different mathematical ways to complicate averaging and to avoid competitive exclusion. While this analysis is mathematically correct in own context, and can be related to field research, it is not very clean mathematically (cf. Barabás et al., 2018) and fully detached from the intuitive concepts, like limiting similarity and niche-segregation.

The status quo is chaotic. Most of the literature equates competitive exclusion with equilibrium resource competition in an often-unclear way and more and more theoretical papers discover violation of that statement in different models. Still, the Chessonian attitude of looking for coexistence-maintaining mechanisms (i.e., considering competitive exclusion, as default) is gaining recognition. Together with losing the intuitive grasp on the issue. The messy state of coexistence theory affects speciation research. As discussed above, the role of ecological adaptation in speciation is becoming more and more recognized. Then, explaining speciation requires a general understanding of the diversity of adaptation possibilities.

Our earlier work

Following Levin (1970), the essential abstraction for clearing up and establishing the ecological basis of adaptive/ecological speciation is the notion of regulating variables. It can be resource concentrations, predation pressure, and many other environmental variables in the feedback loop.

We demonstrated in a model-independent way that the parameter range allowing a coalition of species to coexist shrinks, and disappears, with increasing similarity of the species with respect to the regulating variables (Meszéna et al., 2006). We call it week limiting similarity principle, as there is not a strict lower bound for similarity. The proof is based on sensitivity-analyses of coexistence: linearization around the coexistence fixed point leads to a Lotka-Volterra type behavior generically. The analysis clarifies the sense in which species must differ to coexist: they must differ both in their differential effects on, and in their differential sensitivity to, the regulatory variables. This result implies that Hutchinson's niche space should be identified to the (discrete, or continuous) set of the regulation variables. The niche of the species is determined by the vectors of impacts and sensitivities. The concept was applied to several different ecological situations in later publications, see Barabás et al. (2014) for a summary. (György Barabás is a former student of the PI, who earned a PhD in Michigan and working currently in Sweden. He has made a significant contribution to our theories.) This development became one of the foundations of our textbook (Pásztor et al., 2016).

We demonstrated by functional analytic tools, that any model allowing a continuum of species to coexist must be structurally unstable (Gyllenberg & Meszéna, 2005). This result is important for the interpretation of the discreteness of the species, which is one of the most elementary facts of biology. The theory of adaptive speciation, explained above, is inherently related to this universally discretizing nature of ecological feedback.

Fluctuating coexistence

Interpreting fluctuation-driven coexistence in our terms is of central importance. Barabás et al. (2012) developed this theory for a cyclic (seasonal) environment. It was one of the central issues of the current project to generalize it for an arbitrary, but stationer environmental fluctuation.

Studying population regulation through fluctuating environment in a general way turned out to be quite difficult. The essence of regulation is unchanged relative to the constant-environment case: the long-term growth rate, which is a statistical average, is regulated to zero by the ecological feedback. If the population is too abundant in some averaged sense, the long-term growth rate becomes negative, decreasing the averaged abundance. However, the temporal pattern of the population is also changing while this feedback operates. Based on earlier results on structured populations, we developed the theory of this kind of regulation both in generality and for several specific models.

Despite all the complications, the emerging picture is transparent and intuitive. Fluctuating environment does *not* invalidate the competitive exclusion principle. Instead, it allows a new kind of niche segregation: segregation in resource use between different kind of periods (e.g., dry and wet), as described by time-dependent impacts and sensitivities. There is an analogue of the Lotka-Volterra competition coefficient: it is the temporal covariance of the sensitivity of one species and the impact of the another. Coexistence is maintained if the so-defined averaged competition is smaller between the populations than between them – like in the simplest case of equilibrium competition. The theory reproduces Chesson's one using his approximation and parametrization.

Characterization of fluctuation-mediated coexistence on our way has significant advantages. We can state that there is no essential difference between constant and fluctuating environments, despite the complicacies of the second. It clarifies that limiting similarity in the sense above is the rule of the game, just like in the usual models of resource competition. Last, but not least, the possibility for fluctuation-mediated coexistence may drive speciation like any other types of niche-segregation possibility.

The full mathematical development, both the general theory and specific models, are available for the reviewers of this project in a manuscript by Barabás, Song & Meszéna [7]. As we consider these results essential, we intend to publish it in a top biological journal. To this end the existing purely mathematical manuscript requires significant reworking before submission.

Earlier Szilágyi & Meszéna (2010) investigated the minimal model of fluctuation-maintained coexistence. In this model we had two regulating variables: the average and the variance of the population size. (It corresponded to Chesson's "relative nonlinearity" case.) However, it worked well only on unrealistically large population sizes, otherwise the populations got lost through demographic stochasticity. During the current grant Miklos Gula in his BSc thesis work [10] reinvestigated the model with colored noise. Filtering out the very low frequencies of the noise saved the populations from the harm of demographic stochasticity.

This result points to the importance of time-scale issues. A species may be able to adapt to fluctuations, timescale of which is not much longer than the generation time. Different adaptations to the fluctuation may lead to fluctuation-maintained coexistence. However, no species can adapt to fluctuations over a much longer timescale. It may cope for a while with continuous re-adaptation or go extinct. Still, it seems that the relative nonlinearity type coexistence model is more of a "proof of concept" mathematical demonstration than a realistic description of a real ecological phenomena. Our general model is meant for describing the real thing.

Synthesis paper

After publishing quite a few papers on coexistence, we feel that time is right to write a synthesis on the theory of ecological niche, as we envisage it. While the article Meszéna et al. (2006) was already intended, as a declaration of a general theory, handling the complicacies, like population structure, etc., have remained verbal there. Since then, we clarified many of these details in several publications of different levels of generality. The textbook Pásztor et al. (2016) portrayed the concept as ecological worldview, but in a minimalist way from mathematical point of view.

The envisaged paper consists of a relatively short summary of the biological picture with the top-level mathematics: the regulating feedback and variables, the week limiting similarity and the derived intuitive picture of the niche space. A much longer mathematical appendix will describe the connection between this high-level treatment and the specific details of any specific ecological community. The central issue is the general existence of a long-term exponential growth rate at fixed regulating environment and the time-scale separation between this long term and the other time scales of ecological relaxation processes and fluctuations. Another appendix will discuss the century-old debates about competitive exclusion and the notion of ecological niche. The current state of the manuscript [8] is available for the reviewers. The mathematical appendix is the component that still requires significant work.

Environmental change

Frederik De Leander (Univ. Namur, Belgium) organized a cooperation of studying effect of global change on ecosystems and invited us to cooperate. The first paper from this cooperation was published recently in Ecology Letters [4]. In line with our approach the main question of the paper is, how the parameter-range allowing coexistence is affected by environmental change. It is far from trivial if anything can be stated generally in this respect.

Our paper considers the coexistence of three species in two different arrangements: two trophic levels with two resources, one consumer, or three trophic levels. We studied two types of environmental change: temperature change and pollution. We found some encouraging results, which were in agreement with field data on macroinvertebrate counts in streams across continental USA, as a function of water chemistry variables.

Local interactions

The less developed aspect of our theory is the issue of local interactions, when the individuals are affected by their local neighbors, instead of the population, as a whole.

While this is a very natural ecological situation, most of the ecological theories neglect it, as too difficult. Local interactions are studied usually via individual-based modelling, without the help of analytic support. A small group of people develops analytic descriptions based on pair-approximation, but these efforts are not reconnected to the ecological worldview in any way.

We assume that locality will not invalidate our theoretical picture. A population with local interactions can be considered as a population structured according to the local environments of the individuals. If we develop a pair, or higher moment, approximation, then we can figure out the regulation structure and all high-level theories will be applicable. However, actually doing this for specific models remains a goal for the future.

Bianka Kovács in her thesis work [9] developed a model of competitive coexistence of sedentary organisms with local competition on a 2D continuous plane. The model had two distance scales: the distances of propagation and competition. The essential, and contra-intuitive, result is that locality narrows the parameter range of coexistence, when both distance scale becomes small. We think that the methods we developed directly generalize to more complicated interactions. Investigations into this direction should be continued in the future.

Ongoing thesis work of Gellért Kovács investigates different locality problem [14]. Huston & DeAngelis (1994) raised the issue that resources, e.g, soil water, are not necessarily homogeneously distributed, so counting them, as a single resource, is not necessarily correct. That time it was part of the wider debate about validity and usefulness of the competitive exclusion principle. The issue was forgotten when the whole debate died down into the mess mentioned above. Gellért will investigate.

Eco-evolutionary synthesis and controversies

Darwinian principles

The structure of our theory goes back to Darwin's theory. It's a complicated history. Darwin's non-mathematical and often vague ideas required further development and formalization. The independent formalization of the various sub-issues led to a rich but fragmented intellectual landscape. In recent decades, we have already witnessed a reunification process, both empirically and theoretically. The preprint by Pásztor & Meszéna [6] describes this history on the level of basic scientific principles.

It is a conceptual paper that reveals the fundamental principles required for any explanation of the evolution of biological diversity by connecting the explanatory structure of Darwin's theory and the basic assumptions and results of mathematical evolutionary and ecological theory.

The reconstruction of the fundamental principles of Darwin's theory, besides relying on Darwin's texts, summarizes the relevant research of the historians. The reconstruction of the operational principles of the theory of diversification relies on the theoretical literature and its reviews besides our own work. The paper also discusses the role and significance of these principles for evolutionary studies. A collection of citations supplements the paper.

The crucial population (adaptive) dynamical role of the competitive exclusion principle (Rule of Similarity) and the Principle of Trade-offs in Darwin's theory is demonstrated. Darwin's metaphoric language and concepts are replaced by operational concepts relying on mathematical theory. We formulated six conditions and eight laws as the results of the conceptual analysis of the explanatory structures of the theories. In summary, we concluded that the presented „set of conditions, principles, and logic assumes perspectives utterly different from those presented by the "all is well" framework.

First, the subjects of the principles are the reproducing entities which, depending on the mode of reproduction, may reproduce their alleles and their clonal or species identity – not just genes. Second, the theory aims to reveal the necessary conditions of diversification and extinction instead of determining the conditions of "evolutionary," i.e., gene frequency change. Third, feedback loops, i.e., interactions between the reproducing entities regulating their populations, provide the vantage points, not only those "basic processes" that influence allele frequencies."

Cryptic species

A species pair is called cryptic, if they look identical, but genetic analysis finds them reproductively isolated. Lack of fitness difference between them is the usual, but debatable assumption. Discussion about cryptic species is deeply interwoven with the controversies about competitive exclusion. We have two, unrelated, contributions to this debate.

While the naïve interpretation of competitive exclusion rules out the possibility of coexistence without niche segregation, (neutral) coexistence of ecologically identical species is not mathematically impossible: there is no fitness difference between them, either. Then the question arises: how such a species pair can emerge? McPeek (2019) suggested an interesting solution. Originally, the two species adapted to two different resources. Then, a change in the environment caused them to converge to the same fitness optimum, while remaining reproductively isolated.

In response [2] we showed that the proposed mechanism would only lead to actual coexistence in the converged state if fitness neutrality were maintained continuously during the whole process. It required fine-tuned parameter settings and fully symmetrical staring conditions. E.g., the final optimum should be exactly half-way between the original trait values. Such a special case is highly improbable to be found in nature, therefore convergence is not a probable mechanism for the formation of similar, ecologically equivalent cryptic species.

While neutral coexistence of identical species is mathematically possible, it is expected to be lost over a very long timescale via demographic fluctuations. Gómez-Llano et al. (2021) suggested an interesting new possibility: maybe sexual interactions can maintain regulated coexistence of ecologically equivalent species. This is in line with our feedback-centric approach, but the feedback now is not an ecological one. Fanni Adina Fébert investigated this suggestion in her BSc thesis [13]. She demonstrated in a mathematical model that at least one of the proposed sexual feedbacks is able to maintain coexistence in a regulated way. The topic warrants further investigation.

Review on microbial experiments

The evolution of cross-feeding on metabolites has been studied intensively both in chemostats and batch cultures of *E. coli* for several decades. Liz Pásztor wrote a review paper [3] to demonstrate the importance of the regulating feedback loops and adaptive dynamics in interpreting results of these experiments.

In these experiments bacteria are regulated originally by a single resource, glucose. Therefore, competitive exclusion applies at the start of the process. Later, however, cross-feeding evolves between the organisms: some bacteria begin to consume products by others. This way a new regulation, a new regulating variable arises, allowing evolutionary branching. In the end state different strains of bacteria with different ecologies are living together in a regulated way.

The coincidence of evolutionary and ecological time scales provides an opportunity for demonstrating the mutual role of ecological and evolutionary principles in shaping evolutionary processes. Ecological principles define the ecological conditions under which adaptive branching can occur. However, the potential effects of the feedback environment within the cultures are ignored in the majority of studies. The paper relates the results of theoretical ecology to the selection processes detected in these systems and suggests a way for the inclusion of the ecological conditions into the experimental and modeling studies.

The review demonstrates that the interactions between cells must be mediated by the changing metabolite concentrations in the cultures and that modeling confirms that these changes can control the adaptive dynamics of the clones. In consequence, the potential results of evolution can be predicted at the functional level by evolutionary flux balance analysis (evoFBA), while the genetic changes are more contingent. It is shown that evoFBA follows the scheme of adaptive dynamics theory by calculating the feedback environment that changes during the evolutionary process.

Closing

With several colleagues we launched the International Initiative for Theoretical Ecology, initiated by Axel Rossberg (Queen Mary University, London). It is a charity registered in England & Walles. The goal is “to advocate and develop the role of theoretical ecology in both the scientific community and the public eye”. The PI is one of the trustees and the main organizer of the webinar series of the Initiative. The roughly biweekly series turned out to be a great success. So far, we have had 49 lectures by leading scientists and young researchers. The lectures are available on our YouTube channel. The lecture by the PI is essentially a summary of the work reported here.

Also, a few of us from the Initiative published a call for training more theoretical ecologist in TREE [1].

Outputs

Published

[1] A. G. Rossberg, G. Barabás, H. P. Possingham, M. Pascual, P. A. Marquet, C. Hui, M. R. Evans & G. Meszéna: Let’s train more theoretical ecologists – here is why.

Trends in Ecology and Evolution 34(9): 759-762 (2019)

[2] L. Pásztor, G. Barabás & G. Meszéna: Competitive exclusion and evolution: convergence almost never produces ecologically equivalent species.

American Naturalist 195(4): E112-E117 (2020)

[3] Liz Pásztor: Population regulation and adaptive dynamics of cross-feeding.

Biologia Futura 73:393–403 (2022)

[4] F. De Laender, C. Carpentier, T. Carletti, C. Song, S. L. Rumschlag, M. B. Mahon, M. Simonin, G. Meszéna & G. Barabás: Mean species responses predict effects of environmental change on coexistence.

Ecology Letters (2023)

Preprints

[5] G. Meszéna & U. Dieckmann: Three-phase transitions to reproductive isolation: The roles of utilization mismatch and residual selection.

First version: BioRxiv

New version: Manuscript

Poster at the Gordon Research Conference on Speciation (2023)

[6] L. Pásztor & G. Meszéna: Stable laws in a changing world: The explanatory structure of evolutionary theories over the centuries.

EcoEvoRxiv

Manuscripts under preparation

[7] G. Barabás, C. Song & G. Meszéna: Parameter sensitivity and coexistence in stationary aperiodic environments.

Manuscript

[8] G. Meszéna, G. Barabás, K. Parvinen, A. Szilágyi & L. Pásztor: First principles theory of ecological niche.

Manuscript

Student projects

[9] Bianka Kovács: Spatially explicit modelling of competing populations (2017)

[10] Miklós Gula: Joint dynamics of populations in stochastic environment: relative nonlinearity with colored noise (2019)

[11] Anna Rédl: Adaptive dynamics and speciation (2021)

[12] Krisztián Dobos: Modelling of speciation (2022)

[13] Fanni Adina Fébert: Ecological role of sexual interactions (2023)

[14] Gellért Kovács: Role of spatial resource distribution in plant ecology (in progress)

References

Barabas, G., R. D’Andrea, and S. M. Stump (2018) Chesson’s coexistence theory. Ecological Monographs 88:277-303.

Barabás, G. Meszéna & A. Ostling (2012) Community robustness and limiting similarity in periodic environments. Theoretical Ecology 5:265-282

Barabás, G., L. Pásztor, G. Meszéna & A. Ostling (2014) Sensitivity analysis of coexistence in ecological communities: theory and application. Ecology Letters 17:1479-1494

Barton, N. H., A. M. Etheridge & A. Véber (2017) The infinitesimal model: definition, derivation, and implications. Theoretical Population Biology 118:50-73

Chesson, P. (2000) Mechanism and maintenance of species diversity. Annual Review of Ecological Systems 31:343-366.

Geritz, S.A.H., É. Kisdi, G. Meszéna & J.A.J. Metz (1998) Evolutionary singular strategies and the evolutionary growth and branching of the evolutionary tree. Evolutionary Ecology 12:35-57

Gómez-Llano, M., R. M. Germain, D. Kyogoku, M. A. McPeek, and A. M. Siepielski (2021) When ecology fails: How reproductive interactions promote species coexistence. Trends in Ecology & Evolution, 36:610-622

Gyllenberg, M. & G. Meszéna (2005) On the impossibility of coexistence of infinitely many strategies. Journal of Mathematical Biology 50:133-160

Hardin, G. (1960) The competitive exclusion principle. Science 131:1292-1297

Huston, M. A. (1994) Biological Diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Huston, M. A. & D. L. DeAngelis (1994) Competition and coexistence: the effect of resource transport and supply rates. American Naturalist 144:954-977

Kisdi, É., S. A. H. Geritz (1999) Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. Evolution 53:993-1008

Lawton, J. H. (1999) Are there general laws in ecology? OIKOS 84:177-192

Levin, S. A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. American Naturalist, 104:413-423

McPeek, M. A. (2019) Limiting similarity? The ecological dynamics of natural selection among resources and consumers caused by both apparent and resource competition. American Naturalist 193: E92-E115

Mayr, E. (1942) Systematics and the Origin of Species. Columbia University Press, New York

Meszéna, G., M. Gyllenberg, F. J. Jacobs & J. A. J. Metz (2005) Link between population dynamics and dynamics of Darwinian evolution. Physical Review Letters 95: 078105

Meszéna, G., M. Gyllenberg, L. Pásztor & J.A.J. Metz (2006) Competitive exclusion and limiting similarity: a unified theory. Theoretical Population Biology 69:68-87

Pásztor, L., Z. Botta-Dukát, T. Czárán, G. Magyar & G. Meszéna (2016) Theory-Based Ecology: A Darwinian approach. Oxford University Press

Pennings, P. S., M., Kopp, G., Meszéna, U., Dieckmann, J. Hermisson (2008) An analytically tractable model for competitive speciation. Am Nat 171:E44-E71

Polechová, J., and N. H. Barton (2005) Speciation through competition: a critical review. Evolution 59:1194-1210.

Szilágyi, A. & G. Meszéna (2010) Coexistence in a fluctuating environment by the effect of relative nonlinearity: A minimal model. Journal of Theoretical Biology 267:502-512