Three-phase transitions to reproductive isolation: The roles of utilization mismatch and residual selection

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Dieckmann & Doebeli (1999) studied adaptive speciation with two diploid multilocus traits, an ecological and a mating one. Here we report a reinvestigation and analytic understanding. Frequency-dependent selection against intermediate ecological trait values drives evolution of assortativity. However, assortativity alone cannot ensure reproductive isolation in presence of segregation variance. Fortunately, the selection regime operates also to selectively eliminate genic (and segregation) variance. This process is slow for high locus number. The two processes together can result in strong reproductive isolation. The non-trivial aspect is that selection for assortativity and for decreasing variance are usually attributed to disruptive and stabilizing selection, respectively. Natural origin of this double personality of the selection regime is explained.

„Origin and Persistence"

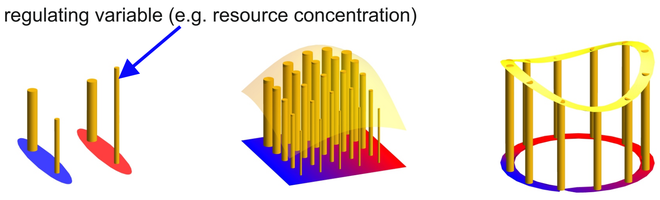
Coexistence = differentiation in regulation

General mathematics: Robust coexistence requires sufficient differentiation between the species in their interactions with the regulating variables (resources, predators, etc.). Weakening differentiation reduces the parameter range allowing coexistence.

G. Meszéna, M. Gyllenberg, L. Pásztor & J. A. J. Metz: Competitive exclusion and limiting similarity: a unified theory, Theor. Pop. Biol. 69:68 (2006)
*G. Barabás, L. Pásztor, G. Meszéna & A. Ostling: Sensitivity analysis of coexistence in ecological communities: theory and application. Ecol. Lett. 17:1479 (2014)
*(Papers dealing with complicated specific situations are cited here.)

Niche space

regulating variable (e.g. resource concentration)



Resources may differ in ether its own quality (e.g. size), or the quality of their location (e.g. cold, or warm habitat). They may be discrete, or form a continuum.

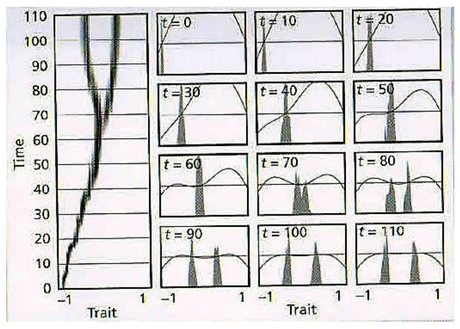
L. Pásztor, Z. Botta-Dukát, T. Czárán, G. Magyar & G. Meszéna: Theory-Based Ecology: A Darwinian approach. Oxford (2016)

Continuos coexistence? NO!

Is it possible for a continuum of species to coexist along a continuous niche axis?
Yes, but it is structurally unstable.
Ecology dictates discrete species.

M. Gyllenberg & G. Meszéna: On the impossibility of coexistence of infinitely many strategies. Journal of Mathematical Biology 50:133 (2005)
P. Szabó & G. Meszéna: Limiting similarity revisited. Oikos 112(3):612 (2006)
G. Barabás & G. Meszéna: When the exception becomes the rule: the disappearance of limiting similarity in the Lotka-Volterra model. JTB 258:89 (2009)
G. Barabás, S. Pigolotti, M. Gyllenberg, U. Dieckmann & G. Meszéna: Continuous coexistence or discrete species? A new review of an old question. Evol. Ecol. Res. 14: 523-554 (2012)

Regulated landscape --> adaptive dynamics



Evolution cannot branch on a frequency independent landscape.
Regulation causes the landscape to evolve.
Diversity of regulating factors often leads to branching evolution.

Origin *vs*. Persistence:
Coexistence is maintained by sufficient difference in the way of regulation, which tends to implement selection pressure for diversification.

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Individual based model

Question

We know that a population with high variance can live in an unselected equilibrium on a resource continuum, without selection for reproductive isolation.

Why speciate, then?

Hint: the unselected equilibrium is structurally unstable, just like continuous coexistence.

J. Roughgarden: Theory of Population Genetics and Evolutionary Ecology. Macmillan (1979)
J. Polechová & N.H. Barton: Speciation through competition: a critical review. Evolution 59:1194 (2005)

Model

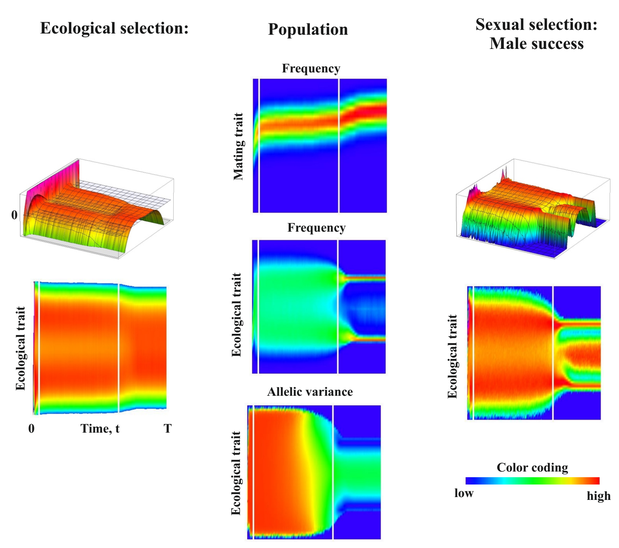
Modified from: Dieckmann & Doebeli (1999)
Aim: deeper understanding of transition
Novelty: High locus number & population size

Ecology: 1D resource axis, Lotka-Volterra competition
Evolving traits: ecological & mating, multilocus
Genetics: multilocus biallelic, additive, free recombination
Isolation: mating trait controls assortativity w.r.t. ecological one

(Meszéna & Dieckmann, BioRxiv)

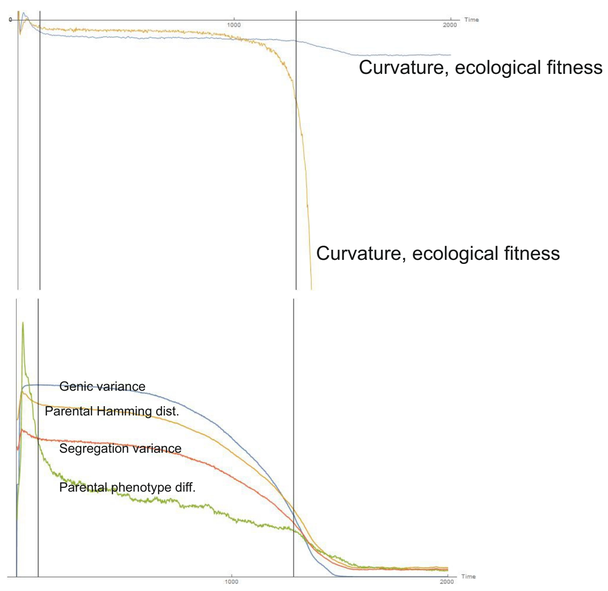
Results

(with platikurtic carring capacity and Gaussian competition kernel)



Three phases:
(1) Fast increase of variance, mismatch remains
(2) Slow transition to bimodality; allelic variance is erroded
(3) Fast completion of isolation via sexual selection.

Time dependencies



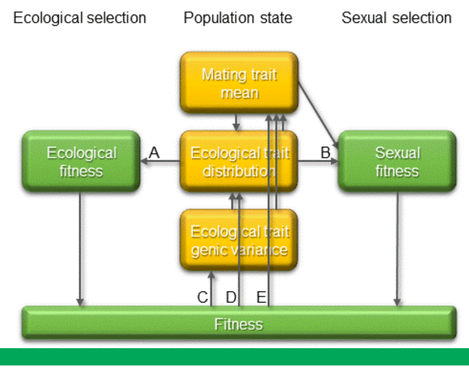
Interpretation

Analitic approximation

High locus number:
Population distribution and gene frequency on an specific locus becomes independent in the limit.

Numerical experience:
The population remains approximately homogeneous both for the mating trait value and for the gene frequencies of the ecological trait.

Three dynamical variables:
(1) Distribution of the ecological trait
(2) Allelic variance of the ecological trait
(3) Mating trait value



How does it work?

(1) The speciation process is intuitively understandable in the high, but not infinite, locus limit, as a correction to the infinitesimal model.

(2) Resource consumption of a random mating population generically cannot match perfectly a wide resource distribution, even if population variance becomes sufficiently large. The emerging residual selection may select for reproductive isolation.

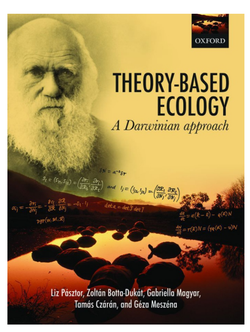
(3) Reproductive isolation developes when selection increases assortativity *and* decreases allelic/segregation variance. This condition seems to require disruptive and stabilizing at the same time. Actually, the two kinds of selection depend on different properties of the fitness function and can be understood exactly.

(4) Selection for decreasing variance becomes slow for high locus number, when the infinitesimal model is approached. Therefore speciation process may require prolonged time, during which gene flow is decreased, but still significant.

(6) The process cannot be described by the symmetric (hypergeometric) approximation, because it assumes maximal allelic variance.

Take home

Ecological speciation is expected to happen, when ecological conditions for coexistence are met and a mechanism for reproductive isolation is available.



An attempt to develop ecology on a clear and unified theoretical basis, which establishes also the clear ecological basis of origin of diversity.