

THEORETICAL BIOLOGY (7)

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Evolutionary Stable Strategies: Theory and Adaptive Dynamics (1.3.7)

Attempts at finding a general fitness concept applicable in a metapopulation context have shown that (a) it is impossible to neglect local chance effects due to the discreteness of the individuals, (b) in the general case it is necessary to determine the dominant Lyapunov exponent of the linear evolution equations for the frequency distribution of all states in which a local community of residents and mutants can be. Only in relatively special cases this system reduces to something more simple. In particular we have developed an effective approximation procedure for the special case where (a) all patches are emptied once a year, to be started again from a well mixed disperser pool, (b) the patches fill up early in the season, and (c) the mutant differs so little from the resident that within patch selection is relatively slow.

We proved for communities described by differential equations that the invasion of a sufficiently similar mutant into a stable point equilibrium leads to a full substitution of the resident by the mutant, after which the community gets to a point equilibrium on the same branch (in the sense of bifurcation theory).

We have, in collaboration with Gza Meszina (Budapest, Hungary), made a start with the development of a bifurcation theory for the evolutionarily singular points of generalised Lotka-Volterra models. Lotka-Volterra models have the advantage that the invasion exponents of their adaptive dynamics can be determined explicitly. Earlier attempts at developing a bifurcation theory for evolutionarily singular points foundered due to the impossibility of finding adequate normal forms. By starting from a known algebraic form this problem can be circumvented. The interaction coefficients of Lotka-Volterra models are replaced locally by polynomials in the strategy variables. We made the first steps towards a classification of the various generic bifurcation patterns in terms of the coefficients of these polynomials.

Together with Yoh Iwasa (Fukuoka, Japan) we developed a model to explain the evolution of genetic redundancy. It is assumed that the fitness depends on the

concentration of a costly gene product, a minimal amount of which is necessary for the development of the optimal phenotype. Errors during development lead to a variable effectively available amount of the gene product. It turns out that there are conditions under which a second gene making the same product can invade if initially only one gene is around which produces the optimal amount of product. These conditions depend on the error probability and the production costs. This conclusion is surprising since the mutants bear higher costs than the residents, and have a higher variance in the amount of available product. Our model shows that, contrary to the current assumption in the literature, gene duplications can evolve under constant environmental conditions.

Together with Olivier Glaizot and Chris Cannings (Sheffield, England) we generalised earlier results about patch depletion under competition for parasitic interactions, to the case where the pay-off of parasites that have already left can still be changed due to the occurrence of superparasitism.

Population Dynamics and Biological Monitoring (2.1.7)

We generalised our results for sequential models for analysing environmental monitoring data, reported in previous annual reports, to higher dimensional and spatial time series.

We extended our previous results on special models for the continental expansion of focal plant diseases, to a number of alternative cases, and embedded the initially purely mathematical results in a richer biological background.

A lot of work was invested in editing a multi-author volume on the mathematical description of, and methods for analysing spatial mechanisms in population dynamics.

Fylogenetic Relationships and Speciation (2.2.7)

In vicariance biogeography three assumptions are used to infer the history of areas from phylogenetic information. For wide-spread taxa these assumptions form a neat hierarchy, so that the sets of compatible area cladograms found under assumptions 0 to 2 are nested, 2 being the least restrictive assumption, which consequently goes with the largest set of cladograms. For sympatric taxa the relationship between the various assumptions is more complex. The inclusiveness of the assumptions was tested for three different methods (Component Compatibility, Brooks Parsimony, and Component Analysis) for all possible cladograms for 3, 4, or 5 taxa.

The folding pathways of viroid RNAs were studied

using computer simulations by the genetic algorithm for RNA folding. The folding simulations were performed for potato spindle tuber viroid (PSTVd) RNAs of both polarities. Simulations of the PSTVd minus strand folding during transcription reveal a metastable hairpin, formed in the left terminal domain region of the PSTVd. Despite high sequence variability, this hairpin is conserved in all known large viroids of both subgroups of PSTVd type, and is presumably necessary to guide the folding of the previously known HP11 hairpin which is functional in the minus strand. The folding simulations are able to demonstrate the changes in the balance between metastable and stable structures in mutant PSTVd RNAs. The stable rod-like structure of the circular viroid (+) RNA is also folded via a dynamic folding pathway. Furthermore, the simulations show that intermediate steps in the forced evolution of a shortened PSTVd replicon may be reconstructed by a mechanistic model of different folding pathway requirements in plus- and minus-strand RNAs. Thus the formation of viroid RNA structure strongly depends on dynamics of competition between alternative RNA structures. This also suggests that the replication efficiency of viroid sequences may be estimated by a simulation of the folding process.

In collaboration with the group of Dr. K. Gerdes (Odense, Denmark), a phylogenetically conserved folding pathway of mRNAs of *hok* family genes is investigated. The folding pathway is evidenced by computer simulations, phylogenetic comparisons and experiments. Such a pathway is necessary to ensure functioning of post-segregational killing mechanism that stabilises inheritance of plasmids by killing plasmid-free cells.

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