The Contribution of the Genetics of Populations to Ecosystem Stability

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Abstract

Taking a system theoretic approach, ecosystem stability can be viewed in terms of adaptedness and adaptability of an open dynamical system to its environmental conditions. The goal of each adaptational process consists in the maintenance of the ecosystem's identity as defined by characteristics of the material, energy, and information balance that are determined by the system's external conditions. The information balance controls the material and energy flows (conversions). Since its material basis is DNA or RNA, this information is organized in the genetic systems of populations, making these the units of adaptation and evolution. The genetic foundation of ecosystem stability thus lies in populations. Interspecific mechanisms of adaptation are put in relation to their intraspecific counterparts, and these are distinguished with respect to their physiological and (micro-)evolutionary components. On the interspecific level, the ecological key species spectrum is closely associated with the ecosystem's identity. Hence, extinctions or substitutions within this species spectrum cannot serve as adaptational mechanisms at this level. Interspecific mechanisms of adaptation may rather be important on the level of the ecological companion species spectrum. The possibility of opportunistic adaptation on the population level associated with "ecologically antagonistic pleiotropy" is pointed out to link adaptational processes at different ecosystem levels in a way that may fundamentally destabilize the system. In conclusion, some common and some more recent methods and parameters of population genetic data analysis are recapitulated with reference to their relevance for the analysis and characterization of adaptational processes and potentials.

Key words: ecosystem stability, system theory, adaptation, open dynamical system, population genetics.

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Introduction

Conditions for stability of ecosystems are usually formulated in terms of biological diversity, temporal and spatial variation in abiotic environmental conditions, or patterns of interaction among species (see the contributions to the book edited by SCHULZE and MOONEY, 1993, or the book of PIMM, 1991, for example). Genetic variation within species is rarely considered in this context, even though it is generally recognized to be a prerequisite for adaptation to both abiotic and biotic factors. Therefore, the involvement of genetic mechanisms in processes of ecosystem stabilization above the species level is usually treated in a more or less implicit manner. The present paper will attempt to clarify this situation by considering the role that genetic variation can play in ecosystem stability.

The following considerations will be based on a system theoretic approach with emphasis on verbal rather than technical formulations. Even though these considerations will be heavily influenced by the characteristics of forest ecosystems, the underlying intention is to develop generalizable concepts. Thus, the concept of adaptation will serve to draw a consistent connection from the level of the ecosystem to the genetically relevant level of the population with reference to the principles of stabilization. The system theoretic approach is a cogent one and continues current tendencies, the experimental aspects of which have been greatly stimulated by research in the field of forest decline (see e.g. the "IMA-Querschnittseminar, Wirkungskomplex Stickstoff und Wald" of the Deutsches Umweltbundesamt, 1995).

Ecosystems as Open Dynamical Systems

Open dynamical systems are characterized by the fact that changes or modifications of their states are governed not only by internal but also by external forces (system inputs). Ecosystems are therefore open dynamical systems, the inputs of which are usually referred to as environmental conditions. The reactions of ecosystems to their environmental conditions and their internal forces define the system outputs, which in turn depend on the current state of the system (for an illustration see *Figure 2*).

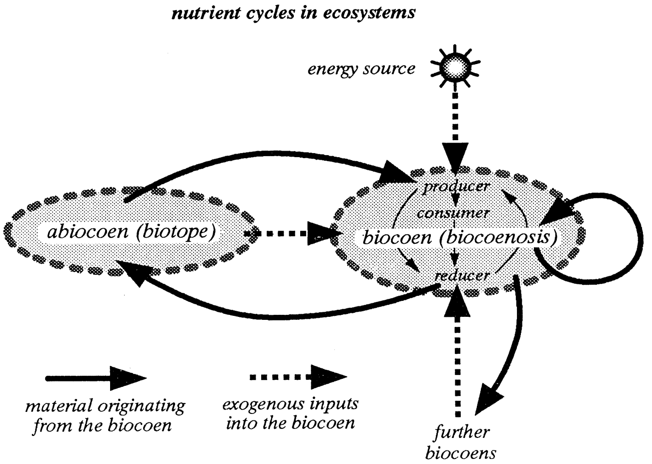

Figure 1. – Nutrient cycle of an ecosystem: Schematic representation of cyclic material conversion driven by an energy source, realized by the biocoen, and drawing from the abiocoen as part of the cycle. Material passing from the abiocoen to the biocoen may, to considerable degrees, originally derive from the biocoen.

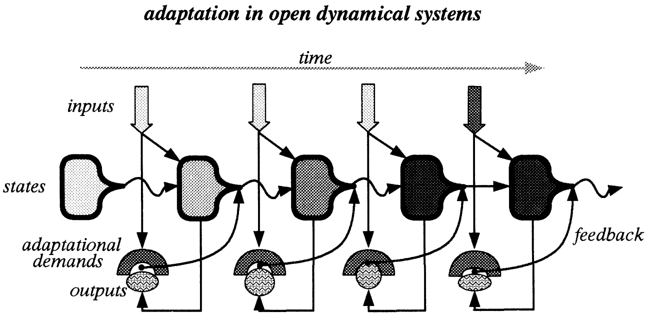

Figure 2. – Adaptation in open dynamical systems: As environmental conditions, inputs determine the adaptational demands, initiate system reactions as outputs via mediation of the system's state, and affect the state dynamics. Adaptedness of outputs to adaptational demands is symbolized by the fit of the 2 pertaining symbols. Feed back arrows indicate the control of the state dynamics by the degree of adaptedness.

Ecosystems can be subdivided into 2 elementary subsystems comprising the biocoen (biocoenosis) and the abiocoen (biotope). Under the conditions set by the abiocoen, the biocoen provides the prerequisites for maintenance of the nutrient cycle through producers, consumers, and reducers. This can be realized partially in closed form within the system and in other parts via the balance of system inputs and outputs. Some nutrient cycles can be closed within the biocoen, in which case they would comprise an elementary subsystem. As a rule, however, these cycles pass through both the biocoen and abiocoen subsystems. This roughly summarizes the generally accepted principles of ecosystem processes (see e.g. the first 4 chapters in the textbook of ODUM, 1971; also compare the explanations of SOLBRIG, 1993, p. 108; *Figure 1* illustrates in gross simplification the components of the ecosystem's nutrient cycle which are of relevance here).

Stability in Open Dynamical Systems

In closed dynamical systems (where system inputs do not exist or are invariant, and where the state dynamics are governed solely by internal forces), which are typical of the model systems of classical physics, stability is chiefly referred to as the potential for stationary system states (or sets of states) to recover from temporary disturbances. These states are commonly identified with characteristics typical of the overall system. Such concepts can be extended to open systems only within narrow limits, since disturbances that take the form of continually (and not just temporarily) varying inputs are an integral part of open systems. Hence, in addition to the internal forces, independently acting external forces participate in the control of the state dynamics (with reference to forest ecosystems see e.g. chapter 1.2.2.1 in RÖHRIG and BARTSCH, 1992). For this reason, the concepts of stationary states or sets of states (such as cycles) are not sufficient for the determination of a system's characteristic attributes.

A generalized concept of stability is therefore indispensable for the analysis of open systems. In such a concept, stability of a system's characteristic attributes (its *identity* or *integrity*) does not necessarily require stationarity of certain system states. The emphasis is now rather on a system's capacity to maintain its characteristic attributes under not just temporarily acting disturbances. This may entail changes in system state. Persistence in the sense of maintaining identity under varying external conditions (inputs), in turn, captures the essence of adaptation and thus relates to an innately biological principle. The implied generalization also allows the expressive definition of *stability in open dynamical systems* as adaptedness or adaptability to their inputs. However, the usage of this term requires more precise explanation of the system theoretical concept of adaptation, particularly in ecology.

The Notion of Adaptation

As indicated above, the generalized concept of adaptation is closely associated with the maintenance of the identity of a system influenced by forces of external origin. Thus, *adaptedness* to the respective external conditions (inputs) can be claimed for a system if it has the capacity to react to these conditions in a manner not impairing its identity or integrity. The *adaptational demands* to be met in order to maintain identity are determined by the system's inputs. The system's reactions (outputs) are then required to conform with these demands so as to establish adaptedness of outputs to inputs. It has to be taken into account that a system's reactions to its inputs basically depend on its current state, while the adaptational demands are solely determined by the system's inputs (this representation of adaptation goes primarily back to MESAROVIČ, 1968 a and b; see also GREGORIUS, 1993; *Figure 2* may serve as an illustration).

Adaptation, in turn, describes all processes contributing to the attainment and maintenance of adaptedness to the external conditions, and which thus serve to secure the system's identity. This includes the possibility that an adaptational process fails. If, however, the adaptational process is successfull in ultimately reaching persistent adaptedness, *adaptability* to the respective conditions can be claimed. In this case, situations of insufficient adaptedness are always of a temporary nature, even though they can be considered as characteristic of adaptational processes.

If adaptedness cannot be achieved without state changes, the system is forced to deploy its intrinsic dynamical capacities. The resulting state changes entail further opportunities for adaptation of system reactions to changed conditions. Since different initial states qualify the system for different adaptational reactions, the *adaptational potential* is defined for a specified initial state and reflects the set of all inputs to which the system is adaptable when starting from this state. State changes may or may not be involved in the process of adaptation, and this gives rise to the distinction between *structural* and *regulatory adaptation*, respectively (GREGORIUS, 1993).

A basic example of adaptational processes on the ecosystem level is provided by the balancing between material input and output. This balance appears to be frequently realized in the form of steady (to be distinguished from stationary) states, which gave rise to considering the establishment of such states as a general stability characteristic of ecosystems (see e.g. ULRICH, 1992). As the above explanations confirm, the establishment of steady states has to be viewed as a special case of the more comprehensive concept of adaptation and adaptedness (also cf. GREGORIUS, 1993). Therefore, the observation of steady states may have only limited significance in a general attempt to characterize stability conditions for biological and, in particular, for ecological systems. The present explanations on stability in open dynamical systems moreover demonstrate that, in general and in contrast with conventional concepts, *stability of an ecosystem state* becomes manifest in its adaptability as specified by its adaptational potential.

Control of Adaptational Processes on the Ecosystem Level

In every instance, the species composition of an ecosystem depends on the respective local living conditions. To allow for the establishment of persistent nutrient cycles, these external conditions (such as provided by the soil or climate) ought to be distinguished by a certain constancy or regular recurrence over time. Therefore, the *identity of an ecosystem* can be regarded as the totality of those characteristics of its material, energy, and information balance that are specifically determined by the system's external conditions. Adaptational or stabilizing processes of ecosystems should thus serve the maintenance of this system identity.

The fact that material conversion requires, releases or stores energy always guides studies of material and energy balances of biological systems in an obvious manner. In contrast, information frequently has a very vaguely defined meaning in connection with balances, and probably for this reason it has rarely been a subject of experimental causal analysis (cf. DEGEN and SCHOLZ, 1996). Basically, it can be stated that the *information balance* of an ecosystem determines the laws controlling the material and energy flows (conversions) of the system. Adaptation of these flows to variable external conditions is among the most fundamental tasks of such control. On the one hand, variability of the information controlling the adaptational processes is thus indispensable. On the other hand, a certain degree of constancy of this information is required in order to guarantee consistency of adaptational processes. Apparently, *this information must be of a biological nature, and has its material basis in the hereditary substance DNA* (or RNA in some cases), as is well known. The implied temporal continuity of this information is realizable only within populations, the genetic systems of which organize the information balance.

The *genetic system*, in turn, covers all mechanisms involved in the organization, expression (manifestation), creation, recombination, and maintenance of hereditary information, as well as its transmission over the generations and its dispersal over space and time. The direct control of adaptational reactions of the ecosystem therefore takes place on the level of the population, which makes populations the elementary *units of adaptation and evolution.* The genetic basis of ecosystem stability is thus located on this level.

Before entering into some of the details of adaptational mechanisms of populations and their effects on the ecosystem level, it is necessary to briefly refer to the special significance of populations as part of the species spectrum.

Species Spectrum and Ecosystem Stability

With respect to its significance for the maintenance of the nutrient cycle, the species composition of an ecosystem can be divided into the ecological key species spectrum and the companion species spectrum. Populations from the *ecological key species spectrum* are characterized by the fact that their removal from the community would, even under favourable conditions, be followed by a decoupling of the nutrient cycle. This spectrum forms the backbone of the system and its populations represent each of the 3 groups, producers, consumers, and reducers. They have an essential share in the determination of an ecosystem's identity. Reductions or losses of adaptability to variable environmental conditions among populations belonging to the ecological key species spectrum would have particularly grave consequences for the stability of the ecosystem.

The notion of companion species is applied in different contexts. For the present purpose, the significance of the *ecological companion species spectrum* lies in its effects on the adaptability of the populations of the associated key species spectrum. These effects may be of a *probiotic* or of an *antibiotic* nature, where the first is reflected in an extension and the second in a reduction of adaptability and thus of adaptational potential of the members of the key species spectrum. The probiotic effect of a companion species may be so strong that the identity of an ecosystem can be maintained under conditions that would have implied a collapse of the community in the absence this companion species (cf. e.g. the section starting at p. 34 in the textbook of FUTUYMA, 1986; BERTNESS and SHUMWAY, 1993; or GREGORIUS, 1994, 1995). Hence, in some cases the assignment of a species population to the group of the ecological key or companion species spectrum may be very difficult or even impracticable.

On the ecosystem level, structural adaptational processes are likely to be confined to changes in the ecological companion species spectrum. This form of *interspecific adaptation* may take place via substitution or simple loss of resident species, or it may imply the non-replacing establishment of a new species. *Intraspecific adaptation* represents a form of regulatory adaptation on the ecosystem level, and it accounts primarily for the elementary requirements of short-term adaptation. By definition, these processes do not involve changes in the species composition and can be considered as reactions to more or less regularly varying environmental conditions. As was emphasized above, the intraspecific adaptational potentials of the ecological key species spectrum are very likely to play a dominant role in the stabilization of ecosystems.

Adaptational Mechanisms of Populations

The regulatory or intraspecific capacities of adaptation on the ecosystem level trace back to the adaptational potentials of the populations. The population's adaptational mechanisms, in turn, consist of the physiological response ranges of its members on the one hand. On the other hand, these response ranges may vary on genetic grounds and under the control of the respective genetic system. Accordingly, one distinguishes *physiological* from *evolutionary* adaptational mechanisms, and these determine the regulatory and structural capacities of adaptation, respectively, on the population level.

Genetically caused variation in individual physiological response ranges increases the adaptability of a population solely by the fact that it implies adaptational (physiological) optima in different environments for different genotypes. In the absence of genetic variation among the members of a population existing in a heterogeneous environment, a certain fraction of the population would always be forced to exist under suboptimal conditions. Hence, genetic variation offers the chance to meet the variable demands of a natural environment with a variety of genotypes showing higher physiological adaptability or adaptedness to the respective conditions. By this a population also increases its adaptational potential. Furthermore, the genetic system enables forms of (micro-)evolutionary dynamics which even allows the maintenance of some genetic information that endows its carriers with insufficient physiological capacity to adapt to their environmental conditions. In a changing environment, this information can turn out to lay the basis for successful adaptation of the population and thus contributes to its adaptational potential.

A central, though largely ignored problem of ecosystem stability consists in the conflict that may arise from the adaptational pressures that force populations to react immediately and without having received any feedback on the long-term consequences of their reactions for the nutrient cycles. Hence, an *adaptational conflict* between different ecosystem levels may emerge if evolutionary adaptation of a population to an environmental factor (such as the development of resistance to a parasite) leads to the formation of morphological structures or to the secretion of substances that stress the ecosystem's nutrient cycle by impeding litter decomposition, for example. The developed structure would thus pleiotropically affect resistance and decomposability. In this case of *ecologically antagonistic pleiotropy*, the opportunistic adaptational success of a population may destabilize its ecosystem. Consequently, this opportunistic adaptation can persist only to the point where the impediment of the nutrient cycle acts back upon that population. A guard against such a threat would require mechanisms of the genetic system favouring the establishment of genetic variants in populations, which contribute to the stabilization of the ecosystem's nutrient cycle. On an interspecific level of adaptation, this task would have been carried out either by extinction of that population, if it did not belong to the ecological key species spectrum, or by substitution by a population representing a different species.

The classification of the different forms of intra- and interspecific interactions with respect to this apparent conflict may imply a special challenge. Intra- or interspecific competition leading to a more efficient utilization of limited resources, for example, would have to be considered with respect to its effect on the nutrient cycles in order to be able to evaluate its significance for ecosystem stability. As a result, the ecological and evolutionary relevance of competition might be looked at from a different perspective. The possibility that ecologically antagonistic pleiotropy links adaptational processes at different ecosystem levels may turn out to be an interesting and probably important source of new testable hypotheses on mechanisms of ecosystem stabilization.

To conclude and round out the present consideration, some of the population genetic methods will be recapitulated that are applied in order to obtain characteristics of the genetic structure that allow for inferences on the adaptedness and adaptability of populations. More detailed explanations of these methods can be found in HATTEMER et al. (1993), for example. GREGORIUS (1995) provides an overview with special reference to problems of adaptation and introduces new methods.

Genetic Parameters of Adaptation

Studies on adaptability or adaptational potentials of populations require genetic traits, particularly in the form of gene markers. The 2 basic characteristics of genetic markers, function and inheritance, can be used in different ways. Concerning function, genetic markers are of interest for studies of both physiological and evolutionary adaptation, where adaptation to special environmental conditions has priority.

Concerning inheritance, knowledge of the mode of inheritance is indispensible both for studies of descent and for representation of functions determined by the genetic background. The latter is realizable through genomic associations. In both of these cases the actual function of the considered genetic trait is of secondary relevance. Even DNA-segments of completely unknown function can be applied meaningfully here, provided they together with their methods and techniques of representation fulfill the conditions for a gene marker. Yet, it should be emphasized that for the study of adaptational potentials, many genetic traits are of interest for their functional aspects as well as for aspects of their modes of inheritance. Isoenzymes still constitute the most important and extensively used group of traits in population genetics.

Apart from a population's genetic state components, adaptational potentials are determined by additional state components, such as physiological, demographic (age class composition, system of sexuality and mating, spatial distribution, etc.) and social (competition, etc.) components. However, the genetic components of a population's state occupy a central position, since as the fundamental carriers of information they establish the principles according to which all of the other state components are realized. Unfortunately, almost insurmountable experimental problems are encountered when attempting direct identification of adaptational potentials, including their genetic components. Therefore, adaptational potentials are specified with the help of populational state characteristics representing *adaptational capacities*. The genetic adaptational capacities are therefore determined by characteristics of the genetic state components (the genetic structure) of a population.

With respect to the effective environmental conditions, *operational capacities of adaptation* can be distinguished from *latent capacities.* The former refer to capacities securing adaptedness to the current conditions; their structures are widely represented in the population. The latter constitute capacities of adaptation to currently non-prevailing environmental conditions, and their structures have low representation. The correspondence of regulatory and structural potentials of adaptation of a system's state to processes of adaptation to regularly and newly occurring environmental conditions, respectively, draws the connection to the operating and latent capacity of adaptation.

This roughly describes the frame within which a considerable part of population genetic methods and parameters for the characterization of adaptation can be classified. Taking account of its function and mode of inheritance, a genetic trait can be analysed as a direct subject of adaptation or as an accumulating indicator of phenomena of adaptation realized in the genetic background. This allows for studies of more specific and more general problems of adaptation. The following compilation of some of the commonly applied and a few more recently suggested methods and parameters follows this distinction. Each parameter is introduced by a short verbal definition and a statement as to its adaptational correspondence. If not obvious from the definition, a brief explanation of the adaptational context is provided.

Directly interpretable distributional characteristics of genetic traits

Diversity: Effective number of (number of prevalent) genetic types. It corresponds via the operating capacity of adaptation to the variety of currently operating adaptational demands.

Evenness: Degree of equality in the representation of genetic types. It corresponds to the equality in the effects of the currently operating adaptational demands.

Differentiation: Difference in genetic composition among several demes or populations. It corresponds to the adaptational differentiation among demes in the presence of sufficient gene flow among them. In the absence of adaptational differentiation gene flow would even out genetic differences.

Heterozygosity: Parameters of the distribution of the number or proportion of heterozygous loci of the members of a deme. They correspond to the degree of ontogenetically (temporally) varying adaptational demands when measured among adult members.

Profile separation: Distinguishability between prevalent and rare types in frequency profiles (absence of types of intermediate frequency). It corresponds to the distinguishability between genetic types with operating and with latent adaptational function; it enables estimation of the shares of operating and latent capacity in the total capacity of adaptation.

Distributional characteristics of genetic traits serving as background indicators

Genomic association: In combination with the respective mating systems and modes of inheritance, the mutual functional and structural relationships between large parts of the genome can lead to the establishment of stochastic associations between these parts on the population level (genomic association). With the help of genetic traits, these associations can be utilized to characterize processes or states in other parts of the genome that are not accessible to direct observation (genetic background).

(1) Capacities of adaptation to stressing environmental changes – they can be quantified by comparison of distributions of genetic traits in different phenotypic groups.

(2) Parameters of heterozygosity – based on suitable knowledge on species-specific characteristics of the reproduction system (selfing, reproductively effective deme sizes, etc.), these parameters provide information on the adaptational signifi-

cance of heterozygosity under the respective environmental conditions of a population (associative selection).

(3) Selection parameters – they aid the estimation of lower bounds of intensities of adaptational processes in the genetic background (selection load).

Reconstruction of descent: Differences in genetic traits can be utilized in various ways for the exclusion of identity by descent of their carriers. Based on this principle, methods of reconstruction of descent may serve the estimation of quite different elementary determinants of adaptation.

(1) Parameters of the reproduction system – refer to estimation of self- and cross-fertilization, preferential mating among neighbours, functional sex, reproductively effective deme size. The associated parameters are directly related to the capacity of a population to maintain genetic polymorphisms and thus the potential for adaptation for which they code.

(2) Dispersal parameters – estimate pollen and seed dispersal.

(3) Rates of gene flow – specify degrees of fragmentation and reproductive isolation. Together with the dispersal parameters, they provide information on the extent to which populations can enlarge or restore their potentials of adaptation when needed (metapopulation principle).

(4) Assurance of provenance – can be achieved with the help of genetic methods of exclusion of common descent by way of comparing the potential descendants (reproductive material) with claimed parental (basic) material. This assures primarily that the genetic basis for adaptation claimed for the original material is sufficiently represented in the derived material.

(5) Phylogenetic relations – chiefly concern opportunities for reconstruction of macro-evolutionary relationships between populations and species. Apart from general aspects of biological systematics, problems of adaptational history (migrational paths, variation in population size, selective reduction, hybridization, introgression, etc.), and thus of delimitation of species-specific potentials of adaptation, can be treated.

It should be emphasized that, as mentioned above, the validity of most of these methods depends on certain assumptions which may need testing. Particularly in the first section about directly interpretable genetic traits, the assumption of adaptiveness of the trait is implied in many of the statements. Yet, for many genetic markers such as isozymes, there exists still some disagreement on their adaptational significance (see e.g. Savolainen and Hedrick, 1995; as opposed to Gregorius and Bergmann, 1995). In contrast, in the second section about background indicators, selective neutrality of the applied genetic marker can be desirable for some of the problems mentioned under both of the headings ”genomic association“ and ”reconstruction of descent“. The early paper of Langner (1952) gives an excellent, still up-to-date account of the likelihood that common forest management practices exert selective effects. Such detailed pre-information may be very helpful in formulating hypotheses on the degree of selection that is to be expected in the genetic backgrounds of the respective markers.

Finally, explicit consideration of knowledge available about other state components of a population, such as concerning its demographic characteristics (see above), may provide important details with direct implications for the estimation of adaptational capacities. Among these details are effective population sizes, mating system characteristics, and spatial distribution. Genetic markers may then be applied as a tool aiding further specification and validation of the estimations.

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