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# Preface

Temporal and spatial variability is one of the intricacies of the real world that ecologists have long been aware of but have by and large ignored. In the 1960s and 1970s, theoretical ecologists were busy with other issues, and the study of variability had to wait. Incorporating variability into theories of competition and predation tends to make things more complicated, conceptually and mathematically — to say nothing about the work of the experimentalist. It seems reasonable enough that models were first formulated and many problems were solved in the case of a constant environment, with the tacit assumption (and hope) that variability would not make a big difference.

Today, some of the most interesting developments in theoretical and population ecology have much to do with variability, and with situations in which the very existence of a phenomenon, for example, the coexistence of competitors, crucially depends on variability. This is the reason why a number of ecologists active in this field were invited to lecture at the Nordic Council for Ecology (NCE) post-graduate course on temporal and spatial variability in population ecology. The meeting was held at the Hyytiälä Forest Research Station, southern Finland, on 21 to 25 September 1987. This issue of *Annales Zoologici Fennici* includes eight lectures given during the meeting and one paper that was submitted independently.

It is clearly impossible, with this collection of nine papers, to provide a comprehensive overview of the ecological significance of temporal and spatial variability — the field is huge, in comparison with the limited funds that were available to invite speakers. These papers nonetheless cover several themes that are currently under intensive study. Most of the papers are reviews, and many of them discuss a healthy mixture of theory, experiments and observational data. It is hoped that this issue will be of value to population and community ecologists, including post-graduate students, interested in temporal and spatial variability in ecology.

The papers have not been divided into separate categories, but it may be helpful here to briefly outline the topics that are covered and to indicate which papers are related to each other.

There are four papers dealing primarily with temporal variability. As Chesson & Huntly point out, the general feeling of many ecologists is that temporal variability should make the coexistence of competitors easier. This is not always the case: in some models and under certain assumptions coexistence is facilitated by temporal variability, but other assumptions and other models lead to the opposite prediction. Chesson & Huntly develop a general model incorporating the different elements that affect coexistence in a variable environment. They emphasize how the community level phenomenon of coexistence often crucially depends on the life history traits of the component species. It is also important to realize that the "new" non-equilibrium theory by no means implies that the "old" equilibrium theory can be ignored; Chesson & Huntly are able to provide, for a particular model, a coexistence criterion that involves both equilibrium and non-equilibrium mechanisms.

Two botanical papers discuss temporal variability in plant communities. Liljelund, Ågren & Fagerström demonstrate that the lottery model of competition for space can generate successional changes in species composition, based only on variation in species' lifetime seed production and longevity. If species are selected so that they have complementary seed production and longevity, the species may be able to coexist in the same community without any resource partitioning. Furthermore, if the abundance of all species is perturbed to a low value — such as occurs in the beginning of secondary succession — the model predicts an early dominance by short-lived species with high seed production, which are gradually replaced by long-lived species with lower seed production. This model provides a simple "null hypothesis" for secondary succession, incorporating only the most essential life history parameters.

Grubb's paper discusses an aspect of plant population ecology that has remained little explored in the literature, the degree of coupling of disturbance events and recruitment in plant communities. Grubb examines a continuum from tight coupling to no coupling at all, and gives a range of examples from in between. The different kinds of seed banks in plants are related to this continuum, and the implications for regional persistence are discussed in this framework.

The succession model of Liljelund et al. is based on an extreme assumption in Grubb's scheme, this being that all species germinate immediately after the disturbance event.

Multiannual dormancies in plants may have two different functions — the timing of germination to coincide with a favourable period for seedling growth, and "bet-hedging", spreading the germination of offspring over several years to minimize the possibility of total failure due to an exceptionally bad year (note that bet-hedging generally assumes parental control over dormancy). Multiannual dormancies with these functions are not restricted to plants. Hanski reviews what he calls extra long diapause in insects: some individuals miss one or more breeding opportunities by spending longer in diapause than others in the population. Extra long diapause may be achieved either by entering diapause earlier, or by staying in diapause longer than others in the population, and diapause induction may be density-independent or density-dependent. These possibilities combine to produce a rich variety of interactions between life histories and population dynamics, as illustrated by Hanski with numerous examples. In their paper, Chesson & Huntly divided life history traits into "buffers" and "amplifiers" on the basis of their effect on coexistence in a variable environment. Risk-spreading multiannual dormancies function as buffers, though one does not need to invoke interspecific competition to explain their evolution in the first place.

Another set of four papers explores spatial variability, covering predator-prey and competitive interactions in patchy environments.

Hassell & May discuss the dynamics of coupled host-parasitoid interactions in patchy habitats. Patchiness is generally considered to promote stability in these interactions but, contrary to a widespread belief, the reason why patchiness is important is not related so much to spatial density-dependence as to increased variation in the likelihood of different prey individuals being parasitized. Regardless of whether parasitism is spatially density-dependent, inversely density-dependent, or density-independent, aggregated parasitism tends to promote stability. As Hassell & May point out, their conclusions raise serious questions as to exactly what should be measured in the field if one is interested in understanding the dynamics of host-parasitoid interactions. No definite answer yet exists.

The focus of Taylor's paper is at the regional (metapopulation) scale, in systems of local populations connected by dispersal. Does dispersal among local populations increase the persistence of predator-prey interactions with unstable local dynamics? To answer this question Taylor presents a comprehensive review of the relevant theory, and he summarizes the few laboratory and field studies that are available. Taylor concludes that a spatially divided population structure may indeed enhance regional persistence, provided a sufficient degree of asynchrony exists in the dynamics of local populations. The main issue is how this asynchrony is maintained. Several unanswered questions still await theoretical studies, but the greatest lack now is in field studies attempting to assess the role of dispersal in natural predator-prey interactions.

Another pair of related papers, by Ives and Marino, focus on competition in patchy environments. Coexistence in patchy habitats is often facilitated by classical resource partitioning, as is the case in non-patchy habitats, but species may also coexist due to extinction-colonization dynamics, and a trade-off between dispersal and competitive abilities, as first suggested by Hutchinson and Skellam in 1951. Ives reviews a model which provides a third possible explanation, and which is particularly relevant for insects breeding in ephemeral, patchy microhabitats, such as carrion, dung and fallen fruits. The key point in this model is that intraspecifically aggregated spatial distributions of the competing species shift the balance between intraspecific and interspecific competition towards relatively stronger intraspecific competition, and thereby facilitate coexistence. Ives describes the model assumptions and predictions, and he reviews examples from the literature and from his own studies on carrion-breeding flies. It is worth emphasizing that the crucial point is not spatial aggregation, as such, but large variance between individuals in the frequency of competitive interactions; spatial aggregation is only one — though probably very important — mechanism causing such individual differences.

There is a noteworthy common element between the host-parasitoid models reviewed by Hassell & May and the competition model reviewed by Ives: in both cases intraspecific aggregation increases intraspecific competition and reduces that species' effect (competitive or predatory) on the other species. One could even picture the host-parasitoid interaction as competition between a superior (parasitoid) and an inferior competitor (host), both competing for the same patchy resource, host pupae, notwithstanding that resource renewal is here dependent on the number of "inferior" competitors surviving to breed. Stability is promoted, in this perspective, by sufficient parasitoid aggregation leaving enough "resource patches" for the host to survive. The analogy applies, however, only to within-generation effects of aggregation, the between-generation dynamics of competition and predator-prey interactions being fundamentally different.

Marino reports a case study of four species of mosses in the family Splachnaceae with a unique life history: the species colonize dung pats using dung-visiting flies as vectors. These mosses are singularly suitable for a detailed, experimental analysis of dispersal and competition, the two key processes in systems of competing species in patchy environments. Marino examines the various mechanisms that may facilitate coexistence at local, regional and continental scales. Processes occurring at the intermediate scale are found to be most significant for coexistence, suggesting that regional dynamics are indeed the key to coexistence in this system.

The papers by Marino and Taylor complement each other by examining competition and predator-prey interactions, respectively, at the metapopulation level. Taylor emphasizes how the regional persistence of a predator and its prey depends on asynchrony of their dynamics in different local populations. The same applies to competitors that cannot coexist locally.

The final contribution, by Pamilo, reviews genetic variation in heterogeneous environments. Much of the genetic response of populations to environmental variability is due to indirect effects, environmental variability first affecting population demography (ecology), which affects the processes determining genetic variation. Pamilo's message is that most natural populations are less, not more, heterozygous than predicted by the null model, the neutral theory of genetic variation. The real question, Pamilo concludes, may be how environmental variability reduces rather than how it maintains genetic variation in populations. It may be recollected here that Chesson & Huntly emphasized how variability may increase, decrease, or have no much effect at all on species diversity — but what happens in the real world is a challenge to all of us.

If one particular aspect of the talks given during the meeting and the papers in this issue should be singled out, I would choose the interaction between species' life histories and their population dynamics. The questions — how the dynamics of populations and communities depend on the life history attributes of the species, and vice versa — are not unknown to ecologists, but this is a field in which further studies can make significant contributions and improve our understanding of nature. Surely it is a welcome sign of maturation when the previously distinct fields of behavioural and evolutionary ecology (individual ecology), population ecology and community ecology are finally and, one hopes, irreversibly merging together.

The ambience during the meeting was genuinely friendly and warm — and not only in the sauna. The credit goes to all the participants from the different Fennoscandian countries, the UK, and the USA.

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