Richard Law

Life in the Undergrowth

Born: London 1950. First degree: 1971, University of York: Biology. PhD: 1975, University of Liverpool: Colonization and evolution of life histories in *Poa annua.* Research Fellow: 1975-1976, University College of North Wales, Bangor. Lecturer: 1976-1983, University of Sheffield. 1983-1996, University of York. Reader, 1996- present. Guest Scientist: 1992-1993, Forschungszentrum Jülich. Research interests: Plant community dynamics; Dynamical systems theory in ecology; Assembly of ecological communities; Management of biological resources; Evolutionary dynamics of symbioses; Evolution of ecological and genetic systems. — Address: Department of Biology, University of York, PO Box 373, GB-York YO1 5YW.

I came to the Wissenschaftskolleg to work on an interdisciplinary project with a theoretical physicist, Ulf Dieckmann, and a plant ecologist, Tomas Herben. Our programme was to develop techniques for the analysis of spatio-temporal dynamics of plant communities. For me, this was a once in a lifetime opportunity to bring together two seemingly remote subject areas in search of a common goal, and I am very grateful to the Wissenschaftskolleg for making it possible.

Plant community ecology has developed in two directions: the analysis of pattern of plants (space), and the analysis of community dynamics (time). Neither of these is sufficient as a basis for understanding the dynamics on its own, because these dynamics depend on interactions in small spatial neighbourhoods; one needs to study the spatial and temporal processes together. In spite of a widespread awareness that this is so, plant ecology is far from achieving a successful synthesis in the form of a spatio-temporal framework for community dynamics. This is due to both the practical difficulties of obtaining the data needed and the lack of appropriate mathematical tools. But some data sets are now becoming available and developments in mathematics and theoretical physics have reached a stage such that a synthesis may be possible. It was this that we set out to explore.

Tomas Herben was able to place at our disposal twelve years of detailed spatio-temporal data on a montane grassland in the Northern Bohemian Mountains in the Czech Republic. These data were to

provide an anchor for the development of our ideas. The intention was to construct stochastic models based on the primary events of birth, death and movement of plants, and to estimate the parameters of the models from the field data. Investigating the dynamics of such models is problematic because of their very high dimensionality, and this motivated the second main part of our programme: to explore ways in which the dimensionality could be reduced without losing the spatial information essential for the dynamics.

We made substantial progress on the problem, although inevitably we would like to have made even more. Constructing the stochastic models both in discrete and continuous space was relatively straightforward. Parameter estimation was more challenging. In particular, estimating the strength of interactions between species turned out to be a major and interesting problem to solve. These interactions are the building blocks of community ecology and are responsible for communities being more than just the sum of the species they contain. But the interactions are notoriously difficult to determine. Plant ecologists have tried experimentally perturbing communities, to see what changes occur to one species when the density of another is altered; they have also tried using properties of plants that might be said to be related to their interactions. We were able to develop two new techniques from which the interactions among species can be estimated non-invasively, simply using information on the turnover of species on a fine spatial scale. These techniques hold promise as a key for unlocking some secrets of plant communities that have been well guarded in the past. The computations involved sometimes seemed to take over most of the workstation resources available at the Wissenschaftskolleg, and many thanks are due to Dr. Lindenberg for his help with the computational aspects of the research.

A major drawback of spatio-temporal models is their high dimensionality. This makes it hard to gain insight into their dynamical behaviour, and often one can do little more than investigate their dynamics by numerical simulation. But it seems likely that such processes can be reduced to a small number of dimensions without losing their major properties. We set out to explore the possibilities of dimension reduction, starting from individual-based spatio-temporal stochastic process and deriving dynamical systems for their first- and second-order moments. At the time of writing, this looks promising, although we have yet to see it through to completion.

With the support of the Wissenschaftskolleg, our group was able to host a workshop on `Strategies in spatial ecological modelling' in early July. This provided us with the opportunity for discussions with other

researchers from Germany and Hungary actively researching the dynamics of spatio-temporal processes. The discussions centred around the reliability, robustness and generality of spatio-temporal models, and led to a lively exchange of views between groups with interestingly different perspectives. I don't know whether the wine of the Wissenschaftskolleg or the strong views of the participants were responsible, but the arguments seemed to continue far into the night. For myself, the meeting helped to clarify how important it is to find suitable measures for comparing simulated and field spatial patterns, and the need to develop systematic methods for estimation of parameters of the models.

I imagine that, in all interdisciplinary research, there are gaps in language and concepts that need to be bridged. A plant ecologist may wonder if it is really appropriate to represent a plant as a Dirac delta function. A physicist may wonder at how a leaf of *Deschampsia flexuosa is* to be distinguished from one of *Festuca rubra.* Our bridge building was completed one wet June day as we crouched in driving rain on a windswept grassland in the Krkonoge Mountains of North Bohemia examining the plants previously known to two of us only from the computer screen.

Outside our collaborative research programme, I was able to spend some time at the Wissenschaftskolleg developing other lines of research. The dynamics of over-exploitation of biological resources have been of particular interest to me as a problem which cuts across traditional subject boundaries of ecology, economics and social behaviour. The Wissenschaftskolleg provided me with a welcome opportunity to share and develop ideas with fellows from these other subject areas; this taught me a lot, not least about the dangers of stepping incautiously into other disciplines. I am very grateful to my colleagues for discussing the ideas and patiently explaining the complexities involved in these other areas.