

## **Chapter 7. Conclusions and future work**

### **7.1 Introduction**

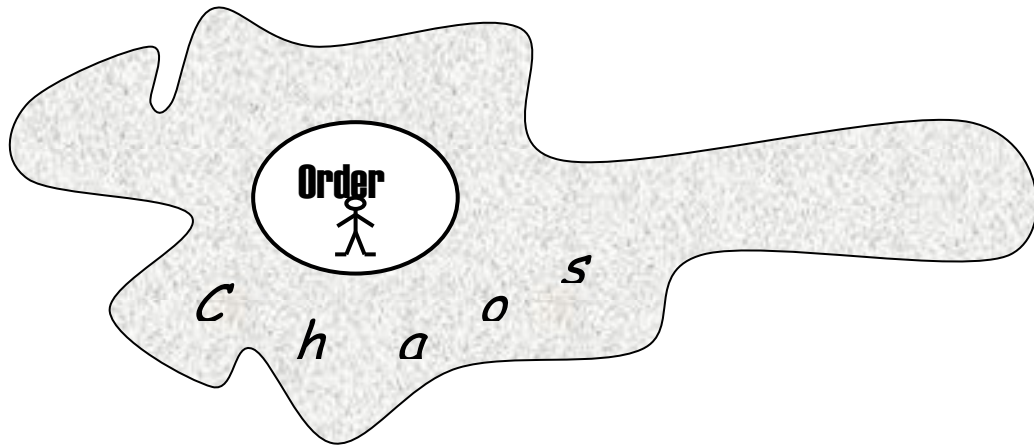
‘Nature is surprisingly devoid of the classical Euclidean forms developed by Greeks to describe it.’

Young and Crawford (1991), p. 187

The development of science can be seen as an expansion of our world view from a little sphere around us to an unimaginably complex world without bounds (Figure 7.1). From a view of the world as a mechanism with many parts working together as a clock, science has ventured into the world of chaos, fractals, fuzzy logic and genetic algorithms, where a whole can be much more than the sum of its parts, and where each particle exists in many places at once. In short, the worldview of science has become rather complex. So complex, in fact, that it can perhaps begin to explain ecosystems. The development of ecology has been slow. In fact, ecology has few known laws (Lawton 1999). Great advances in thought, such as Darwin’s theory of evolution, Turing’s morphogenesis, and mathematical population modelling, have been made. However, ecology is only starting to be able to grasp the complexity of interactions in even the simplest ecosystems. The body of knowledge about ecosystems is very large. However, it has only just been discovered, for example, that there is a mutualistic relationship between salmon and trees (Helfield and Naiman 2001).

### **7.2 From the individual to the ecosystem**

This work has explored one aspect of ecosystem complexity: the diversity of individuals and their interactions. It addressed questions regarding origins of diversity, mechanisms generating diversity patterns, and the relationship between diversity and ecosystem function. The importance of the variability of individuals and individual interactions is becoming increasingly recognised as a factor shaping ecosystem



**Figure 7.1** World as a sphere of order surrounding humans, and 'chaos' around.

dynamics (Huston 1994). In this work, an individual is considered as the unit of an ecosystem, and is defined in terms of physiological traits. A community is defined by the range and the distribution of trait values of the individuals in that community. Using this approach, it was convenient to represent individual variability and interactions in the models. Moreover, it was possible to connect individual dynamics to community dynamics and function across scales.

Small-scale plant communities were studied in this work. Plant communities were chosen since this work was done as a part of a project exploring the diversity of Scottish grasslands. Therefore, experimental data describing the physiological properties of plants was available. However, the approach in this work is generic and can be easily adjusted to suit other organisms (as was done in Chapter 6). The communities were simulated as isolated patches of vegetation without the effects of immigration. Diversity in systems with immigration have been studied with some detail in the context of metapopulation theory (Hubbell 2001).

Biodiversity has become a particularly pressing issue since it has become obvious that it is disappearing at alarming rates (Chapin *et al.* 2001). Several questions regarding the importance of diversity for ecosystem health and functioning have presented challenges for ecologists. Two of the most important questions are the relationships between diversity and productivity and between the diversity and stability of ecosystems. These relationships have not yet been elucidated because they depend on a range of environmental conditions and underlying diversity mechanisms (Loreau

2000). The mechanisms producing diversity in communities have presented another challenge for ecologists. Some of them, such as trade-offs between properties of interacting species and spatio-temporal heterogeneity and disturbance, have been explored. However, several questions have not yet been answered. For example, some patterns in community diversity, such as the species-area relationship and the species abundance distribution, have not been explained on all scales.

Two types of models were employed to explore origins and patterns of diversity: a mean-field differential equation model and a spatially explicit individual-based model. The mean-field model was defined to explore whether the basic traits of individuals can be linked to community diversity. It was found that individual traits are important for the existence of diversity in a community. Diversity required certain relationships (trade-offs) between the individual traits. The form of the trade-off defined the distribution of individuals over trait values. The nature of interactions between individuals was found to be critical for both system stability and the form of the trade-off. Hence, a need for a more explicit definition of physiological processes and interactions between individuals was suggested. An individual-based model was formulated to accomplish this. The individual-based model simulated discrete individuals that were explicitly defined by their traits, with a fuller description of the physiological parameters and spatially explicit interactions.

Using the individual-based model, diversity patterns and effects of diversity on productivity were explored. As in the mean-field model, a particular relationship between physiological traits was found to be responsible for the generation of diversity in the model. This relationship was the trade-off between time to reproduction and reproductive biomass.

Moreover, the incorporation of space and explicit individual interactions led to diversity patterns in the model that had the same form as the patterns observed in biological communities. Since a community was defined in terms of individuals in it, the communities that could be simulated were relatively small, due to computational limitations (100 to 2500 individuals or approximately 1 to 25 m<sup>2</sup> in terms of the plant model parameterisation). This suggests that the observed diversity patterns operate on small, as well as large, scales in a community. If the mechanisms responsible for generating the patterns can be understood on the small scale, then the same reasons may explain the patterns on larger scales as well. Connection between scales has

emerged as a major issue in ecology (Levin 1992). It is still a relatively unexplored area that may be very fruitful in formulating a general theory of ecosystem processes.

The individual-based model was also used to explore the mechanisms affecting the relationship between diversity and productivity. Community productivity was found to be a result of the community composition (*i.e.* the distribution of trait values in the community), environmental conditions, and the response of the community to environmental conditions. The individual properties responsible for changing the productivity under different conditions were found. They were related to plant resource uptake.

Variation in time to reproduction was necessary for the existence of diversity in the model. This variation introduced temporal separation of the reproduction events of different plant types, hence reducing competition for space. Therefore, local competition for space may be very important for community diversity. However, competition for space is only one of the ways in which individuals interact. There are other individual interactions widely present in communities. This work explored the effect of one of these interactions, the mutualistic relationship between individuals. The reason for choosing mutualistic interactions was the relative lack of knowledge about their effect on community dynamics. The effect of trophic interactions has been studied more widely in the context of predator-prey models (Hastings, 1997) and artificial life models (Holland 1995, Ray 1991). In this work, it was found that mutualistic relationships between individuals could increase diversity, both in the number of persisting individuals and in the range of the parameter space that a community occupied.

### **7.3 Challenges and future directions of the mean-field model**

The mean-field model showed that community diversity requires a particular relationship between the basic traits of individuals: the number of offspring (per unit time), reproduction rate and death rate. In particular, the ratio of number of offspring to death rate must be a decreasing and concave-up function of the reproduction rate. This trade-off is one of several that have been found to generate or promote diversity. A current work by Adler and Mosquera (2000) explores the trade-off between mortality and competitiveness. The connection between these two trade-offs can be explored.

The discrete version of the model has presented a challenge, since the linear stability analysis did not determine stability in all cases. Also, the curious separation of peak spacing did not lend itself to a complete solution. In those cases, simulation results were used. Further analysis may be possible. However, the general aim of the model was accomplished in 1) emphasising the importance of traits of individuals in determining diversity, and 2) directing attention to the importance of discreteness in a community.

A general analysis of the model, with the introduction of a genetic coupling function, was performed. The results suggest that genetic coupling plays as important a role for community diversity as the trade-off between individual traits. This is an area can be explored further. The effects of various forms of genetic coupling, and also the introduction of mutation, can be explored. The analysis of the model with genetic coupling was complicated. A complementary study of genetic coupling using both the analytical and simulation models might be the most fruitful approach in this case.

#### **7.4 Challenges and future directions of the model of plant communities**

There are several directions in which the plant model can be extended. For example, it can be extended to include other trophic levels such as insects and other predators. The introduction of other trophic levels can strongly affect community diversity. For example, introduction of predators has been shown to increase diversity, since predators affect highly abundant species the most (Huston, 1994). An extension and parameterisation of the model for three trophic levels: plants, insects, and insect predators, is currently being researched by John Hillier in a joint collaborative project between the SIMIBOS Centre and Scottish Crop Research Institute. In this context, the effect of plant heterogeneity on the diversity of higher trophic levels can also be explored.

A seedbank may also have a big effect on community dynamics in the following way. Seeds may not germinate immediately, but persist in the soil for some time before germination. This may lead to temporal variation in plant germination. In the current model, temporal variation was found to be the driving force leading to diversity. Therefore, seedbank dynamics may provide another mechanism for coexistence. A seedbank also allows rarer species to persist as seeds even if they are not able to find space to germinate above ground. These seeds can persist in soil until an opportunity

for germination arises. This might also alter community dynamics. This work is being conducted by Alistair Eberest in SIMBIOS Centre. The relationship between seed size and plant abundance is another area of possible research. Some studies have shown a relationship between seed size and abundance patterns in communities, but the nature of this relationship is still unclear (Leishman and Murray 2001). Another area related to seed production is seed dispersal. Dispersal has been shown to be important in determining community diversity (Tilman 1999). Its effect on diversity patterns can be investigated using the model.

This work presented a sample parameterisation of the model. However, some data were unavailable and some experimental data were not collected with the intention of being used in mathematical models. There is a need for collaborative work between experimental ecologists and mathematical modellers. In this work, experimental data were used for parameterisation of the individual-based model, and the model results suggested hypotheses that could be tested in ecological communities. For example, with regard to community diversity, the spread of time to reproduction, and its relationship reproductive biomass can be measured. With regard to community productivity, the response of communities under different conditions can be tested and then applied to ecosystems.

It would be also interesting to incorporate the mechanisms generating the lognormal distribution into a mathematical model. The lognormal distribution in the model was generated by few mechanisms: variation in time to reproduction, the trade-off between time to reproduction and fecundity, death rate, and competition for space. These factors could be used to define a mathematical model. In this manner, a simulation model could inform and lead to a more theoretical (and manageable) analytic model.

The model was parameterised for only one species. Other parameterisations could be done. There is data available for other grassland species from the same area, and the model will be parameterised for these species. This will allow the comparison of community dynamics under different parameterisations. Moreover, communities consisting of individuals from both species can be simulated in the same environment, and the dynamics of their interactions can be explored. This would explore the range of the trait space. In addition, the distributions of the plant traits were assumed to be normal. The effect of changing the shape of the distributions can be explored.

As has been mentioned before, the mean-field model suggested that geneflow can affect dynamics significantly. Geneflow can be incorporated into the plant model, and the effects of various geneflow scenarios on the community dynamics could be investigated. This will allow for the trait space occupied by a community to change and evolve in simulations. The effect of geneflow on mechanisms of diversity, diversity patterns and community response to environment are some of the questions that could be addressed. A project investigating these questions is underway in SIMBIOS Centre led by Professor John Crawford.

Another interesting question to explore is that of limiting similarity. Limiting similarity refers to the question of how similar two species can be while still able to coexist. In 1930's Gause has formulated a principle of competitive exclusion that two competing species could not share the same niche and both survive (Rosenzweig 1995). Limiting similarity explores just how similar two species can be. This question has mainly been addressed in analytic models (Rosenzweig 1995). The principle of competitive exclusion works in stochastic, but not in deterministic models. This is due to the fact that in stochastic models, if the abundance of a species is low, there is a probability for it to go extinct. On the other hand, deterministic models allow species with very low abundances to persist indefinitely. The question of limiting similarity has not been addressed in individual-based models. The plant model presented indications that there may be a minimum distance necessary between species for them to be able to coexist. This is an interesting question to address in the framework of an individual-based simulation model.

In the model, plant type abundances were variable, but the overall shape of the plant type abundance distribution remained stable. This is consistent with the observation that species ranking in biological communities may not be static, and a snapshot of species ranks at a single time may not correspond to the most often occurring abundances. The stratification of species ranking observed in the model may give a convenient way of separating species of a community into groups. This separation may be related to the concept of 'functional groups'. Functional groups are groups of species that perform the same function in a community. On large scales, community function can be understood in terms of its functional groups. Walker *et al.* (1999) and Loreau (1992) have suggested that different mechanisms are responsible for supporting species abundance at different levels. They proposed that competition governs the abundance of the very abundant species, and that species that have intermediate abundances are competitively equivalent. In the intermediate abundance levels,

stochastic variation drives the abundances of species, while keeping them within a certain range. This may correspond to the stratification of plant types observed in the model. The mechanisms behind the stratification can be investigated.

In this work, the temporal structure of the plant abundances and diversity was not explored in detail. Cumulative measures were used to compare dynamics in different communities. The temporal structure and autocorrelation in the time series of abundances and diversity is an interesting question that can be explored. A recent work by Kaitala *et al.* (2001) found temporal self-similarity in a spatial individual-based model of population dynamics. It would be interesting to investigate the temporal structure exhibited in the model used in this work.

### **7.5 Challenges and future directions of the organism interaction model**

The organism interaction model presented here is very simple. It includes only a few basic mechanisms of individual interaction, which is far removed from the complexity of reality. The aim of this study was to explore whether it was possible for mutualistic interactions to affect diversity in simple systems: it was. This knowledge can be used to extend the model to more complex situations. It can be enriched to include the possibility of larger mutualistic webs and other individual interactions, such as predation. This work is currently progressing in collaboration with Tim Taylor and Jason Sundram in a collaborative project between SIMBIOS Centre and IC-Cave at the University of Abertay Dundee. To make such interactions possible, it is necessary to define a system with more flexible interactions, possibly adding mobility or sensory ability to an individual's capabilities.

These investigations would be most beneficial if coupled with biological studies, so that the modelling could be informed, guided, and checked. The model could be informed by biological systems where mutualistic interactions play a central role such as tree-mycorrhizal and plant-bacterial communities (as described by Kiers *et al.* 2000, and Wilkinson and Parker 1996).

The organism interaction model resides in the realm between artificial life and ecology. The model of plant communities was readily modified into the organism interaction model. Although the changes may appear substantial since the organism interaction model represents a very different community and is much more abstract, in reality

there are the two models are very similar. The ecological and artificial life models often have a similar basic setup, but there have been few connections between them. In general, individual-based ecological population models have concentrated on smaller scale populations with a rather detailed description of the individuals (Grimm 1999). The artificial life models, on the other hand, have concentrated on processes on evolutionary scales, with the main questions centring around the evolution and persistence of diversity and complexity (Adami *et al.* 1998). Since models in the two areas are similar in their basic structure, it may be fruitful to investigate possible connections between them. It will also lead to the question of how the two scales of population dynamics and evolutionary dynamics can be connected, and whether population dynamics has lasting consequences for evolutionary dynamics.

The theoretical question behind the model was how complexity could arise in systems. The model was designed so that the possibility of relationships was governed by evolution, rather than being imposed. Evolution is sometimes referred to as ‘open-ended evolution’ in systems which have been created with the potential for increasing complexity (Taylor 1999). The definition of such a system may provide an insight into the mechanisms generating complexity and diversity in biological systems.

## **7.6 The conclusion of the conclusion**

It is an exciting time in ecology, since there are now tools that allow us to begin to understand ecosystems. Perhaps ecology is ‘the final frontier’. Humans have travelled in space and made a map of human genome, but ecosystems still contain many a mystery. Their diversity, complexity, and unpredictability enables, pushes, and dares us

‘To see a world in a grain of sand  
And a heaven in a wild flower,  
Hold infinity in the palm of your hand  
And eternity in an hour.’

William Blake