Why it takes all kinds:

Diversity mechanisms and patterns in ecological communities

E Pachepsky

PhD Theoretical Biology

2002

School of Computing
University of Abertay Dundee

Why it takes all kinds:
Diversity mechanisms and patterns in ecological communities

E. Pachepsky

A thesis submitted in partial fulfilment of the requirements of the University of Abertay Dundee for the degree of Doctor of Philosophy

This research programme was carried out in collaboration with Scottish Crop Research Institute

October 2001

I certify that this thesis is the true and accurate version of the thesis approved by the examiners.

Sign[redacted] Date..25/10/02........

(Director of studies)

Abstract

This work explores the effect of diversity of individuals on a community. The mechanisms generating diversity are explored, their effects on patterns of diversity are examined, and the impact of diversity on community properties (such as productivity and stability) is investigated. Three individual-based models are employed: 1) a mean-field differential equation model, 2) a simulation model of plant populations, and 3) a simulation model of interacting organisms.

The mean-field model is used to show that the traits of individuals in a community affect community diversity. The mathematical analysis, supported by numerical simulations, demonstrates that trade-offs between the individual traits are required for community diversity to exist. Moreover, the form of the trade-offs defines the equilibrium distribution of the population over the trait values. The nature of interactions among individuals (in particular, competition) determines the stability of the equilibrium state.

For a more realistic representation of the community, a more detailed and spatially explicit model of a community is defined. This model simulates each individual explicitly, with a fuller description of the physiological traits and interactions. The model is parameterised using experimental data from a grassland species *R. acetosa.* Diversity patterns in the modelled communities are of the same form as the patterns observed in biological communities. The mechanisms generating diversity patterns are examined. As in the mean-field model, analysis of the simulation model shows that a trade-off between physiological traits is responsible for generation of diversity in the simulation model also. Moreover, it affects the form of the diversity patterns. Community productivity results from the interplay of community diversity and environmental conditions.

To further explore the effect of individual interactions on community diversity and stability, a model of interacting organisms is developed. This model is a modification of the plant model, with the possibility of two-way mutualistic interactions between organisms. The mutualistic interactions are found to increase community diversity in space and time and to promote community stability under environmental disturbance.

The impact of individual-scale processes on community-scale dynamics has recently been recognised as an important factor contributing to ecosystem dynamics. This work defines and explores some of the links between individual and community scales within ecological communities. In particular, it shows that individual traits in a community can affect community-scale properties such as diversity patterns and productivity, while individual interactions are important for community diversity and stability.

Acknowledgements

I would like to thank my supervisor John Crawford for superlative and superior supervision. His direction, inspiration, and endless enthusiasm about the world have made my work much more interesting. I would like to thank him for patience, understanding and believing that I can self-manage. A large part of this work uses a model written by Jim Bown. I greatly appreciate his help with the model and his (quite extensive) patience. I would also like to thank him for being considerate and helpful in a whole range of matters, which include valuable comments on my thesis. I would like to thank Geoff Squire for his help throughout my studentship, and for providing invaluable expertise and discussions with regard to matters relating to biological world. A part of this work was done in collaboration with Tim Taylor. His expertise in artificial life and enthusiasm for collaboration made our work together possible and enjoyable. A thank you goes to Peter Millard and Ursula Bausenwein for providing the experimental data, without which the plants in the model would be much less real. A project on the diversity of Scottish grasslands funded by SERAD provided me with my studentship, for which I am grateful.

I would like to thank my parents without whom this PhD would not be. This work is dedicated to them. Their help ranged from the scientific to the material to the spiritual, and every bit of it was greatly appreciated. To Jason Sundram goes out a thank you as big as a mountain for invaluable comments on the thesis, and for his understanding and patience. He has made writing and living in general so much happier for me.

Contents

Chapter 1. Introduction and conceptual approach

Chapter 2. Mean-field model of diverse populations

Chapter 3. Individual-based model of diverse populations

Chapter 4. Origins and patterns of diversity in the individual-based model

Chapter 5. Effects of diversity on productivity and stability of communities

Chapter 6. Individual interactions and community diversity

Chapter 7. Conclusions and future work

Appendix A. Linear stability analysis

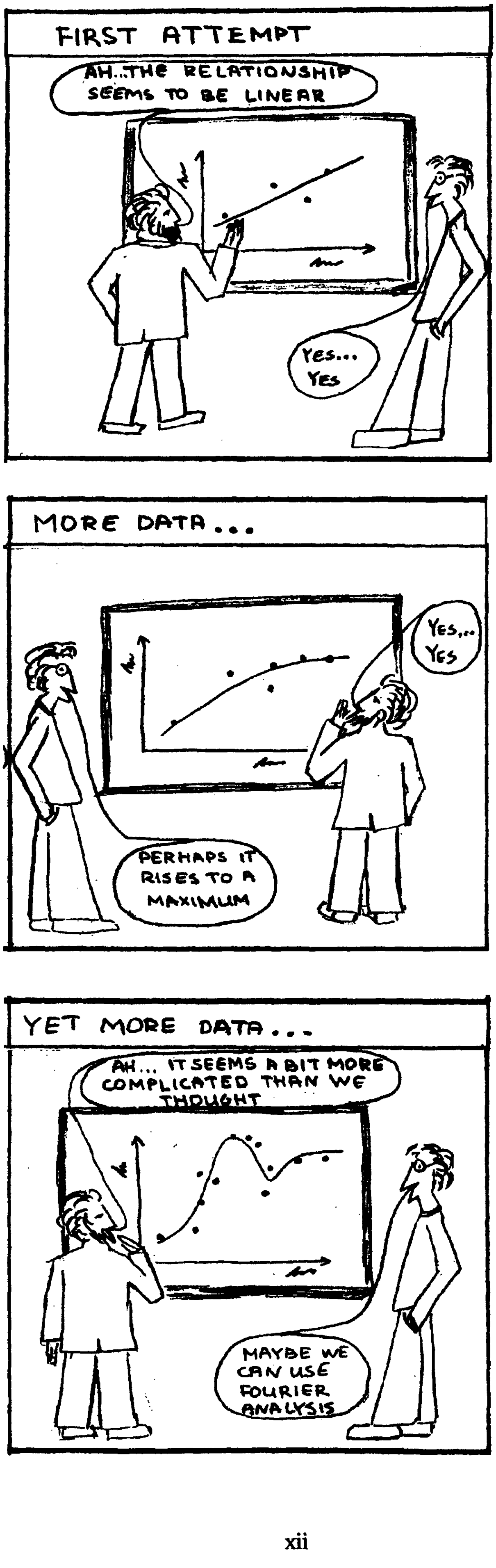
Appendix C. Choosing a model for the parameter *essential uptake*, $U_e(s)$

List of figures and tables

Figures

Tables

Modelling real life



Chapter 1. Introduction and conceptual approach

1.1 Will we live with or without biodiversity?

Humans have 'conquered' the world (Figure 1.1), and now it is time to face the consequences. The world is changing:

> '...Fossil-fuel combustion and deforestation have increased the concentration of atmospheric carbon dioxide (CO_2) by 30% in the past three centuries... We have more than doubled the concentration of methane... In the next century ... greenhouse gases are likely to cause the most rapid climate change that the Earth has experienced since the end of the last glaciation 18,000 years ago... Humans have transformed 40–50% of the ice-free land surface, changing prairies, forests and wetlands into agricultural and urban systems... We use 54% of the available fresh water... [The] mobility of people has transported organisms across geographical barriers that long kept the biotic regions of the Earth separated...' (p. 234, Chapin III *et al.* 2000)

Overpopulation, pollution, thinning of the ozone layer, global warming (or cooling), toxic wastes, new deadly diseases, and a rapidly growing number of extinct species: these are some of the challenges for humans to overcome. In biological disciplines, science has made giant steps, such as evolutionary theory, the human genome project, and heart transplants. However, we are still unable to control the common cold, predict the weather, or assess the damage caused by species extinctions. Some of these questions are more pressing than others. Species extinction was recognised as a potential problem only in the last few decades. There is evidence that human impact on the rate of species extinction may be great: '...recent calculations suggest that rates of species extinction are now on the order of 100 to 1000 times those before humanity's dominance of Earth... At present, 11% of the remaining birds, 18% of the mammals, 5% of fish, and 8% of plant species on Earth are threatened with extinction' (Vitousek *et al.* 1997).

Why is it important to have diversity? There are several reasons, among them the medicinal value of plants in disappearing tropics, diversity's stabilising effect on

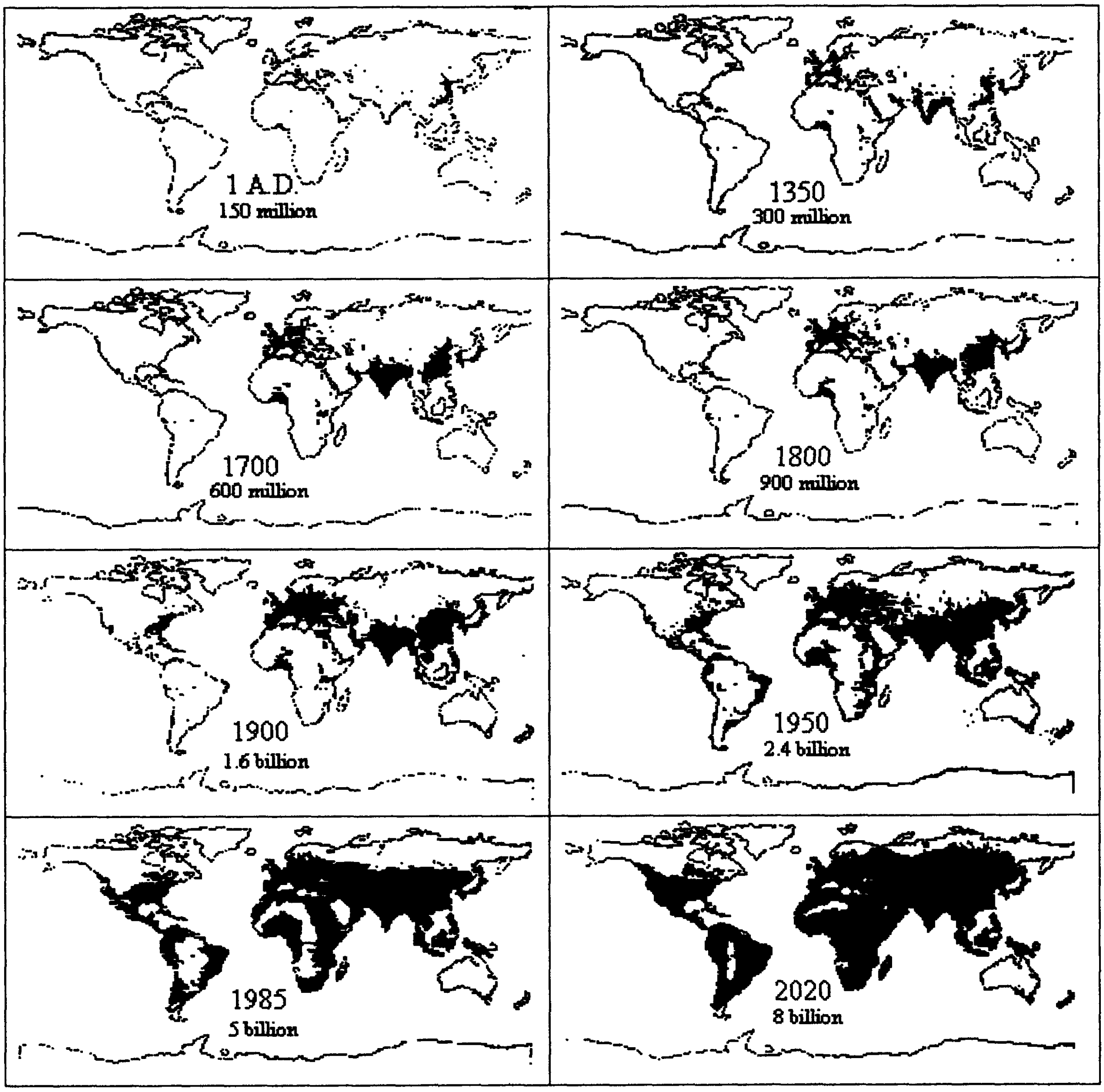


Figure 1.1 The spread of humanity from 1 A.D. to 2020 (from Tanton 1995).

ecological systems, uses of wild species for agriculture, and ethical and esthetic considerations. But more importantly, we are not sure how and when diversity is important. Such an answer, while policy makers do not usually accept it as an urgent call for action, should be taken extremely seriously. If the role that diversity plays in ecosystem functioning and health is not understood, it might not be possible to estimate the dangers. Perhaps much of diversity is redundant – but perhaps it is not. Perhaps, tomorrow or next year it will be too late. Because we do not have a precise understanding of our impact on ecosystems, it is important to realise the necessity of research, in the face of the gravity of the possible consequences. 'In view of the genuine possibility of a global collapse of biodiversity in the near future, it is unconscionable that we still have no serviceable general theory of biodiversity.' (p. x), wrote Hubbell in his book on the theory of biodiversity (Hubbell 2001). Can we understand the consequences of our actions to ourselves and our environment? Can we understand other ecological systems so that we may manage them prudently? These questions may be vital to our survival, and are tests of whether human intelligence - which makes us 'so special' - can help us to use our environment wisely.

1.2 *Explaining biodiversity*

1.2.1 Measuring biodiversity

The incredible diversity of natural communities is apparent to even the most uninformed observer. The multitude of shapes, colours and sizes that exist in ecosystems, ranging from the rainforest to our backyard, is striking. However, in order to study diversity in communities, it is necessary not only to observe but to measure diversity. Measures of diversity can incorporate a range of information such as simply the number of species in an area, or the kinds of species present in a community and their abundance.

The available measures of diversity are 1) measures of the species number, 2) species indices (which incorporate information about the distribution of species in a community), and 3) diversity patterns (such as the species abundance distribution or the species-area relationship). The first type includes three measures which express the number of species, defined by Whittaker (1970). The α diversity is the number of species at a particular location. The β diversity is the rate at which species accumulate as the observer moves away from a point, in a line. The γ diversity is the number of species in a particular region (Rosenzweig 1995).

Diversity indices are commonly used in field ecology. One of the earliest indices is Fisher's α (Rosenzweig 1995), which is a measure that does not depend on sample size. It is based on the assumption that species abundance fits a log-series distribution, *i.e.* if the total number of individuals, in a community is N, then, for a constant proportion p, the most common species has pN individuals, the next common $p(1-p)N$ individuals, the next $p(1-p)^2N$, etc. If the species abundance in a community fits such a distribution, then the number of species S in a sample is:

$$S = -\alpha \ln(1-x)$$

where α is a constant that depends on diversity, and x is a variable that depends on the size of the sample, and satisfies:

$$\frac{S}{N} = \left(\frac{x-1}{x}\right)\ln(1-x).$$

There are many other indices of diversity: for example Shannon's index, Simpson's index, McIntosh's index, and others (Rosenzweig 1995). These indices incorporate the number of species and their distribution in various ways. Currently, the importance of incorporating differences between species in terms of their contribution to community functioning was highlighted (Nijs and Roy 2000). Progress towards this was made by Shimatani (2001), who described a diversity index incorporating species differences in terms of their genetic relatedness to each other. Diversity indices are useful for tracking the evolution of diversity in a community. However, those that have been devised to date do not provide insight into the underlying community processes that lead to diversity.

One of the remarkable characteristics of diversity is that, in various communities, it exhibits consistent patterns, such as the species-area relationship and the species abundance distribution. For a detailed treatment of diversity patterns see Rosenzweig (1995). One of the most well known ecological studies is the study of species richness (the number of species in a particular sampling area) on islands of different sizes conducted by MacArthur and Wilson (1963, 1967). They found a linear relationship on a log-log scale between the island size and the number of species found on the island. Since then, this relationship has been observed in many other communities and contexts. The same linear relationship on a log-log scale was observed if mainland plots of different sizes were considered. However, the slope of the linear relationship changes with the scale of considered. Crawley and Harral (2001) analysed data for plants in Great Britain, and found that the slope was small (around 0.1 to 0.2) at small scales (less than 100 m^2), larger (0.4 to 0.5) for the intermediate scales (less than 1 hectare), and low again (0.1 to 0.2) for the largest scales (regions of Great Britain). Rosenzweig (1995) presents Preson's species-area curve for land birds, in which the slope is higher (approximately 0.5) for the intermediate area (less than 0.5 km^2), lower (approximately 0.2) for the regional areas (*e.g.* Pennsylvania), and high again (approximately 0.6) for the global scale (*e.g.* continents).

In a seminal paper, Preston (1948) collected ecological data on species abundances in communities, and formulated the theory of the canonical lognormal distribution of species abundance. He postulated that species number as a function of abundance is lognormally distributed. Moreover, it is canonical, *i.e.* there is a relationship between the parameters of the distribution. His work attracted attention, especially when some of the data sets were analysed to show that the lognormal distribution was not always evident. Instead, in some communities, the distribution of species abundances appeared to fit a geometric distribution better, and some exhibited distributions somewhere in between (Pielou 1977). MacArthur in 1957 formulated the 'broken-stick' theory of species abundance. In this theory, the species abundance distribution was assumed to arise from randomly splitting the total population into S segments, where S is the number of species in a community (MacArthur 1957). The lognormal distribution on log scale is a normal curve, and the geometric distribution is a horizontal line, MacArthur's distribution had a shape flatter than a normal curve, but not quite a horizontal line. Another species abundance theory was proposed by Whittaker (1965). This theory, dubbed 'niche pre-emption', assumes that each species, in order of decreasing competitive dominance, takes a fraction of the remaining resource available in the system. Sugihara (1980) put forward yet another theory of abundance distribution, the sequential breakage theory. This theory assumes that the species abundance distribution can arise from the following process: the total number of individuals in a community is divided randomly into two parts, then one of these parts is picked randomly and randomly split in two again, etc. Hubbell (2001) developed a theory of biodiversity on large scales. He considered a community consisting of many populations which interact by migration. He connected his theory to the work of MacArthur and Wilson (1967) and showed that the resulting species abundance distribution could be lognormal or negatively skewed. In general, a comparison of different communities shows that geometric distribution is characteristic of a community under stress or disturbance, or a young community in the r-selection stage (*i.e.* the population density is low, and the individuals with high growth rates are favoured). The lognormal distribution is characteristic of undisturbed long-existing communities. As May (1976) put it: '... [a] lognormally distributed community tends to be an egalitarian socialist society compared with the feudal hierarchy characteristic of early succession.' (p.216)

1.2.2 Modelling approaches

Explanations of diversity in biological systems were sought in theoretical biology and mathematical population ecology. Theoretical biology characterised species in terms of their habitat space, both in terms of spatial distribution and resource requirements. The species' habitat space is its niche, within which it competes with other species. Considered in these terms, species diversity is the sum of all the species that can pack themselves into the niches of the environment. While appealing on theoretical level, such an explanation is hard to test in real communities. Measuring a species niche is difficult since it is defined by many parameters (*e.g.* various environmental gradients, species resource preferences and responses to environmental conditions). However, attempts to measure a species niche have concentrated on measuring differences in one or a few properties, such as size or resource preferences (Gordon 2000).

Another area of ecology exploring diversity was mathematical population modelling. In this area, studies focused on coexistence mechanisms. Species coexistence studies began with Lotka-Volterra models defined in the 1920s. These models consisted of two coupled differential equations. They expressed the interactions of two species, predator and prey. The results showed that coexistence between the two species is possible when cyclic oscillations in both populations occur (Murray, 1989). To estimate the possible number of coexisting species in a community, a model was developed where the species were limited by different resources (Levin 1970). This model showed that the species number in a community is equal to the number of resources. However, this answer was unsatisfactory since many diverse communities are limited by just one resource, *e.g.* in grasslands (Gleeson and Tilman 1990). Huisman and Weissing (1999) showed that under certain conditions coexistence of many species in an environment limited by few resources is possible in resource competition models.

In the 1970s, population dynamics turned to investigate the effect of spatial configurations on community diversity (influenced by the work of Turing (1952) on morphogenesis, the generation of patterns from a uniform initial state). Levin (1974) wrote:

> 'The distribution of a species over its range of habitats is a fundamental and inseparable aspect of its interaction with its environment, and no complete study of population dynamics can afford to ignore it. This point was emphasized over 20 years ago by Skellam (1951) and Hutchinson (1951); and yet, until recently, the mathematical theory of population dynamics has largely ignored spatial considerations.' (p.207)

Levins was responsible for the introduction of spatial considerations into modelling. He defined an analytical model of species living in many habitat patches (Levins 1969). (This occurred around the same time as MacArthur and Wilson published their work on the species-area relationship.) This approach developed into an area of ecological modelling called 'metapopulation modelling' or 'patch modelling'. Metapopulation models showed that coexistence between superior and inferior competitors is possible in a community consisting of many separated populations interacting with each other. This occurs through the emigration of the inferior species, which can 'escape' from the competition. This concept is sometimes referred to as 'regional coexistence' (Levins and Culver 1971 and Slatkin 1974, discussed in Levin 1974). These results have been confirmed more recently (Shmida and Ellner 1984). In a host-parasitoid system, Hasell *et al.* (1994) showed that spatial segregation occurs among the coexisting species.

To represent the diversity of individuals in a particular characteristic such as age on size, analytic models of physiologically structured populations were developed (Metz and today is Diekmann, 1986). These systems were defined with implicit space (i.e. there is no spatial dimension in the model, but spatial interactions are expressed through the formulation of the model, e.g. density dependent growth) and explicit space (where the model is defined with explicit definition of spatial dimensions and processes occurring in space). These models used a combination of analytical and numerical simulation approaches to explore population dynamics in these systems, and were used successfully to predict population dynamics in some systems, such as *Daphnia* communities (Metz *et al.* 1988). However, local interactions and spatial heterogeneity rendered the models too complicated for analysis (Metz and de Roos 1992).

Another modelling approach of representing individual diversity in a population was developed by Caswell (1989). He developed age- or stage-structured models (also known as matrix models). Matrix models consider a population consisting of groups of individuals varying in one particular parameter (*e.g.* age or weight). The dynamics of a population are simulated by defining source ('birth') rate, sink ('death') rate, and transition probabilities between the groups. Age- and stage-structured models are used widely as prediction tools for population dynamics (Hastings, 1997).

In the 1980's, technological advances in computational power led to the development of individual-based modelling (also known as agent-based modelling). In this approach, the behaviour of each individual in the modelled community is simulated explicitly. This became possible only when computers became powerful enough to simulate populations of individuals in a reasonable amount of time. Individual-based modelling was developed to relax two assumptions made in most mean-field models that a) all individuals are identical, and b) that all individuals are affected by each other and their environment in the same manner, in an effect called 'mixing' (Huston *et al.* 1988). In most biological communities, individuals interact with other individuals only within a certain neighbourhood. This neighbourhood can be of different sizes, include different number of various individuals, and can move if the individual in question is mobile. Individual-based models are used to explore the effects of individual interactions and variation on community dynamics, often in a spatially explicit environment (for further descriptions of this approach see Hogeweg and Hesper 1990, Uchmanski and Grimm 1996, Grimm 1999, Lomnicki 1999). Individual-based modelling has been used to investigate the dynamics of both animal and plant populations (for a general review see Grimm 1999; for a review of models of animal populations see Dunning *et al.* 1995; for a review of models of marine populations see Botsford 1992; for some examples of forest models see Mladenoff and W. Baker 1999, Köhler and Huth 1998, Kubo and Ida 1998, Shugart 1984).

The individual-based approach is especially relevant to modelling vegetation systems, since plants are sessile organisms, and neighbourhood interactions are restricted to individuals in the immediate area around the plant. Hence, neighbourhood interactions are especially pronounced and may affect ecosystem dynamics. Grassland individual-based models include models by Weiner and Conte (1981), Pacala and Silander (1985), Pacala (1986, 1987), Crawley and May (1987), Humphries *et al.* (1996), Warren and Topping (1999), Winkler *et al.* (1999), and Kleidon and Mooney (2000). Spatially explicit models allow explicit definition not only of the plant locations, but also of environmental variables for each of the locations. Therefore, environmental heterogeneity and disturbances can be simulated in individual-based models. Individual-based models have been used to show that the introduction of description of spatial interaction in the models can have a strong impact on population dynamics (Tilman and Kareiva 1997). In particular, several studies showed that spatial arrangements of individuals, environmental heterogeneity, and environmental disturbances can alter interactions and, in some cases, promote the coexistence of species (Levin 1974, Weiner and Conte 1981, Green 1989, Chesson 1994, Tilman 1994, Lavorel and Chesson 1995, Weber *et al.* 1998, Winkler 1999).

1.2.3 The role of trade-offs in sustaining diversity

Spatial and temporal heterogeneity are the external environmental factors that can promote coexistence. What are the mechanisms within a community that promote coexistence? Why does a 'superspecies' (a species best at everything) not exist? Ecologists have noted that species superior in one aspect with respect to others are inferior in other aspects (for example, organisms which grow very fast do not have long life spans). This is believed to happen due to the existence of physical/physiological constraints on organisms. These constraints can be described in terms of trade-offs between traits of organisms.

Several trade-offs have been shown to lead to community diversity. One of these is a trade-off between competitive ability and dispersal, *i.e.* the superior competitors disperse at slower rates. This trade-off has been shown to make coexistence of species possible in the context of the metapopulation modelling (Levins and Culver 1971, Hastings 1990, Shmida and Ellner 1984). The same conclusion was reached by Weiner and Conte (1981) applying a different method - a spatial simulation model with neighbourhood competition. The model showed that a trade-off between competitive ability and dispersal rate can retard or prevent competitive elimination. Crawley and May (1987) modelled a two species community consisting of an annual plant species dispersing by seed and a perennial plant species invading only by lateral growth. They employed a spatially explicit neighbourhood model, and found that coexistence was possible due to the competition/colonisation trade-off, if the perennial species was a better competitor. Tilman (1994) further explored the role of trade-offs in coexistence mechanisms. He investigated coexistence in analytic models that assume local interactions on a homogeneous resource. Coexistence in these models was possible given two- or three-way interspecific trade-offs among competitive ability, colonisation ability, and longevity.

Lavorel and Chesson (1995) explored the effect that germination played in the coexistence mechanisms of ecological communities. They employed a two-species simulation model of annual plants with periodic disturbance. They found that a dispersal/germination strategy trade-off can lead to species coexistence. In other words, coexistence was possible if the species with shorter dispersal ranges had higher probabilities of germination. Diversity in seed production strategies was explored by Rees and Westoby (1997) and Geritz *et al.* (1999). In both studies, analytic models were considered in an evolutionary context. That is, plants' persistence was evaluated using a fitness function based on competitive ability and abundance. They showed that coexistence is possible due to a trade-off between seed size and seed number, provided that seedlings from large seeds were more competitive and viable. Evidence for the existence of this trade-off was examined by Guo *et al.* (2000), who inspected plant data in northern England and the Chihuahuan Desert of Arizona, USA. The results of the study show that a trade-off between seed number and size exists (species with small seeds produce more of them). However, they also show that small seeds have higher viability than large ones, contrary to the assumptions of the analytic models. In the study of a diverse grassland site with nitrogen as one limiting nutrient, Gleeson and Tilman (1990) stipulated that coexistence between species may be possible due to the trade-off in resource allocation to roots *vs.* reproduction.

1.3 Some open problems

> '... we do not know how many species inhabit the Earth or even a small part of it... We know even less about how and where most species on Earth originate, live and die.'
>
> Hubbell (2001), p. ix

In addition to an incomplete catalogue of existing species, several other issues have been plaguing ecologists. One of them is the relationship between diversity and ecosystem functioning (*e.g.* its productivity and stability). This relationship has been a subject of an ongoing debate in ecology (Tilman 1999). Whether an increase in species diversity leads to an increase in ecosystem productivity, and whether diversity impacts system stability are two questions that have been much debated. The collection of studies on these topics (Loreau 2000, Schwartz *et al.* 2000, Hector *et al.* 1999, Tilman 1999, Tilman and Downing 1994, Naeem *et al.* 1994, Schulze and Mooney 1994) shows that these questions have not been amenable to straightforward answers. These studies lead to the conclusion that ecosystem functions are related not to one, but to a collection of diversity characteristics (which include the number of species, types of species, and their proportion in a community). The exact effect of various diversity characteristics is unclear. Moreover, there is evidence that this effect depends on environmental conditions (Cardinale *et al.* 2000, Yachi and Loreau 1999). Therefore, understanding an ecosystem in terms of relationships between one property and one ecosystem function seems not to be possible.

While macroscopic patterns in diversity such as species abundance distribution and species-area relationship exist, the question of their origin is still unanswered. Their existence points to regular behaviour emerging from complexity at the individual level and offers constraints on proposed mechanisms. Most of the theories explaining the patterns are abstract, untestable, and do not explain the observed variation in patterns (see section 1.2.1). A recent book by Hubbell called *The Unified Neutral Theory of Biodiversity and Biogeography* (2001) describes a theory of the mechanisms on the metapopulation scale (*i.e.* a large scale of community consisting of many smaller populations). According to this theory, the species-area relationship and species abundance distribution are of the same form as those observed in ecological communities. However, the mechanisms generating diversity patterns on smaller scales are not yet known.

1.4 Challenges in understanding biodiversity

> 'Variety is charming
> and not at all alarming'
>
> 16th century English folk song

1.4.1 Complexity

It is not surprising that ecosystem dynamics have not yet been fully understood. An ecosystem is 'all the interacting parts of the physical and biological worlds' (Ricklefs and Miller 1999). It is a collection of entities sized from millimetres (*e.g.* microorganisms) to kilometres (*e.g.* lakes). These all interact with each other in various ways: along and across scales, locally and globally. Moreover, several types of heterogeneity are present in ecosystems on various scales: in abiotic environmental factors, in the spatial distribution of individuals, and between individuals themselves. It is difficult (an understatement!) to map out these interactions, decide which are important for the questions at hand, and capture them meaningfully in a model.

1.4.2 Defining diversity

To distill any understanding from the complexity of ecosystems, simplifications are necessary. One of these simplifications is in the definition of diversity. Most ecological models view ecosystems at the species scale. Originally, species were defined as 'groups of populations that can actually or potentially exchange genes with one another and that are reproductively isolated from other such groups' (Mayr 1942). This definition is convenient for evolutionary studies, which follow the genetic evolution of groups of populations in higher kingdoms (*e.g.* animals). In the plant and lower kingdoms, interspecific exchange of genetic material is common; this erases the genetic distinctions and makes the term 'species' unusable. However, describing diversity in terms of species is not informative if the question at hand is the relationship between the function of a community and the function of its subsets. Species are characterised genetically and often phenotypically, but genetic and phenotypic differences do not always correspond to differences in function. Functional variation between individuals within species is often great (Huston 1994, Briggs and Walters 1997). In addition, ecosystem processes affect all individuals, no matter what species. Huston (1994) expressed this point: 'The basic rules of competition and predation among individuals are the same regardless of whether the individuals are of the same or of different species.'(p. 178)

On larger scales, this difficulty has been addressed by separating species into 'functional groups', which are groups of species that perform the same function in a community (Köhler and Huth 1998, Walker *et al.* 1999, Tilman 1999, Loreau 2000, Nijs and Roy 2000). Experimental studies have been done to assess the effect of different functional groups on ecosystem processes. The results are not consistent. Some studies found that functional groups were very important for ecosystem productivity, stability and other processes (Symstad and Tilman 2001, Tilman *et al.*, 1997). Other studies found no significant effect of removing functional groups (Hooper and Vitousek 1997). The major difficulty with the concept of 'functional groups' is in their definition, because it requires species to be related to functions. This is possible but difficult since species were not defined to be related to function.

1.4.3 Connecting models and reality

Most of the current ecological community models do not have much relevance to ecosystems, and offer, at best, qualitative results. The main reason for this is the difficulty in linking models to real ecological systems. In order to keep models manageable, they often lack much ecological detail and, therefore, relevance. The results of a highly simplified model are hard to relate to the ecological communities on which the model is based. It is also difficult to translate ecological observations and measurements into parameters of highly simplified models. Such parameters are, for example, competition or invasion coefficients and rates of replacement (Weiner and Conte 1981, Crawley and May 1987, and Sivertown *et al.* 1992). These describe the competitive effect that one species has on another. Experimental studies to determine these effects have been done (Naeem *et al.* 2000, Silvertown *et al.* 1992). However, as mentioned in the work by Naeem *et al.* (2000), the variation of this effect, which depends on environmental conditions and particular species arrangement, is likely to be great. As a result, there has been little connection between ecological models and experimental ecology (Schmitz 2000). This is now changing, particularly in the field of individual-based modelling, where individuals in the models are defined in terms of measurable characteristics (Warren and Topping 1999, Grimm 1999).

1.5 The conceptual approach of this work

> 'After we reject the ideas of the identity of individuals within a species and of the homogeneity of ecological space, a different picture of natural communities emerges, in which individual variation, spatial heterogeneity, behavioural interaction between individuals, and migratory behaviour do determine the dynamics and stability of ecological systems.'
>
> Lomniki (1988), p. 203

1.5.1 Re-defining diversity

In this work, diversity is defined in terms of individuals. Consider a community in which each individual is described by a set of basic traits (*e.g.* lifetime, fecundity etc.).

The traits define the functions and interactions of an individual with its environment and other individuals. The values of a trait for all individuals in a community define a distribution for that trait. The community diversity can then be defined as the range and distribution of the trait values in the community.

This idea can be conveniently expressed in mathematical notation. Suppose that individuals in a community are defined by n physiological traits, with each individual defined by a set of values for each of the traits. An individual can then be defined as a point in the n-dimensional space of traits. For example, Figure 1.2 shows a distribution of individuals in the 3-dimensional space of three traits: growth rate (g), death probability (d) and fecundity (b). The diversity of a population can then be defined as the frequency distribution of individuals (*i.e.* points) in the n-dimensional space of individual traits.

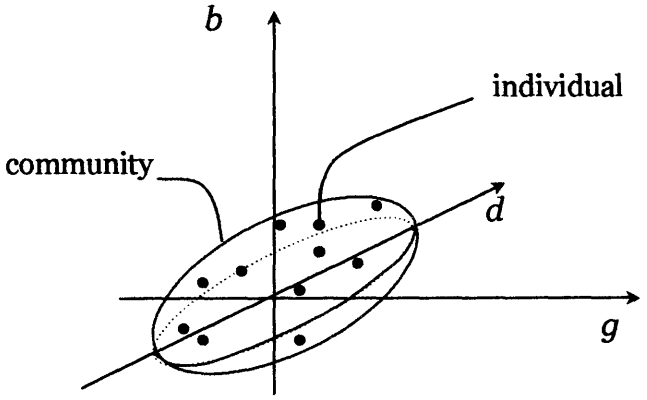


Figure 1.2 A representation of community as a collection of points in n-dimensional (3-dimensional in this case) space of physiological traits. Here, g is growth rate, b is fecundity, and d is death probability.

Using the described framework, the modelling is more closely tied to experimental ecology. Defining the community in terms of basic physiological traits has an advantage: the traits are measurable. It is experimentally feasible to measure the properties of individuals; however, it is much more difficult to measure individual interactions and other community-scale properties. Hence, a model with input parameters that are physiological characteristics of individuals is more amenable to parameterisation (as shown in Ch. 3 of this work).

1.5.2 Questions addressed in this work

This work addressed the questions posed in section 1.3 of this chapter. Diversity patterns are consistent across a range of different life forms and environments. This suggests that the mechanisms responsible for these patterns are fundamental, and depend on characteristics that are common among different communities and conditions. This in turn implies that the key to understanding the patterns lies in the basic properties of the life cycle (*e.g.* birth, death, reproduction), and the basic properties of the environment (*e.g.* space, spatial interactions, and spatial variation). In this work the link between the properties of individuals to community properties is explored. This connection is then used to gain insight into the origins of diversity patterns.

Linking the properties of individuals and a community across scales offers an *opportunity to gain insight into the nature of the relationship* between community function and diversity. The simplistic view of relating community function to diversity by defining diversity as the number of species in a community can be modified. An alternate definition of diversity – as the range of values of physiological traits in a community – is linked to community productivity and stability. This definition incorporates the concepts of species richness, species evenness, and difference between species. All these diversity characteristics have been shown to have a significant effect on community dynamics (Nijs and Roy 2000). Since this definition of diversity (unlike species) describes community variability in terms of functional differences, it is possible in this work to elucidate the mechanisms -- on the scale of individual -- responsible for the generation of community behaviour.

Chapter 2. A mean-field individual-based model

2.1 General form and introduction

> 'Modelling is a way of enforcing constraints on otherwise wishful thinking.'
>
> Giulio Ruffini

In this chapter a mean-field model of two coupled differential equations of diverse communities is considered. The model is defined in order to establish whether traits of individuals have an important role in determining community diversity. The model is very simple, containing only a few basic mechanisms, and was designed to give general clues that might guide more detailed and realistic models. In this model, space is not defined explicitly. Instead, interactions between individuals with different trait values are explored. In the model, individuals are described by three physiological traits: lifetime, time to reproduction, and number of progeny produced per unit time. The model of a population such that the time to reproduction varies between individuals (*i.e.* there exists diversity in the time of reproduction) is now defined.

The biological system under consideration is a population of plants, since this work was conducted as a part of a project investigating the diversity of Scottish grasslands. Suppose there is a population consisting of F adult plants and S seeds. Suppose further that adult individuals reproduce at intervals of $1/\lambda$ (time to reproduction), *i.e.* λ is the rate of reproduction. Assume that the seedlings compete with each other. The aim is to express the density dependence of seed germination as a function of the seed population. Call the number of germinated seeds in one season G. Then define G as follows (Harper 1977):

$$G = \frac{\lambda S}{1 + KS}$$

where K is a constant determining the strength of competition (competition increases as K increases). The shape of the curve is shown in Figure 2.1.

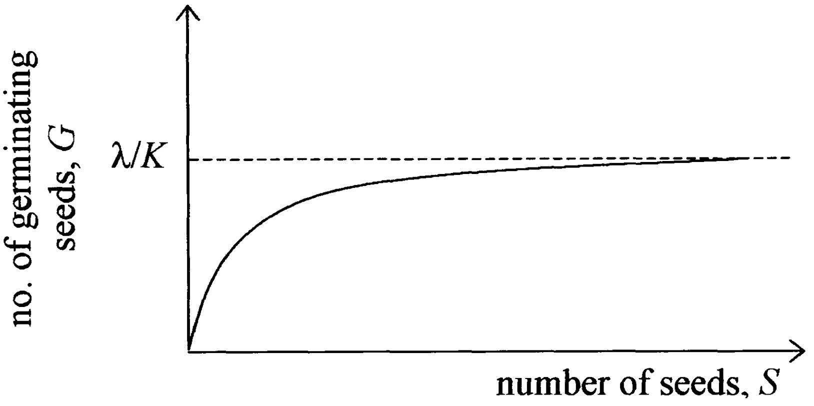


Figure 2.1 The number of germinating seeds as a function of the total number of seeds. This relation expresses competition that seeds experience in the presence of other seeds.

Suppose that within the population, there are individuals with a range of reproduction rate values $(0, \lambda_c)$, where λ_c is the upper limit of λ. First, suppose that each seed competes with all other seeds. Then S and G are functions of λ. For a given value of λ, $S(\lambda)d\lambda$ is the number of seeds corresponding to individuals with reproduction rates in the range λ to $(\lambda+d\lambda)$, and $G(\lambda)d\lambda$ is the number of those that germinate. In this case

$$G(\lambda) = \frac{\lambda S(\lambda)}{1 + K\int_0^{\lambda_c} S(l)dl}$$

where the integral represents the total number of seeds in a population.

Other competition scenarios can be expressed by introducing a kernel into the integral in order to characterise the extent to which seeds with different reproduction rates contribute to competition:

$$G(\lambda) = \frac{\lambda S(\lambda)}{1 + K\int_0^{\lambda_c} \kappa(l,\lambda)S(l)dl}$$

where $\kappa(l,\lambda)$ is the kernel.

For example, suppose that individuals with reproduction rate λ_i only have to compete with individuals of higher reproduction rate to reach maturity. Then the kernel can be described as:

$$\kappa(l,\lambda)=\begin{cases}0 \text{ if } l<\lambda \\ 1 \text{ if } l\geq\lambda\end{cases}$$

and

$$G(\lambda_i)=\frac{\lambda_i S(\lambda_i)}{1+K\int\limits_{\lambda_i}^{\lambda_c} S(l)dl}. \qquad (2.1)$$

Now consider a population consisting of seeds and adults, with seeds being produced at rates in the interval $(0,\lambda_c)$. Let $S(\lambda, t)d\lambda$ be the number of seeds in the population corresponding to individuals with reproduction rate in the range λ to $(\lambda+d\lambda)$, and let $F(\lambda, t)d\lambda$ be the corresponding number of adults, at a given time t. The evolution of the adult population over time can be described as

$$\frac{\partial F}{\partial t}=G(\lambda)-aF(\lambda,t) \qquad (2.2)$$

where a is the death rate of adult individuals. Substituting (2.1) into (2.2),

$$\frac{\partial F}{\partial t}=\underbrace{\frac{\lambda S(\lambda,t)}{1+K\int\limits_{0}^{\lambda_c}\kappa(l,\lambda)S(l,t)dl}}_{\text{germinated seeds}}-\underbrace{aF(\lambda,t)}_{\text{adult death}}\ . \qquad (2.3)$$

To describe the evolution of the seed population over time, it is necessary to define the process of geneflow. Consider the simple case when all adults cross with all other adults (*e.g.* by pollen mixing). Also suppose that at each crossing there is a probability $\rho(\lambda\mid x,y)$ that a seed of an individual with reproduction rate λ will be produced by two parents with reproduction rates x and y, respectively. Then the number of seeds $B(\lambda, t)d\lambda$ produced at time t with reproduction rate in the range λ to $(\lambda+ d\lambda)$ can be described by

$$B(\lambda,t)=b\frac{1}{2}\int\limits_{0}^{\lambda_c}\int\limits_{0}^{\lambda_c}\rho(\lambda\mid x,y)F(x,t)F(y,t)dxdy$$

where b is the number of seeds produced per unit time when an adult with reproduction rate x crosses with an adult with reproduction rate y.

The more general case can be considered when not all adults cross with each other. Suppose a function $Q[F(x,t),F(y,t)]$ describes the frequency of crossing for two individuals with reproduction rates *x* and *y*. Then *B*(λ, *t*) can be defined as follows:

$$B(\lambda,t)=b\int_0^{\lambda_c}\int_0^{\lambda_c}\rho(\lambda\,|\,x,y)Q[F(x,t),F(y,t)]dxdy \qquad (2.4)$$

The change in seed population over time can then be described as:

$$\frac{\partial S}{\partial t}=B(\lambda,t)-c\lambda S(\lambda,t) \qquad (2.5)$$

where *c*λ is the proportion of seeds that die and become adult. Substituting (2.4) into (2.5),

$$\frac{\partial S}{\partial t}=\underbrace{b\int_0^{\lambda_c}\int_0^{\lambda_c}\rho(\lambda\,|\,x,y)Q[F(x,t),F(y,t)]dxdy}_{\text{rate of production of seeds}}-\underbrace{c\lambda S(\lambda,t)}_{\substack{\text{rate of seed death}\\ \text{and germination}}} \qquad (2.6)$$

A coupled system of differential equations can now be described by combining equations (2.3) and (2.6) as follows:

$$\begin{cases}\dfrac{\partial F}{\partial t}=\dfrac{\lambda S(\lambda,t)}{1+K\displaystyle\int_0^{\lambda_c}\kappa(l,\lambda)S(l,t)dl}-aF(\lambda,t)\\[2ex] \dfrac{\partial S}{\partial t}=b\displaystyle\int_0^{\lambda_c}\int_0^{\lambda_c}\rho(\lambda\,|\,x,y)Q[F(x,t),F(y,t)]dxdy-c\lambda S(\lambda,t)\end{cases} \qquad (2.7)$$

This system can be non-dimensionalised as follows. Let *τ=at*, then

$$\begin{cases}\dfrac{\partial F}{\partial \tau}=\dfrac{\lambda S(\lambda,\tau)/a}{1+K\displaystyle\int_0^{\lambda_c}\kappa(l,\lambda)S(l,\tau)dl}-F(\lambda,\tau)\\[2ex] \dfrac{\partial S}{\partial \tau}=b/a\displaystyle\int_0^{\lambda_c}\int_0^{\lambda_c}\rho(\lambda\,|\,x,y)Q[F(x,\tau),F(y,\tau)]dxdy-c\lambda S(\lambda,\tau)/a\end{cases} \qquad (2.8)$$

Define $\lambda^*=\lambda/\lambda_c$, $l^*=l/\lambda_c$, $x^*=x/\lambda_c$, and $y^*=y/\lambda_c$. Then

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda^* S(\lambda^*\lambda_c,\tau)\lambda_c / a}{1+K\lambda_c \int_0^1 \kappa(l^*\lambda_c,\lambda^*\lambda_c)S(l^*\lambda_c,\tau)dl^*} - F(\lambda^*\lambda_c,\tau) \\ \dfrac{\partial S}{\partial \tau} = b/a\int_0^1 \int_0^1 \rho(\lambda^*\lambda_c \mid x^*\lambda_c, y^*\lambda_c)Q[F(x^*\lambda_c,\tau),F(y^*\lambda_c,\tau)]dx^*dy^* - c\lambda^* S(\lambda^*\lambda_c,\tau)\lambda_c / a \end{cases} \tag{2.9}$$

Let $S^*(\lambda^*,\tau) = S(\lambda^*\lambda_c,\tau)$, $F^*(\lambda^*,\tau) = F(\lambda^*\lambda_c,\tau)$, $\kappa^*\left(l^*,\lambda^*\right) = \kappa\left(l^*\lambda_c,\lambda^*\lambda_c\right)$, and $\rho^*(\lambda^* \mid x^*, y^*) = \rho(\lambda^*\lambda_c \mid x^*\lambda_c, y^*\lambda_c)$.

Let

$$\frac{\lambda_c}{a} = R^* = \frac{\text{lifetime}}{\text{minimum time to repoduction}}, \tag{2.10}$$

$$\frac{b}{a} = P^* = \frac{\text{(lifetime)(number of offspring)}}{\text{time}} \tag{2.11}$$

$= $ total number of offspring produced by an individual.

Then the system becomes:

$$\begin{cases} \dfrac{\partial F^*}{\partial \tau} = \dfrac{R^*\lambda^* S^*(\lambda^*,\tau)}{1+K\lambda_c \int_0^1 \kappa^*(l^*,\lambda^*)S^*(l^*,\tau)dl^*} - F^*(\lambda^*,\tau) \\ \dfrac{\partial S^*}{\partial \tau} = P^*\int_0^1 \int_0^1 \rho^*(\lambda^* \mid x^*, y^*)Q[F^*(x^*,\tau),F^*(y^*,\tau)]dx^*dy^* - R^* c\lambda^* S^*(\lambda^*,\tau) \end{cases} \tag{2.12}$$

2.2 A model with clonal reproduction and hierarchical competition

2.2.1 Model definition

Consider a simplification of (2.12) where reproduction is clonal:

$$\begin{cases} \dfrac{\partial F^*}{\partial \tau} = \dfrac{R^*\lambda^* S^*(\lambda^*,\tau)}{1+K\lambda_c \int_0^1 \kappa^*(l^*,\lambda^*)S^*(l^*,\tau)dl^*} - F^*(\lambda^*,\tau) \\ \dfrac{\partial S^*}{\partial \tau} = P^* F^*(\lambda^*,\tau) - R^* c\lambda^* S^*(\lambda^*,\tau) \end{cases} \tag{2.13}$$

To reduce the number of parameters, let $S^{**}(\lambda^*,\tau) = \lambda_c K S^*(\lambda^*,\tau)$ and let $F^{**}(\lambda^*,\tau) = \lambda_c K F^*(\lambda^*,\tau)/R^*$. The kernel function does not change since

$$\lambda_c K\int_0^1 \kappa^*\left(l^*,\lambda^*\right)S^*\left(l^*,\tau\right)dl^* = \int_0^1 \kappa^*\left(l^*,\lambda^*\right)K\lambda_c S^*\left(\lambda^*,\tau\right)dl^* = \int_0^1 \kappa^*\left(l^*,\lambda^*\right)S^{**}\left(\lambda^*,\tau\right)dl^*$$

For convenience of notation, the superscripts * and ** on λ, *l*, κ, *x*, *y*, S and *F* are left out below:

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda S(\lambda,\tau)}{1+\int_0^1 \kappa(l,\lambda)S(l,\tau)dl} - F(\lambda,\tau) \\ \dfrac{1}{R^*}\dfrac{\partial S}{\partial \tau} = P^* F(\lambda,\tau) - c\lambda S(\lambda,\tau) \end{cases} \qquad (2.14)$$

Let $P = R^* P^*$ and $C = R^* c$. Then (2.14) becomes:

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda S(\lambda,\tau)}{1+\int_0^1 \kappa(l,\lambda)S(l,\tau)dl} - F(\lambda,\tau) \\ \dfrac{\partial S}{\partial \tau} = PF(\lambda,\tau) - C\lambda S(\lambda,\tau) \end{cases} \qquad (2.15)$$

Considered boundary conditions are: $\lambda \in [0,1]$ and $F(0,\tau)=S(0,\tau)=F(1,\tau)=S(1,\tau)=0$. This means that there are no individuals that grow at a rate λ = 0, and no individuals that grow at a rate λ = 1 (since this was defined as the upper limit of λ). Now several forms of $\kappa(l,\lambda)$ can be considered.

First, consider a simple form of the kernel $\kappa(l,\lambda)$, which expresses strictly hierarchical competition, *i.e.* an individual competes equally with all individuals that grow as fast or faster than it does:

$$\kappa\left(l,\lambda\right) = \begin{cases} 0 \text{ if } l < \lambda \\ 1 \text{ if } l \geq \lambda \end{cases}$$

The system (2.15) becomes:

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda S(\lambda,\tau)}{1+\int_\lambda^1 S(l,\tau)dl} - F(\lambda,\tau) \\ \dfrac{\partial S}{\partial \tau} = PF(\lambda,\tau) - C\lambda S(\lambda,\tau) \end{cases}$$

Other forms of κ will be considered in section 2.5.

Let $H(\lambda,\tau) = 1 + \int_{\lambda}^{1} S(l,\tau)dl$.

This means that the system can be rewritten as

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = -\lambda \dfrac{\partial H}{\partial \lambda}\dfrac{1}{H} - F(\lambda,\tau) \\ -\dfrac{\partial^2 H}{\partial \tau \partial \lambda} = PF + C\lambda \dfrac{\partial H}{\partial \lambda} \end{cases} \tag{2.16}$$

Here,

$$S(\lambda,\tau) = -\frac{\partial H}{\partial \lambda}. \tag{2.17}$$

$H(\lambda, \tau)$ has several constraints. First, since $S(1,\tau) = 0$ is a boundary condition, this means that

$H(1, \tau) = 1.$ (2.18)

Also, since $S(\lambda,\tau)$ must be non-negative,

$$\frac{\partial H}{\partial \lambda} \le 0 \text{ on } [0, 1].$$

And if $S(\lambda,\tau)$ must be positive (*e.g.* for a non-zero steady state),

$$\frac{\partial H}{\partial \lambda} < 0 \text{ on } [0, 1]. \tag{2.19}$$

2.2.2 Steady states and stability

Let $H(\lambda,\tau) = h(\lambda) + \tilde{h}(\lambda,\tau)$ and $F(\lambda,\tau) = f(\lambda) + \tilde{f}(\lambda,\tau)$ where (f, h) is a steady state, *i.e.*

$$-\lambda \frac{\partial h}{\partial \lambda}\frac{1}{h} - f = 0 \tag{2.20}$$

and

$$Pf + C\lambda \frac{\partial h}{\partial \lambda} = 0 \tag{2.21}$$

Now (2.20) implies that

$$\lambda \frac{\partial h}{\partial \lambda} = -hf \qquad (2.22)$$

Plugging this in into (2.21)

$$Pf - Chf = 0$$

or

$$f(P - Ch) = 0$$

This means that either $f = 0$ or $h = P/C$ or both.

If $h = {}^{P}\!/_{C}$ (2.23)

then

$$\begin{aligned} f &= -\lambda \frac{\partial h}{\partial \lambda} \frac{1}{h} \\ &= -\lambda \frac{\partial (P/C)}{\partial \lambda} \frac{C}{P}. \end{aligned} \qquad (2.24)$$

Until this point no conditions on $\frac{P}{C}$ were imposed. However, (2.24) implies that the ratio $\frac{P}{C}$ must be a function of λ. Moreover, the steady state of the system depends on this ratio and its derivative. Two constrains on $\frac{P}{C}(\lambda)$ can be derived. First, from (2.18) and (2.19) $\frac{P}{C}(1) = 1$. Second,

$$\frac{\partial \left({}^{P}\!/_{C}\right)}{\partial \lambda} < 0 \qquad (2.25)$$

on [0, 1]. This implies that $\frac{P}{C}(\lambda)$ is a decreasing function of λ. Now, $\frac{P}{C}(\lambda) = \frac{b}{ca}(\lambda)$. Therefore, inequality (2.25) imposes constraints on the relationship between the physiological parameters necessary for coexistence. The inequality requires the ratio of the number of offspring (per unit time) and the product of adult death rate and juvenile death and maturations rates to be a decreasing function.

Boundary conditions also imply that since $\frac{\partial h(1)}{\partial \lambda} = 0$, $\frac{\partial \left({}^{P}\!/_{C}\right)(1)}{\partial \lambda} = 0$.

Note that $f = 0$ then (2.22) implies that $\frac{\partial h}{\partial \lambda} = 0$, *i.e.* $h = h_0$ where h_0 is a constant. Since a steady state with seeds and no flowers is impossible, h_0 is 1, which corresponds to $s_0 = 0$. Therefore, this state represents extinction of seeds and flowers. Also, note that if $\frac{P}{C}$ is a constant, then $\frac{\partial \left(P/C \right)}{\partial \lambda} = 0$, and therefore *f*=0.

Therefore, steady states are

(f, h) and $(0, h_0)$.

It was not possible to conduct a full analytical treatment of the linear stability analysis (Appendix A). Therefore, the stability of the system was explored numerically.

2.2.3 Numerical simulation results

In order to explore the stability of steady states described in the previous section, the system was simulated numerically. An ODE solver (ordinary differential equation solver) by Hairer *et al.* (1993) was used. The solver simulates the evolution of the system from a given initial state. It uses the Runge-Kutta method of order 8 with step size control and dense output.

In the system under consideration, both $F(\lambda, \tau)$ and $S(\lambda, \tau)$ are defined for values of λ in the range (0, 1). To represent the distributions of $F(\lambda, \tau)$ and $S(\lambda, \tau)$ along λ, the system was discretised along λ. To discretise λ, the interval was divided into even λ-steps, $\Delta\lambda$. The continuous function $S(\lambda, \tau)$ was then discretised to become $S(\lambda_i, \tau)$ where $\lambda_i = 0$, $\Delta\lambda$, $2\Delta\lambda$, ..., 1. Similarly, $F(\lambda, \tau)$ was discretised. To represent $\int_\lambda^1 S(l, \tau)dl$ the trapezoidal approximation was used. That is $\int_\lambda^1 S(l, \tau)dl$ was approximated by

$$\Delta\lambda \left[\frac{1}{2} S(\lambda_i, \tau) + \sum_{j=i+1}^{n-1} S(j, \tau) + \frac{1}{2} S(1, \tau) \right]$$

where λ from the integral was in the interval $(\lambda_i, \lambda_i + \Delta\lambda)$.
Therefore, the continuous system was replaced by a system of equations

$$\begin{cases} \dfrac{dF(\lambda_i,\tau)}{d\tau} = \dfrac{\lambda_i S(\lambda_i,\tau)}{1+\Delta\lambda\left[\dfrac{1}{2}S(\lambda_i,\tau)+\sum\limits_{j=j+1}^{n-1}S(\lambda_j,\tau)+\dfrac{1}{2}S(1,\tau)\right]} - F(\lambda_i,\tau) \\ \dfrac{dS(\lambda_i,\tau)}{d\tau} = PF(\lambda_i,\tau) - C\lambda_i S(\lambda_i,\tau) \end{cases}$$

First, the steady state $(f, h) = (0, h_o)$ is explored. This corresponds to the steady state $(f, s) = (0, 0)$. The stability analysis revealed that this steady state is a stable node if $\frac{P}{C}(\lambda) < 1$. To confirm this, simulations were performed with $\frac{P}{C}(\lambda) < 1$: case 1) P=0.2, and C=0.5; case 2) $P=4\lambda^2$ and C=0.5. Two sets of initial conditions were used: 1) $(F(\lambda), S(\lambda)) = (1, 1)$ and 2) $F(\lambda)$ and $S(\lambda)$ picked randomly from the range (0, 100). In all simulations, the system immediately settled to the (0, 0) state.

To explore the stability of the non-zero steady state, two functions of $P(\lambda)$ were used for simulations:

Case 1: $P(\lambda) = (\lambda - 1)^2 + 1.5$ and C=1.5. Substituting for $\frac{P}{C}(\lambda)$ in (2.17) and (2.23),

$$s(\lambda) = \frac{4}{3}(1-\lambda),$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.24),

$$f(\lambda) = 2\frac{\lambda - \lambda^2}{(\lambda-1)^2 + 1.5}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing on the interval (0,1), and ${}^{P}\!/_{C}(1) = 1$.

Case 2: $P(\lambda) = \dfrac{1}{2\lambda - \lambda^2 + 1} + 1$ and C=1.5, which meant that the analytical non-zero steady state was the following.

Substituting for $\frac{P}{C}(\lambda)$ in (2.17) and (2.23),

$$s(\lambda) = \frac{4}{3}\frac{(1-\lambda)}{\left(2\lambda - \lambda^2 + 1\right)^2},$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.24),

$$f(\lambda) = 2\frac{\lambda - \lambda^2}{\left(2\lambda - \lambda^2 + 1\right)^2 \left(\frac{1}{2\lambda - \lambda^2 + 1} + 1\right)}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing on the interval (0,1), and $P/_C(1) = 1$.

To explore the stability of the steady state, experiments were conducted with $F(\lambda)$ and $S(\lambda)$ at various values away from the analytically determined steady state. The simulations were performed with the following initial states:

1) setting $F(\lambda)$ to the steady state values $f(\lambda)$, and setting $S(\lambda)$ to values a) $s(\lambda) \pm 0.001\, s(\lambda)$; b) $s(\lambda) \pm 0.01\, s(\lambda)$; c) $s(\lambda) \pm 0.1\, s(\lambda)$; d) $s(\lambda) \pm 0.5\, s(\lambda)$; if the assigned value was negative, then its absolute values was used (since $F(\lambda)$ and $S(\lambda)$ cannot take on negative values);
2) setting $S(\lambda)$ to the steady state values $s(\lambda)$, and setting $F(\lambda)$ to values a) $f(\lambda) \pm 0.001 f(\lambda)$; b) $f(\lambda) \pm 0.01 f(\lambda)$; c) $f(\lambda) \pm 0.1 f(\lambda)$; d) $f(\lambda) \pm 0.5 f(\lambda)$;if the assigned value was negative, then its absolute values was used (since $F(\lambda)$ and $S(\lambda)$ cannot take on negative values);
3) $F(\lambda)=S(\lambda)=1$ on $\lambda \subset (0, 1)$;
4) $F(\lambda)$ and $S(\lambda)$ assigned random values from 0 to 100.

The λ-step, Δλ, was set to 0.01. The simulations were not sensitive to the value of λ-step as long as λ-step was below 0.1. In all cases, the simulations converged to the steady state before 400,000 time steps. An example of a simulation for the initial condition of 1 is presented in Figures 2.2 and 2.3, which show the distribution of $F(\lambda)$ and $S(\lambda)$ at four different time points (plots 2.2 and 2.3 a, b, c, and d) as the system approached the predicted steady state. Figure 2.4 shows sample phase plane plots for two values of λ (λ=0.9 and λ=0.7). The phase plane plots show oscillatory behaviour that is more pronounced for smaller values of λ. Another phase plane plot is shown in Figure 2.5, for the initial state when $S(\lambda)$ was set to the steady state $s(\lambda)$, and $F(\lambda)$ was set to $F(\lambda) \pm 0.5 f(\lambda)$ (with constraint that it is always positive). The plot shows oscillatory behaviour, as in Figure 2.4. However, in this case the oscillatory behaviour is not as uniform, possibly due to the random variation of the initial condition for $F(\lambda)$. The same behaviour is observed for all values of λ, but the oscillations are more frequent for smaller values of λ.

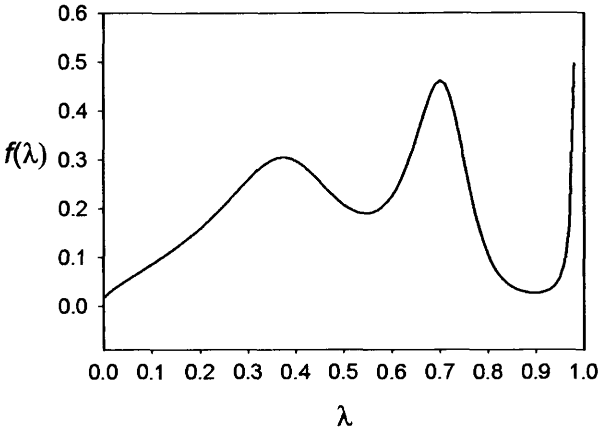


Fig. 2.2 a) time step 300;

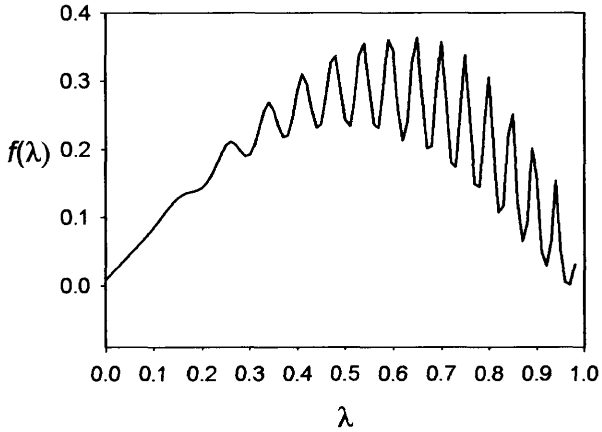


Fig. 2.2 b) time step 1,000;

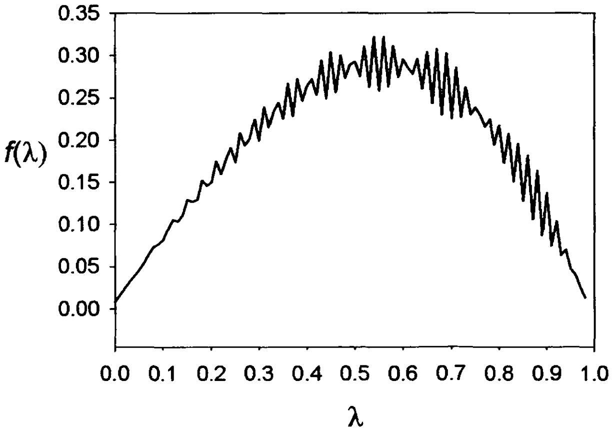


Fig. 2.2 c) time step 100,000;

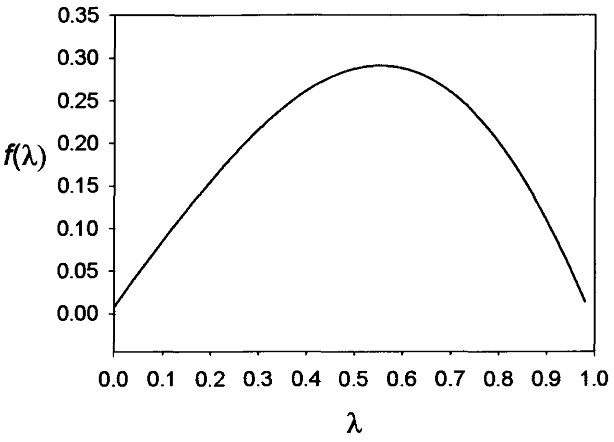


Fig. 2.2 d) time step 400,0000 – steady state.

Figure 2.2 Simulation of the distribution of the fecund individuals across λ. The simulation evolved through states shown in a) and b) towards c) which is the steady state predicted by analysis. Initial conditions for the simulation were: $F(\lambda)=1$, $S(\lambda)=1$ for $0<\lambda<1$; $F(\lambda)=0$, $S(\lambda)=0$ for $\lambda=1$ (the upper limit of λ values). However, the simulation outcome did not depend on the initial conditions.

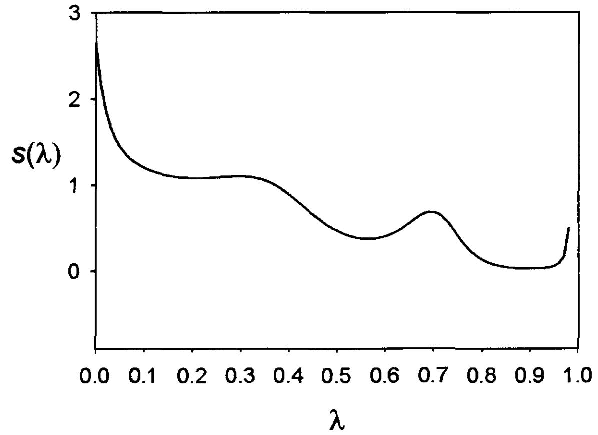


Fig. 2.3 a) time = 300;

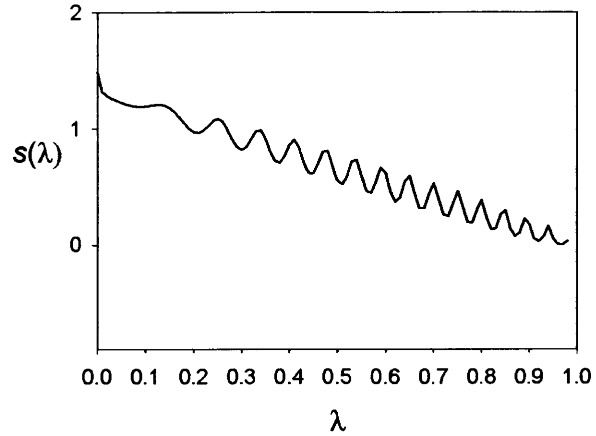


Fig. 2.3 b) time step=10,000;

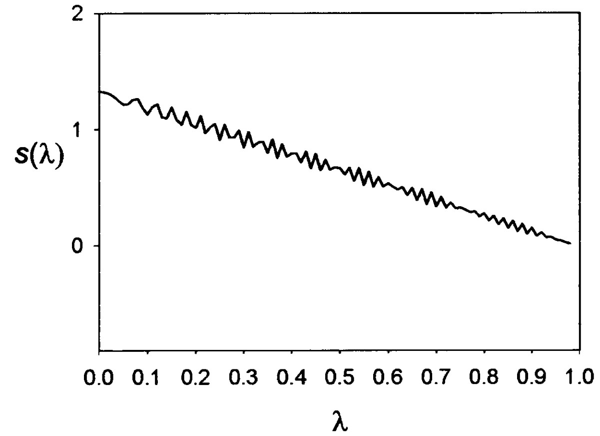


Fig. 2.3 c) time step 100,000;

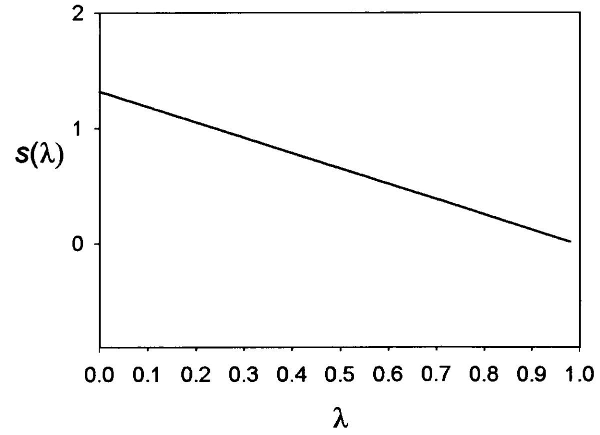


Fig. 2.3 d) time step 400,000 – steady state.

Figure 2.3 Simulation of the distribution of seeds across λ. The simulation evolved through states shown in a, b and c towards d) which is the steady state predicted by analysis. Initial conditions for the simulation: $F(\lambda)=1$, $S(\lambda)=1$ for $0<\lambda<1$; $F(\lambda)=0$, $S(\lambda)=0$ for $\lambda=1$ (the upper limit of λ values). However, the simulation outcome did not depend on the initial conditions.

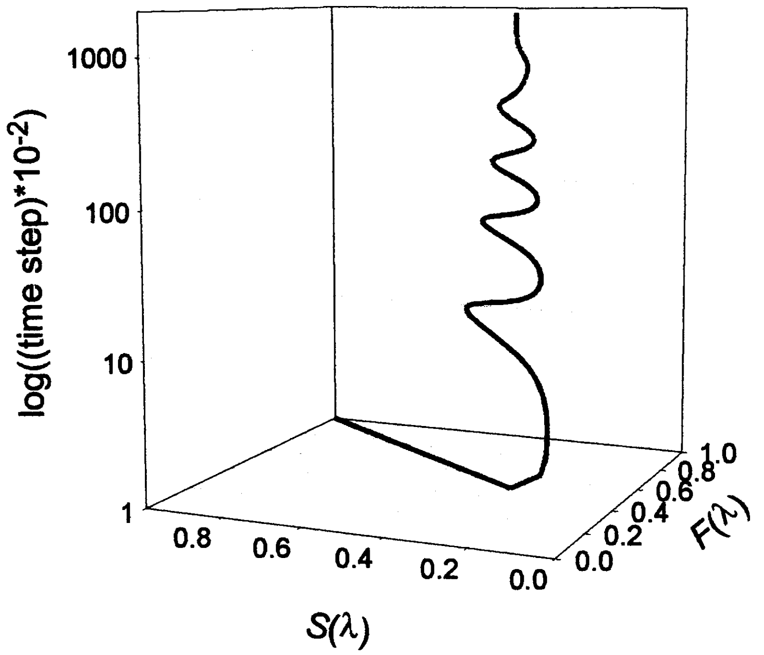


Fig. 2.4 a) Phase plane plot for $F(\lambda)$ and $S(\lambda)$ at λ=0.9. Note that time is shown on log scale.

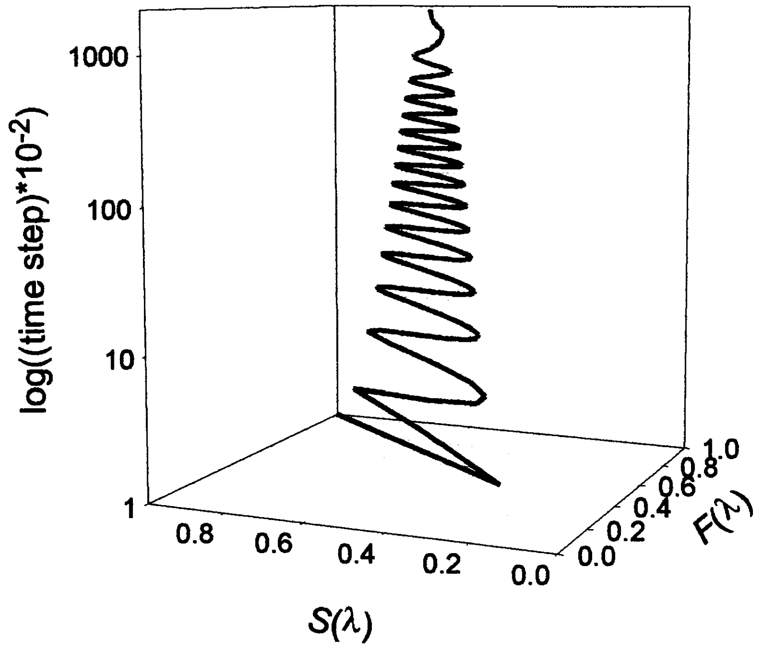


Fig. 2.4 b) Phase plane plot for $F(\lambda)$ and $S(\lambda)$ at λ=0.7. The dynamics are the same as in the phase plant plot for λ=0.9, but with more fluctuations. In general, for smaller λ values, there are more fluctuations than for larger λ.

Figure 2.4 Phase plane plots for $F(\lambda)$ and $S(\lambda)$ observed in the simulations with initial state (1, 1).

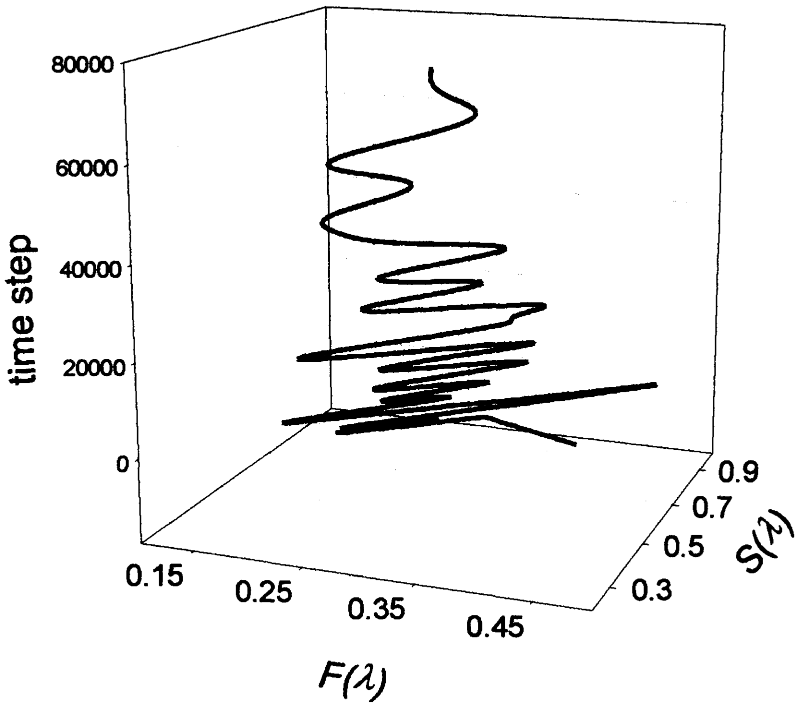


Figure 2.5 Phase plane plots for $F(\lambda)$ and $S(\lambda)$ observed in the simulations with initial state ($f(\lambda) \pm 0.5 f(\lambda)$, $s(\lambda)$).

2.3 Implications for diversity maintenance

The model was formulated to explore the connection between the basic physiological traits of individuals in a community and community diversity. The results show that a relationship among the individual traits is necessary in order to maintain diversity in the system. In particular, $\frac{P}{C}(\lambda)=\frac{b}{ca}(\lambda)$, the ratio between the number of offspring (per unit time) *b* and the product of death rate of adult plants, *a*, and death and maturation rate of juvenile plants, *c*, had to be a decreasing function of the reproduction rate λ. In other words, plants that reproduced at a smaller rate had to have a bigger number of offspring to death and maturation rates ratio (Figure 2.6). This shows that the trade-off among traits of individuals needs to be of a particular form in order for community diversity to exist.

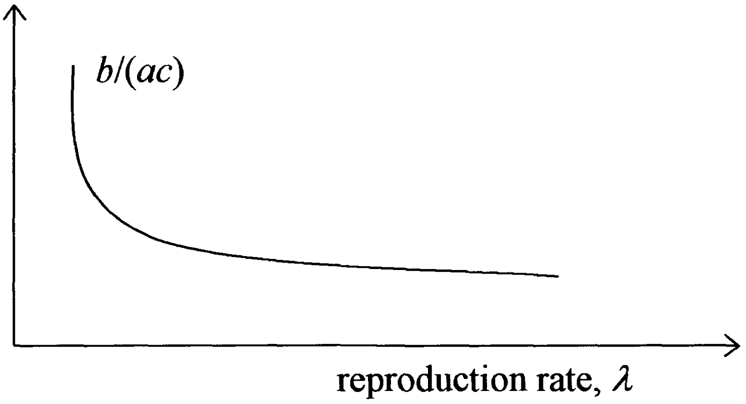


Figure 2.6 Ratio of number of offspring (per unit time), *b*, to the product of adult death rate, *a*, and juvenile death and maturation rate, *c*, is a decreasing function of the reproduction rate λ.

In addition to determining community diversity, the form of the trade off also determined the relative abundance of individuals with different trait values. The stable steady states of the systems were shown to be a function of the ratio $\frac{b}{ca}(\lambda)$. Therefore, the shape of function determined the final shape of the population distribution (Figure 2.7).

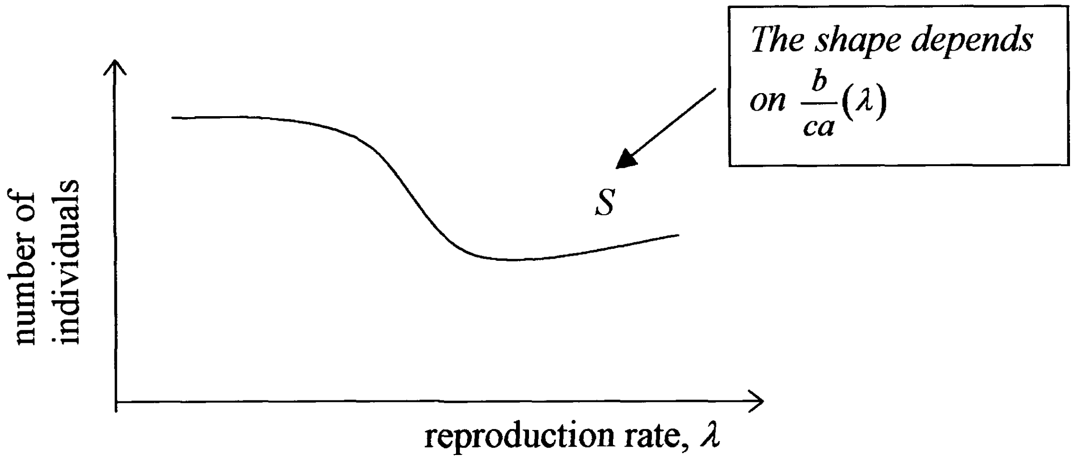


Figure 2.7 Example of the distribution of $S(\lambda)$ (the number of seeds in a population) as a function of the reproduction rate λ. $S(\lambda)$ is a function of $\frac{b}{ca}(\lambda)$.

2.4 A model with genetic coupling and hierarchical competition

2.4.1 Model definition

This section explores the effect of genetic coupling on the system requirements for diversity. Returning to eq. (2.12)

$$\begin{cases} \dfrac{\partial F^*}{\partial \tau} = \dfrac{R^*\lambda^* S^*(\lambda^*,\tau)}{1+K\lambda_c\int\limits_0^1 \kappa^*(l^*,\lambda^*)S^*(l^*,\tau)dl^*} - F^*(\lambda^*,\tau) \\ \dfrac{\partial S^*}{\partial \tau} = P^*\int\limits_0^1\int\limits_0^1 \rho^*(\lambda^* \mid x^*,y^*)Q[F^*(x^*,\tau),F^*(y^*,\tau)]dx^*dy^* - R^*c\lambda^*S^*(\lambda^*,\tau) \end{cases}$$

To reduce the number of parameters, let $S^{**}(\lambda^*,\tau) = \lambda_c KS^*(\lambda^*,\tau)$ and $F^{**}(\lambda^*,\tau) = \dfrac{\lambda_c KF^*(\lambda^*,\tau)}{R^*}$. The kernel function does not change since

$$\lambda_c K\int_0^1 \kappa^*\left(l^*,\lambda^*\right)S^*\left(l^*,\tau\right)dl^* = \int_0^1 \kappa^*\left(l^*,\lambda^*\right)K\lambda_c S^*\left(\lambda^*,\tau\right)dl^* = \int_0^1 \kappa^*\left(l^*,\lambda^*\right)S^{**}\left(\lambda^*,\tau\right)dl^*$$

Then the system can be rewritten as

$$\begin{cases} \dfrac{\partial F^{**}}{\partial \tau} = \dfrac{\lambda^* S^{**}(\lambda^*,\tau)}{1+\int_0^1 \kappa^*(l^*,\lambda^*)S^{**}(l^*,\tau)dl^*} - F^{**}(\lambda^*,\tau) \\ \dfrac{\partial S^{**}}{\partial \tau} = (R^*)^2 P^* \int_0^1 \int_0^1 \rho^*(\lambda^* \mid x^*,y^*)Q[F^{**}(x^*,\tau),F^{**}(y^*,\tau)]dx^*dy^* - R^* c\lambda^* S^{**}(\lambda^*,\tau) \end{cases}$$

Let $P=(R^*)^2 P^*$ and $C=cR^*$. For clarity of notation, eliminate the subscripts * and ** on λ, l, κ, x, y, S and F. Then:

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda S(\lambda,\tau)}{1+\int_0^1 \kappa(l,\lambda)S(l,\tau)dl} - F(\lambda,\tau) \\ \dfrac{\partial S}{\partial \tau} = P\int_0^1 \int_0^1 \rho(\lambda \mid x,y)Q[F(x,\tau),F(y,\tau)]dxdy - C\lambda S(\lambda,\tau) \end{cases}$$

Consider the form of the kernel from section 2.2.1. Then the system becomes

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = \dfrac{\lambda S(\lambda,\tau)}{1+\int_\lambda^1 S(l,\tau)dl} - F(\lambda,\tau) \\ \dfrac{\partial S}{\partial \tau} = P\int_0^1 \int_0^1 \rho(\lambda \mid x,y)Q[F(x,\tau),F(y,\tau)]dxdy - C\lambda S(\lambda,\tau) \end{cases}$$

Let $H\left(\lambda,\tau\right)=1+\int_\lambda^1 S\left(l,\tau\right)dl$. Then the system becomes

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = -\lambda\dfrac{\partial H}{\partial \lambda} - F(\lambda,\tau) \\ -\dfrac{\partial^2 H}{\partial \tau \partial \lambda} = P\int_0^1 \int_0^1 \rho(\lambda \mid x,y)Q[F(x,\tau),F(y,\tau)]dxdy + C\lambda\dfrac{\partial H}{\partial \lambda} \end{cases}$$

2.4.2 Steady states and stability

Let $I(\lambda)=P\int_0^1 \int_0^1 \rho(\lambda \mid x,y)Q[F(x,\tau),F(y,\tau)]dxdy$.

If (*F*, *H*)=(0,0), the system is in a steady state. Let (*f*, *h*) be a non-zero steady state. Then:

$$\begin{cases} 0 = -\lambda \dfrac{\partial h}{\partial \lambda} - f(\lambda,\tau) \\ 0 = I(\lambda) + C\lambda \dfrac{\partial h}{\partial \lambda} \end{cases}$$

Then,

$$-\lambda \frac{\partial h}{\partial \lambda} \frac{1}{h} = f(\lambda), \tag{2.26}$$

and

$$I(\lambda) = -C\lambda \frac{\partial h}{\partial \lambda}. \qquad \text{with} \tag{2.27}$$

Combining (2.26) and (2.27)

$$h(\lambda) = \frac{I(\lambda)}{Cf(\lambda)}. \tag{2.28}$$

Boundary conditions state that *h*(1)=1. Therefore,

$$\frac{I(1)}{f(1)} = C. \tag{2.29}$$

Substitute (2.28) into (2.27):

$$I(\lambda) = C\lambda\left(-\frac{1}{C}\frac{d}{d\lambda}\left(\frac{I(\lambda)}{f(\lambda)}\right)\right)$$

$$I(\lambda) = -\lambda \frac{d}{d\lambda}\left(\frac{I(\lambda)}{f(\lambda)}\right)$$

$$I(\lambda) = -\lambda \frac{f(\lambda)(dI(\lambda)/d\lambda) - I(\lambda)(df(\lambda)/d\lambda)}{f^2(\lambda)}$$

$$f^2(\lambda)I(\lambda) = -\lambda f(\lambda)\frac{dI(\lambda)}{d\lambda} + \lambda I(\lambda)\frac{df(\lambda)}{d\lambda}$$

$$f^2(\lambda)I(\lambda) + \lambda f(\lambda)\frac{dI(\lambda)}{d\lambda} - \lambda I(\lambda)\frac{df(\lambda)}{d\lambda} = 0 \tag{2.30}$$

This is a Bernoulli equation, and it can be solved as follows.

First, divide (2.30) by $-\lambda I(\lambda)$:

$$\frac{I(\lambda)}{-\lambda I(\lambda)} f^2(\lambda) - \frac{\lambda dI(\lambda)}{d\lambda}\frac{1}{\lambda I(\lambda)} f(\lambda) + \frac{df(\lambda)}{d\lambda} = 0$$

and therefore

$$-\frac{1}{\lambda} f^2(\lambda) - \frac{d(\ln I(\lambda))}{d\lambda} f(\lambda) + \frac{df(\lambda)}{d\lambda} = 0 \tag{2.31}$$

Let $v = \frac{1}{f(\lambda)}$, (2.32)

then $\frac{dv}{d\lambda} = -\frac{(df(\lambda)/d\lambda)}{f^2(\lambda)}$.

Now divide (2.31) by $f^2(\lambda)$.

$$-\frac{1}{\lambda} - \frac{d(\ln I(\lambda))}{d\lambda}\frac{1}{f(\lambda)} + \frac{df(\lambda)}{d\lambda}\frac{1}{f^2(\lambda)} = 0$$

which is

$$-\frac{1}{\lambda} - \frac{d(\ln I(\lambda))}{d\lambda}v - \frac{dv}{d\lambda} = 0 \text{ or}$$

$$\frac{1}{\lambda} + \frac{d(\ln I(\lambda))}{d\lambda}v + \frac{dv}{d\lambda} = 0. \tag{2.33}$$

To solve this, let $u = e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}$ be an integrating factor. Multiply (2.33) by *u*.

$$e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}\frac{1}{\lambda} + e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}\frac{d(\ln I(\lambda))}{d\lambda}v + e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}\frac{dv}{d\lambda} = 0$$

$$\frac{d}{d\lambda}\left(e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}v\right) + \frac{1}{\lambda}e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}} = 0$$

This equation has a solution

$$v = \frac{\int \frac{1}{\lambda}e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}d\lambda + q}{e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}}} \tag{2.34}$$

where *q* is a constant.

Note that

$e^{\int \frac{d(\ln(I(\lambda))}{d\lambda}} = I(\lambda)$ and therefore (2.34) becomes

$$v = \frac{\int \frac{I(\lambda)}{\lambda}d\lambda + q}{I(\lambda)}.$$ Using (2.32)

$$f(\lambda) = \frac{I(\lambda)}{\int \frac{I(\lambda)}{\lambda}d\lambda + q}.$$

Unfortunately, a full stability analysis was intractable for this particular system and is the subject of further work. However, the above analysis shows that genetic coupling, along with the ratio $\frac{b}{ca}(\lambda)$, determines: 1) whether or not diversity is present, and 2) the distribution of the population along values of λ.

2.5 Relaxing hierarchical competition for the model with clonal reproduction

2.5.1 Model definition

Consider a model with clonal reproduction (as in section 2.2), but in the case where competition between individuals is not strictly hierarchical; instead, an individual competes with all individuals that grow faster than it, and also some proportion of individuals that grow slower than it. This can be expressed by the kernel in the competition integral in (2.15), of the following form:

$$\kappa(l,\lambda)=\begin{cases}0 \text{ if } l<\varepsilon\lambda\\ 1 \text{ if } l\geq\varepsilon\lambda\end{cases}$$

where $0 < \varepsilon < 1$.

The system looks as follows:

$$\begin{cases}\dfrac{\partial F}{\partial\tau}=\dfrac{\lambda S(\lambda,\tau)}{1+\int\limits_{\varepsilon\lambda}^{1}S(l,\tau)dl}-F(\lambda,\tau)\\ \dfrac{\partial S}{\partial\tau}=PF(\lambda,\tau)-C\lambda S(\lambda,\tau)\end{cases}\qquad(2.35)$$

Let $H(\lambda,\tau)=1+\int\limits_{\varepsilon\lambda}^{1}S(l,\tau)dl$.

This means that the system can be rewritten as

$$\begin{cases}\dfrac{\partial F}{\partial\tau}=-\dfrac{\lambda}{\varepsilon}\dfrac{\partial H(\lambda/\varepsilon,\tau)}{\partial\lambda}\dfrac{1}{H(\lambda,\tau)}-F(\lambda,\tau)\\ -\dfrac{1}{\varepsilon^2}\dfrac{\partial^2 H(\lambda/\varepsilon,\tau)}{\partial\lambda^2}=PF(\lambda,\tau)+C\dfrac{\lambda}{\varepsilon}\dfrac{\partial H(\lambda/\varepsilon,\tau)}{\partial\lambda}\end{cases}\qquad(2.36)$$

Here,

$$S(\varepsilon\lambda,\tau) = -\frac{1}{\varepsilon}\frac{\partial H}{\partial \lambda}. \qquad (2.37)$$

$H(\lambda, \tau)$ has several constraints. First, since $S(1,\tau) = 0$ is a boundary condition, this means that

$$H(1/\varepsilon, \tau) = 1. \qquad (2.38)$$

Also, since $S(\lambda,\tau)$ must be non-negative on [0, 1],

$$\frac{\partial H}{\partial \lambda} \le 0 \text{ on } [0, 1/\varepsilon].$$

And if $S(\lambda,\tau)$ must be positive (*e.g.* for a non-zero steady state), then

$$\frac{\partial H}{\partial \lambda} < 0 \text{ on } [0, 1/\varepsilon]. \qquad (2.39)$$

2.5.2 Steady states and stability

Let $H(\lambda,\tau) = h(\lambda) + \tilde{h}(\lambda,\tau)$ and $F(\lambda,\tau) = f(\lambda) + \tilde{f}(\lambda,\tau)$ where

$$-\frac{\lambda}{\varepsilon}\frac{\partial h(\lambda/\varepsilon,\tau)}{\partial \lambda}\frac{1}{h} - f = 0 \qquad (2.40)$$

and

$$Pf + C\frac{\lambda}{\varepsilon}\frac{\partial h(\lambda/\varepsilon,\tau)}{\partial \lambda} = 0 \qquad (2.41)$$

Now (2.20) implies that

$$\frac{\lambda}{\varepsilon}\frac{\partial h(\lambda/\varepsilon,\tau)}{\partial \lambda} = -hf \qquad (2.42)$$

Plugging this in into (2.21)

$$Pf - Chf = 0$$

or

$$f(P - Ch) = 0$$

This means that either $f = 0$ or $h = P/C$ or both.

If $h = {}^{P}\!/_{C}$ $\qquad$ (2.43)

then

$$f = -\frac{\lambda}{\varepsilon}\frac{\partial h(\lambda/\varepsilon,\tau)}{\partial \lambda}\frac{1}{h}$$

$$= -\frac{\lambda}{\varepsilon}\frac{\partial\left(\frac{P}{C}(\lambda/\varepsilon)\right)}{\partial\lambda}\frac{C}{P}. \qquad (2.44)$$

Also from (2.38) and (2.39) $\frac{P}{C}\left(\frac{1}{\varepsilon}\right) = 1$ and $\frac{\partial\left(P/C\right)}{\partial\lambda} < 0$ on [0, 1/ε].

Boundary conditions also imply that since $\frac{\partial h\left(\frac{1}{\varepsilon}\right)}{\partial\lambda} = 0$, $\frac{\partial\left(P/C\right)\left(\frac{1}{\varepsilon}\right)}{\partial\lambda} = 0$.

If $f = 0$ then (2.22) implies that $\frac{\partial h}{\partial\lambda} = 0$, *i.e.* $h = h_0$ where h_0 is a constant. Since a steady state with a seedbank and no flowers is not possible, h_0 is set to 1, which corresponds to $s_0 = 0$, *i.e.* extinction of seeds and flowers.

Note that if $\frac{P}{C}$ is a constant, then $\frac{\partial\left(P/C\right)}{\partial\lambda} = 0$, and therefore f=0.

Therefore, steady states are

(f, h) and $(0, h_0)$.

Again, it was not possible to complete a full stability analysis for this system and this is the subject of further work. Consequently, numerical simulation were performed.

2.5.3 Numerical simulation results

The results for the stability of the (f, s)=(0, 0) steady state were similar to the results for the model in Section 2.2.2. The simulations revealed that the (0, 0) steady state is a stable node if $\frac{P}{C}(\lambda) < 1$. Simulations were performed with $\frac{P}{C}(\lambda) < 1$: case 1) P=0.2, and C=0.5; case 2) $P=4\lambda^2$ and C=0.5. Two sets of initial conditions were used: 1) ($F(\lambda)$, $S(\lambda)$) = (1, 1) and 2) $F(\lambda)$ and $S(\lambda)$ picked randomly from the range (0, 100). In all simulations, the system immediately settled to the (0, 0) state.

To investigate the stability of the non-zero steady state, two functions of $P(\lambda)$ were used for simulations:

Case 1: $P(\lambda) = (\lambda - 2)^2 + 2.5$ and C=1.5.

If ε=0.5, then substituting for $\frac{P}{C}(\lambda)$ in (2.37) and (2.43),

$$s(\lambda)=\frac{32}{3}(1-\lambda),$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.44)

$$f(\lambda)=16\frac{\lambda-\lambda^2}{(\lambda-2)^2+2.5}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing on the interval (0,1), and ${}^{P}\!/_{C}(1)-1=\frac{4}{3}$ is positive.

Case 2: $P(\lambda)=\frac{1}{4\lambda-\lambda^2+1}+2$ and C=1.5.

If ε = 0.5, then substituting for $\frac{P}{C}(\lambda)$ in (2.37) and (2.43),

$$s(\lambda)=\frac{8}{3}\frac{(2-\lambda)}{\left(4\lambda-\lambda^2+1\right)^2},$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.44),

$$f(\lambda)=4\frac{2\lambda-\lambda^2}{\left(4\lambda-\lambda^2+1\right)^2\left(\frac{1}{4\lambda-\lambda^2+1}+2\right)}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing on the interval (0,1), and $\frac{P}{C}(1)-1=\frac{3}{4}$ is positive.

Simulations were performed with three different initial conditions: the steady state, $F(\lambda)$ and $S(\lambda)$ set to 1 for all λ, and $F(\lambda)$ and $S(\lambda)$ assigned a random value between 0 and 100 (not including endpoints).

When the equation solver was used to confirm the analysis, the predicted steady state was not stable in both cases. In fact, instabilities appeared, and eventually (on the order of 5,000 time steps) the system evolved to a discrete state. Figure 2.8 shows examples of the case 1 with initial conditions set to the steady state, developing instabilities and the stable state of a run with $\varepsilon=0.5$. It was not possible to conduct a complete stability analysis and therefore, at present, the origin of the peaks is not clear. However, there is an important difference in the way that the integral is calculated in the case of $\varepsilon \neq 1$, which leads to an unavoidable error. The competition integral was calculated on the interval $[\varepsilon\lambda, 1)$. When $\varepsilon\lambda$ is calculated, the discretisation leads to the integral for different values of λ to be the same (which should not occur). For example, for $\varepsilon=0.5$ and $\lambda=0.99$ and λ-step of 0.01 the integral should be calculated on the interval [0.495, 1). However, since the λ-step is 0.01, 0.0495 is rounded to 0.49. Now, for $\lambda=0.98$, the interval is also [0.49,1). Refining the discretisation, *i.e.* letting λ-step to be smaller, did not eliminate the peaks, but changed the time at which the instability developed. This was tested for λ-step of 0.1 and 0.002. In case with λ-step 0.1 the discrete state evolved after approximately 1,000 steps, and if λ-step was set to 0.005, the discrete state evolved after approximately 20,000 steps. The change in the resolution of the integration did not affect the location of the peaks and the final state was identical.

The error in the competition integral led to instabilities. However, this 'error' may have its origins in a more realistic representation of the ecosystem. Since, in reality, any ecosystem has a finite number of individuals, the space of λ is occupied at discrete points, with S and F discrete functions. This case is discussed in the following section.

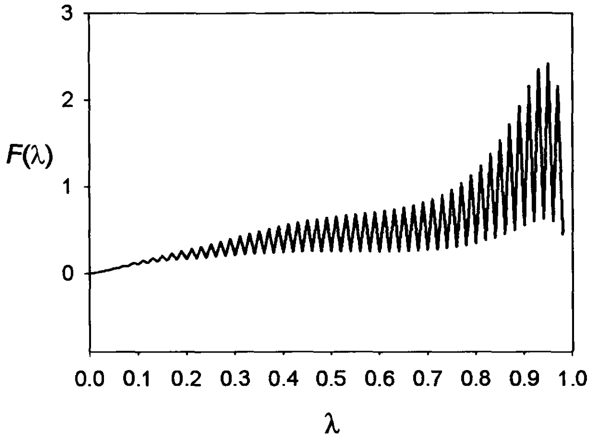


Fig. 2.8 a) time step 300;

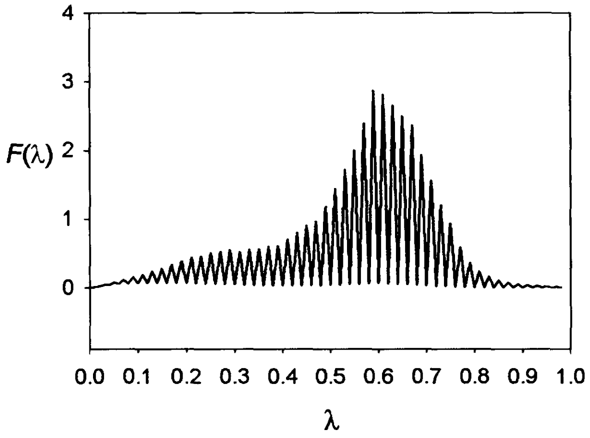


Fig. 2.8 b) time step 1,000;

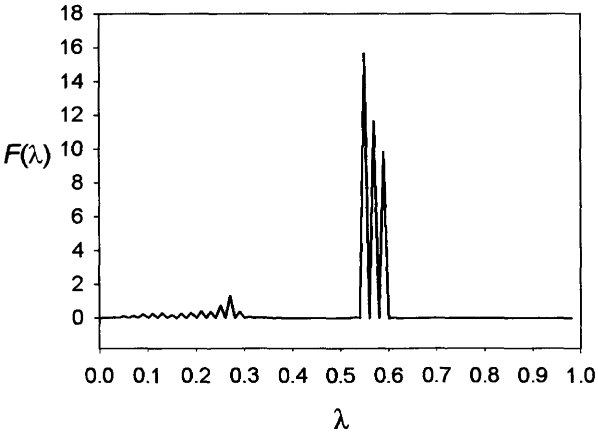


Fig. 2.8 c) time step 3,000;

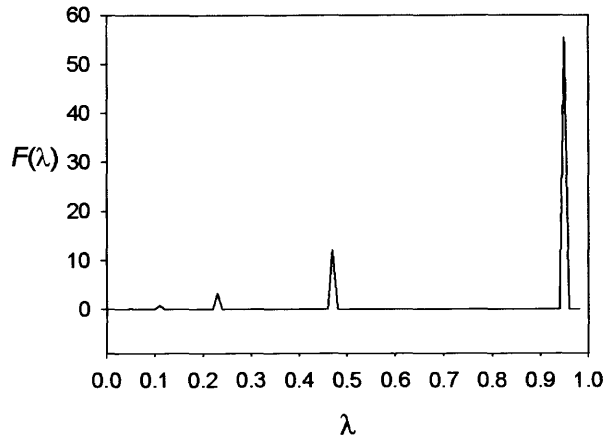


Fig. 2.8 d) the final distribution of the number of adult individuals $F(\lambda)$ across λ values at time step 36,000.

Figure 2.8 An example of numerical simulation results. The distribution of the number of adults $F(\lambda)$ for λ=0.5. The plots a) to d) show development of peaks starting from the steady state predicted by analysis.

2.6 The discrete version of the model

2.6.1 Model definition

Instead of the continuous functions F and S, consider a set of n discrete values (F_i, S_i) for each λ_i, i=1,...,n, with λ_i in the range [0,1). The system (2.35) becomes:

$$\begin{cases} \dfrac{dF_i}{d\tau} = \dfrac{\lambda_i S_i(\tau)}{1+(\Delta\lambda)\sum\limits_{j=i-k}^{n} S_j(\tau)} - F_i(\tau) \\ \dfrac{dS_i}{d\tau} = P_i F_i(\tau) - C\lambda_i S_i(\tau) \end{cases}$$

where $\Delta\lambda$ is the difference between λ_i and λ_{i+1}, and k is a number such that $i\text{-}k=\varepsilon i$.

2.6.2 A simple model of two competing populations

First, consider a simple system of two populations (F_1, S_1) and (F_2, S_2), which affect each other through competition, with values λ_1 and λ_2. The system is the following

$$\begin{cases} \dfrac{dF_1}{d\tau} = \dfrac{\lambda_1 S_1(\tau)}{1+(\Delta\lambda)(S_1(\tau)+S_2(\tau))} - F_1(\tau) = g_1(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \dfrac{dS_1}{d\tau} = P_1 F_1(\tau) - C\lambda_1 S_1(\tau) = h_1(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \dfrac{dF_2}{d\tau} = \dfrac{\lambda_2 S_2(\tau)}{1+(\Delta\lambda)(S_1(\tau)+S_2(\tau))} - F_2(\tau) = g_2(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \dfrac{dS_2}{d\tau} = P_2 F_2(\tau) - C\lambda_2 S_2(\tau) = h_2(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \end{cases}$$

Let f_1, s_1, f_2 and s_2 be the steady state solutions. Then, the possible steady states for this system are:

$$\begin{aligned} \{f_1, s_1, f_2, s_2\} &= \{0,0,0,0\}; \\ &= \{f_1, s_1, 0, 0\} \text{ where } f_1 \neq 0, s_1 \neq 0; \\ &= \{0, 0, f_2, s_2\} \text{ where } f_2 \neq 0, s_2 \neq 0; \\ &= \{f_1, s_1, f_2, s_2\} \text{ where } f_i \neq 0, s_i \neq 0,\ i = 1,2; \end{aligned}$$

For the case $\{f_1, s_1, 0, 0\}$ (where $f_1 \neq 0, s_1 \neq 0$), the steady state is:

$$\begin{cases} 0 = \dfrac{\lambda_1 s_1}{1+(\Delta\lambda)(s_1)} - f_1 \\ 0 = P_1 f_1 - C\lambda_1 s_1 \end{cases}$$

This implies that

$$\frac{1}{1+(\Delta\lambda)s_1} = \frac{f_1}{\lambda_1 s_1} = \frac{C\lambda_1 s_1}{P_1 \lambda_1 s_1} = \frac{C}{P_1} \qquad (2.45)$$

and therefore,

$$s_1 = \frac{1}{(\Delta\lambda)}\left(\frac{P_1}{C} - 1\right)$$

and

$$f_1 = \frac{C\lambda_1 s_1}{P_1} = \frac{1}{(\Delta\lambda)} \frac{\lambda_1 (P_1 - C)}{P_1}.$$

Similarly, for the steady state $\{0, 0, f_2, s_2\}$ (where $f_2 \neq 0, s_2 \neq 0$)

$$s_2 = \frac{1}{(\Delta\lambda)}\left(\frac{P_2}{C} - 1\right)$$

and

$$f_2 = \frac{C\lambda_2 s_2}{P_2} = \frac{1}{(\Delta\lambda)} \frac{\lambda_2 (P_2 - C)}{P_2}.$$

For the steady state $\{f_1, s_1, f_2, s_2\}$ (where $f_i \neq 0, s_i \neq 0,\ i = 1, 2$),

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_1}{C}, \tag{2.46}$$

and

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_2}{C} \tag{2.47}$$

are required for existence of the steady state. This is not possible unless $P_1 = P_2$. Assume that $P_1 = P_2 = P_0$. In that case both populations coexist, and their values are determined by the initial conditions and by the relationship

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_0}{C}, \tag{2.48}$$

and therefore

$$s_1 + s_2 = \frac{1}{(\Delta\lambda)}\left(\frac{P_0}{C} - 1\right).$$

This is the only constraint, and having picked the values of s_1 and s_2, f_1 and f_2 can be found by

$$f_i = \frac{C\lambda_i s_i}{P_0} \text{ for } i=1,2.$$

Linear stability analysis (Appendix A.3) suggests that the zero state is stable if either

a) $P_1 > C$ and $P_2 > C$ or

b) $P_1 < C$ and $P_2 < C$.

Case a) implies that either $C < P_1 < P_2$ or $C < P_2 < P_1$.

Case b) implies that either $P_1 < P_2 < C$ or $P_2 < P_1 < C$.

For the steady state $\{f_1, s_1, 0, 0\}$ (where $f_1 \neq 0, s_1 \neq 0$), linear stability analysis suggests that either

a) $P_1 > C$ and $P_1 > P_2$ or

b) $P_1 < C$ and $P_1 < P_2$.

Case a) implies that either $C < P_2 < P_1$ or $P_2 < C < P_1$.

Case b) implies that either $P_1 < P_2 < C$ or $P_1 < C < P_2$.

Similarly, for the case $\{0, 0, f_2, s_2\}$ (where $f_2 \neq 0, s_2 \neq 0$), the state is stable if either

a) $P_2 > C$ and $P_2 > P_1$, *i.e.* $C < P_1 < P_2$ or $P_1 < C < P_2$ or

b) $P_2 < C$ and $P_2 < P_1$, *i.e.* $P_2 < P_1 < C$ or $P_2 < C < P_1$.

Notice that if

$C < P_1 < P_2$ or $P_2 < P_1 < C$,

then both the zero-state and $\{0, 0, f_2, s_2\}$ are stable, and

if $C < P_2 < P_1$ or $P_1 < P_2 < C$,

then both the zero-state and $\{f_1, s_1, 0, 0\}$ are stable.

For the steady state $\{f_1, s_1, f_2, s_2\}$ (where $f_i \neq 0, s_i \neq 0,\ i = 1,2$), and $P_1=P_2=P_0$, linear stability analysis gives zero for det M. Hence, it does not provide information about stability in this case.

These are the results when individuals have one or two values of the parameter λ. This situation can be extended to more than two values (Appendix B).

2.6.3 Simulation results for a system of two populations

Simulations with two populations were performed, *i.e.* the populations with different values of λ were set to zero for all values of λ but two (with both affecting each other through competition). In that case, as the analysis predicted, population with only one value of λ survived if the values of *P* were different for the two populations. The simulations also showed that the population with a higher *P* value was the one that always survived. If the value of *P* was the same for the two populations, the system settled to the nearest point satisfying (2.48). Simulations with three and seven populations were performed as well, with the same results.

2.6.4 Effects of outside competition on a system with two populations

Now, extend the two population model to any two populations with reproduction rates λ_k and λ_{k-1} with $\lambda_k > \lambda_{k-1}$ for which the competition term, *i.e.* the sum of populations contributing to the competition, is the same. This occurs if $\lambda_{k-1} \subset (\varepsilon\lambda_k, 1)$. Now, suppose there are two populations with λ_k and λ_{k-1}, and the competition term is the same for the two, and $P_k=P_{k-1}=P_0$.

$$\begin{cases} \dfrac{dF_k}{d\tau} = \dfrac{\lambda_k S_k}{1+(\Delta\lambda)(S_k + S_{k-1} + \sum\limits_{j=k+1}^{n} S_j)} - F_k \\ \dfrac{dS_k}{d\tau} = P_k F_k - C\lambda_k S_k \\ \dfrac{dF_{k-1}}{d\tau} = \dfrac{\lambda_{k-1} S_{k-1}}{1+(\Delta\lambda)(S_k + S_{k-1} + \sum\limits_{j=k+1}^{n} S_j)} - F_{k-1} \\ \dfrac{dS_{k-1}}{d\tau} = P_{k-1} F_{k-1} - C\lambda_{k-1} S_{k-1} \end{cases}$$

Let ($s_k, f_k, s_{k-1}, f_{k-1}$) be the non-zero steady state. It exists if

$$1+(\Delta\lambda)(s_k + s_{k-1} + \sum_{j=k+1}^{n} s_j) = \frac{P_0}{C},$$

i.e.

$$s_k + s_{k-1} = \frac{1}{(\Delta\lambda)}\left[\frac{P_0}{C} - 1\right] - \sum_{j=k+1}^{n} s_j .$$

Those s_i in the sum that have the same competition term (the sum of other s values with which s_i competes), call it T_j, can be grouped together. Suppose there are l such groups, and therefore j=1,...,l. Then, in the steady state

$$\sum_{j=k+1}^{n} s_j = \underbrace{\sum_{j=k+1}^{m_1} s_j}_{T_1, P_1} + \underbrace{\sum_{j=m_1+1}^{m_2} s_j}_{T_2, P_2} + \ldots + \underbrace{\sum_{j=m_l+1}^{n} s_j}_{T_l, P_l}$$

In order that s_j within each group can coexist, it is necessary that

$$1+(\Delta\lambda)\sum_{j=m_i+1}^{m_{i+1}} s_j = \frac{P_i}{C} \Rightarrow \sum_{j=m_i+1}^{m_{i+1}} s_j = \frac{1}{(\Delta\lambda)}\left[\frac{P_i}{C} - 1\right],$$

for any i=1,...,l.

This means that

$$\sum_{j=k+1}^{n} s_j = \frac{1}{(\Delta\lambda)}\left[\frac{P_1}{C} - 1 + \frac{P_2}{C} - 1 + \ldots + \frac{P_l}{C} - 1\right]$$

and

$$s_k + s_{k-1} = \frac{1}{(\Delta\lambda)}\left[\left(\frac{P_0}{C} - 1\right) - \left(\frac{P_1 + P_2 + \ldots + P_l}{C} - l\right)\right].$$

Thus, s_k and s_{k-1} can assume any combination of values satisfying the above equality. For $s_k + s_{k-1}$ to be positive,

$$\frac{P_0}{C} - 1 > \frac{P_1 + P_2 + \ldots + P_l}{C} - l,$$

and therefore

$$P_0 > P_1 + \ldots + P_l - C(l-1).$$

This condition means that P_i has to be a decreasing step function of λ, where each step is an interval of λ values on which the corresponding values of s_i have the same competition term.

2.6.5 Simulation results for a system of two populations with outside competition

Simulations were performed using a monotonically decreasing function for $P(\lambda)$ and constant C. This form of $P(\lambda)$ is one of the conditions for the existence of the non-zero steady state in the continuous case. The simulations were started in the non-zero steady state predicted by the analysis. The system did not remain in the 'steady' state, but instead developed instabilities and evolved to a function consisting of discrete peaks (as seen on Figure 2.8 d)). The sequence of λ positions (from 0 through 0.99) at which populations remained was: 0, 0.02, 0.06, 0.14, 0.30, 0.62 (Δλ was 0.01).

The separation of the λ positions can be explained from the considerations outlined in sections 2.6.2 and 2.6.4. Since $P(\lambda)$ is monotonically decreasing,

a) only one population for the interval with the same competitive term (call the interval I_i) can survive;
b) the highest value of $P(\lambda)$ will be the first population at I_i (since $P(\lambda)$ is monotonically decreasing)..

For convenience refer to the positions of λ as 0 through 99 (with 99 corresponding to 0.99).

Look at the intervals I_i:

I_1=[0,1] : $s(\lambda)$ at 0 is has the highest $P(\lambda)$, so there is a population at 0.
I_2=[1,2,3] : $s(\lambda)$ at 1 cannot survive, so $s(\lambda)$ at 2 survives, so $s(\lambda)$ at 3 does not.
I_3=[2,3,4,5] : $s(\lambda)$ at 2 survives, so $s(\lambda)$ at 3-5 do not.
I_4=[3-7] : $s(\lambda)$ at 3 to 5 does not survive, so $s(\lambda)$ at 6 survives and so $s(\lambda)$ at 7 does not.
I_5=[4-9] : $s(\lambda)$ at 6 survives, others do not.
I_6=[5-11] : $s(\lambda)$ at 6 survives, others do not.

I_7=[6-13] : $s(\lambda)$ at 6 survives, others do not.
I_8=[7-14] : $s(\lambda)$ at 14 survives, since all previous do not.
etc...

This scheme produces exactly the spacing of λ resulting in the simulations.
This spacing of populations is

a) independent of the particular shape of $P(\lambda)$, given that it is monotonic decreasing;
b) the λ values for which populations survive depend on the λ step, not on the populations' relative positions in the [0,1) interval.

This scenario is a sequential phenomenon, *i.e.* the outcome at the interval depends on the outcome at the previous interval with lower values of λ. One question regarding this scenario is whether some populations, at λ positions that are predicted to survive, go extinct before the final spacing is reached. In fact, the simulation shows that populations that are predicted to survive can reach very small values (order of magnitude 10^{-7}), but then recover. In real communities, the populations cannot persist as such levels, and will go extinct. This may affect the persistence of individuals with other values of λ.

2.7 Discrete *vs.* continuous – individuals *vs.* populations

Analysis of the continuous and the discrete version of the model revealed some interesting differences between the two. The general requirement for $\frac{P}{C}(\lambda)$ to be a decreasing function was observed in both cases. However, in the continuous case, $\frac{P}{C}(\lambda)$ had to be monotonic decreasing, whereas this condition was weakened in the discrete case and $\frac{P}{C}(\lambda)$ could be a non-increasing step function. Moreover, simulations revealed that the dynamics of the model in the discrete case lead to a steady state consisting of peaks spaced in the manner described above. The difference between the discrete and the continuous models suggests that discreteness resulting from finite populations may play an important role in shaping the relative abundance of individuals across a range of trait values.

2.8 Lessons learned: the role of individuals

The results of the model show a link between physiological traits of individuals and community diversity.

- A trade-off between physiological traits of individuals in the model determined the existence of diversity in the community. Moreover, it determined the relative abundance of individuals across the range of trait values. This gives an indication that individual traits may play an important role in shaping the diversity in the community. The form of the genetic coupling had the same effects on the community.

Discrete and continuous models, while similar in the general conclusion, differed in the steady-state shape of the population distribution along the range of trait values. The simulations of the discrete model consistently produced a steady state distribution with populations located at precise values of the growth rate λ (Figure 2.8 c)). The intervals of separation depended on the description of competition.

- These results show that considering finite populations can have an important impact on the community dynamics. It it crucial to explore this impact, since biological commuities are always discrete in this sense.
- The results also suggested that the nature of competition between individuals in a community may also be important in determining the resulting steady state.

Chapter 3. Individual-based model of diverse populations

3.1 Introduction

The results of the mean-field model showed that the maintenance of diversity in a community depended on particular relationships between the basic physiological traits of individuals in the community. Moreover, the nature of the competition between individuals strongly affected the dynamics of the system. If relationships between physiological traits and interactions between individuals are crucial for community diversity, a more realistic description of individuals and their interactions should provide a more accurate representation of the mechanisms leading to diversity. Individual-based models provide a convenient framework for the description of individuals in terms of their physiological traits. In this work, an individual-based simulation model is used to complement the results of the mean-field model and to explore the effects of local interactions on diversity. The structure of this model was developed elsewhere and is fully described in Bown (2000) and Bown *et al.* (*in preparation*).

Defining individuals in terms of quantifiable physiological traits allows experimental data to be used to parameterise the model. This establishes an important link between the model and the modelled biological community, as has been noted in the introduction. The model can then provide a more realistic representation of the studied community and offer quantitative results. This chapter describes a parameterisation of the model, using experimental data to represent communities of the grassland species *Rumex acetosa* (Bown *et al. in preparation*). The data were obtained from a study that examined individual variation in species-rich grassland. The species *R. acetosa* was chosen for parameterisation because it is common throughout the study sites – *R. acetosa* is a perennial that coexists with many other species in grazed pastures – and had been subject to detailed physiological analysis (Bausenwein *et al.* 2001).

3.2 Model description

> 'Biologists must consider the mathematicians view of logic, low dimensionality, and simplicity; mathematicians must recognize the biologist's tendency to believe that everything is important.'
>
> Gross *et al.* (1992), p. 513.

The model was formulated to represent an isolated patch of plants (*i.e.* without input of seed from outside) on a small scale (1-10 m^2). Space in the model is represented explicitly (*i.e.* plants have locations that define their position with respect to other plants). An explicit representation of space was used to explore the effects of local interactions on the dynamics. The resource was also explicitly defined. Plant interactions occurred through competition for resource and space. A description of plant interactions mediated by resource is easier to parameterise than direct interactions between plants. Measuring the effect of one plant on another, or one species on another, is quite difficult; while measuring plant resource uptake and request (*i.e.* interactions with resource) is feasible and more accurate. The version of the model described here assumes that plants self-replicate (*i.e.* produce offspring identical to themselves), to ignore the effects of genetic coupling. The aim was to explore specifically the physiological, *i.e.* non-genetic, mechanisms generating diversity.

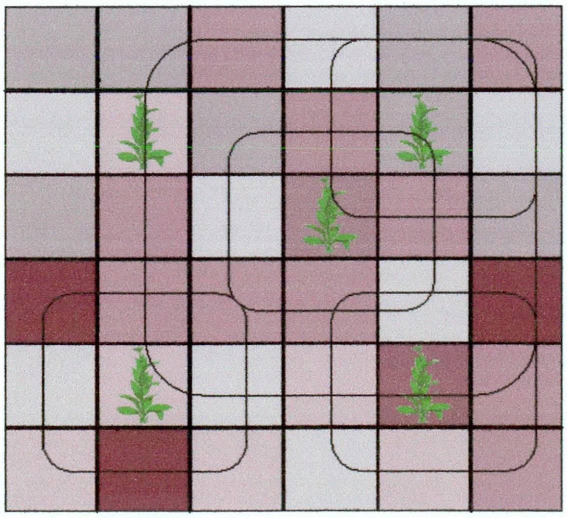


Figure 3.1 A representation of a part of the lattice simulated in the individual-based model. The squares of different shades of brown represent lattice cells with different level of substrate. The rounded squares around the plants cover the lattice sites from which the plants take up resource. Where the rounded squares overlap, the plants compete for resource.

The model simulates plant communities on a 2-D spatial lattice, with at most one plant possible at each lattice cell (Figure 3.1). Space and time in the model are discrete. It is assumed that plant growth is limited by a single resource which is distributed over the lattice. The amount of resource is defined individually for each lattice cell. Competition occurs for resource and for space, as described below. Plants are defined by traits describing essential physiological functions: resource uptake, development and reproduction. Plants develop by progressing along development stages. Those parameters that change with plant development are described as functions of the development stage. The 12 plant traits are listed, along with their numerical values, in Table 3.1 and described below.

Table 3.1 Parameter values and distributions. For parameters which are represented by distributions, sign '±' separates the means and the standard deviations of the distributions (see text for derivation of the values).

Parameter	**Values**
Essential uptake, $U_e(s)$	A sigmoidal curve $y = y_0 + \frac{\alpha}{1+e^{-(s-s_0)/\beta}}$ where s is the development stage. $y_0 = 0.24 \pm 0.310$, $\beta = 8.12 \pm 2.65$, $\alpha = 10.52$, $s_0 = 29.09$.
Requested/essential uptake ratio, r_u	1.1 ± 0.58
Spatial distribution of uptake, D_u	see Table 3.3
Resource storage partition trait, P_s	0.8
General storage release proportion, r_g	0.28 ± 0.143
Surplus storage release proportion, r_s	0.40 ± 0.153
Time dependent reproduction relation, R_t	45 ± 8.6 time steps
Storage-fecundity relation, R_f	$S_r / R_{\min}$ where S_r is the plant's storage available for reproduction, and $R_{\min}=U_e(1)$;
Seed dispersal pattern, D_p	randomly dispersed in an area 5 lattice cells away from parent plant;
Survival threshold, V_t	$0.1*U_e(s)$ where s is plant's current development stage;
Survival assessment period, V_p	5 time steps
Probability of plant death, P_d	0.001

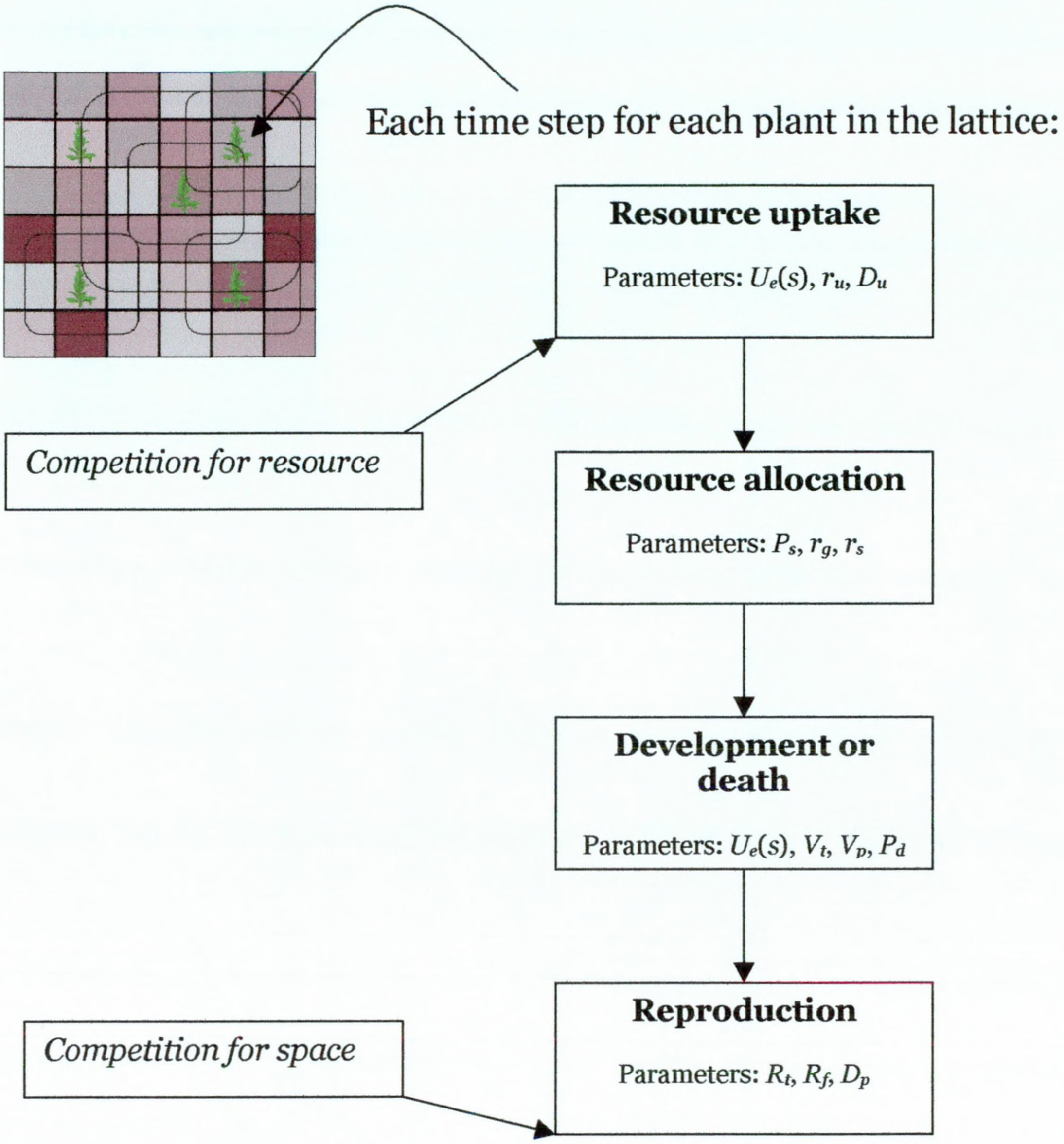


Figure 3.2 A diagram of processes that occur in the model for each plant at each time cycle.

A single time step of the model consists of plant resource uptake, resource storage, development and reproduction (a diagram of the processes that occur for each plant at each time cycle is shown in Figure 3.2). A plant acquires resource from its location and from the cells in its neighbourhood (Figure 3.3). The lattice neighbourhood represents the spatial spread of roots and leaves that the plant uses to acquire resource. The area and the distribution of uptake within this neighbourhood is described by the parameter D_u. Competition for resource occurs when more than one plant demands resource from the same lattice cell, and the demand exceeds the available resource. In this case, the resource available at the lattice cell is distributed among plants in proportion to their requests. More precisely, suppose *n* plants make demands on resource at a lattice cell, and each plant *i* makes a demand D_i. Suppose that T is the total amount of resource at the lattice cell. If $\sum_{j=1}^{n} D_j > T$, then each plant *i* is assigned $T\left(D_i \middle/ \sum_{j=1}^{n} Dj \right)$. This represents the competition that occurs between plants' roots for example. For example, if one plant has few roots in the area, and another plant has most of the roots in that area, the second plant will be able to extract more resource from that site.

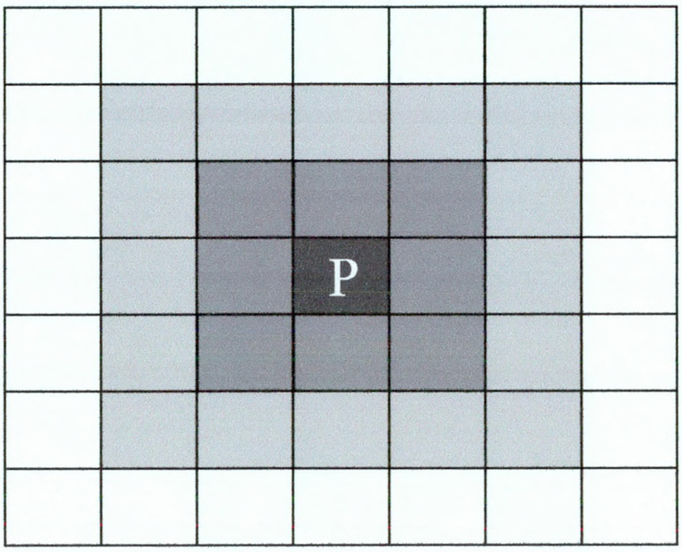


Figure 3.3 An example of a plant's capture area. The squares represent lattice cells. The cell labelled 'P' is the location of the plant. The cells shaded grey represent the area from which the plant acquires resource. The white is the area from which the plant does not request resource. The intensity of grey corresponds to the proportion of the total demand that the plant requests from the environment. For example, at the cell shaded the darkest grey (plant's location), the plant may request 0.5 of its total demand; from the lighter grey area around it 0.3; and from the lightest grey 0.2.

The plant's resource demand is described by two parameters, the essential uptake $U_e(s)$ (a function of the development stage s), and the requested/essential uptake ratio r_u. The essential uptake $U_e(s)$ describes the resource amount necessary for the optimal growth of the plant. A plant places a demand for an amount greater than $U_e(s)$ to increase its chances in the case of competition. Specifically, the amount that a plant demands is $r_u U_e(s)$.

The resource that plants obtained from the environment is allocated to development (*i.e.* growth of structure) and storage. Plants store resource in roots and leaves which can be translocated for use in development and reproduction at a later time. To represent this in the model, the acquired resource R is used by each plant for: a) maintenance of structure, b) development and c) reproduction. If a plant acquires more resource than is necessary for its optimal growth, the excess is allotted to the surplus storage. The proportion of R that is allocated for structure maintenance is described by the parameter P_s, the structural storage proportion. The resource, which is not used for structure, is stored in general storage. The resource in general storage can be used for reproduction and development. Any resource that is obtained in excess of the essential uptake $U_e(s)$ is allocated to the surplus storage.

After resource assimilation, the development stage of each plant is updated. A plant may either develop or die. A plant develops by progressing to the next development stage. A plant is transferred from a development stage s to a development $(s+1)$, if it has acquired an amount of resource $\sum_{i=1}^{s+1} U_e(i)$. A plant can die due to lack of resource or due to some other factor (*e.g.* disease). A plant dies due to lack of resource if it has not acquired enough resource over a specified period of time. The period of time is defined in time steps by the parameter V_p, and the minimum amount of resource required for survival is described by the parameter V_t. Death occurs if a plant's uptake over the last V_p time steps was less than $V_t U_e(s)$ where s is plant's current development stage. Death due to external causes, other than lack of resource, is incorporated by introducing a probability P_d that a plant dies. When a plant dies, the storage it carried is added to the resource level of the lattice cells from which it acquired resource.

Plants in the model reproduce with a frequency defined by the parameter R_t – the number of time steps between reproduction events. Plants produce offspring using storage resource allocated for reproduction. The resource for reproduction is drawn from the general and the surplus storage. The amount of storage used for reproduction from each storage is limited by the general storage release rate r_g, and the surplus storage release rate r_s. That is, the proportion r_g of the resource in the general storage plus the proportion r_s of the resource in the surplus store can be used for reproduction at a single reproduction event. The number of offspring produced is described by the storage-fecundity relation R_f. The parent plant's parameter values are inherited by its offspring. The offspring are distributed on the lattice according to the dispersal pattern of the plant, described by the parameter D_p. To represent an isolated patch, the boundaries of the lattice are absorbing, *i.e.* if an offspring lands outside of the lattice, it effectively dies. Each offspring carries to its site enough resource to progress to the first development stage. This represents the resource storage contained within plant seeds. If the lattice cell where the seed lands is occupied, the offspring dies, and the resource it carried is added to the substrate level of the lattice cell where it landed. After reproduction, plants often lose structure, biomass, and resource store, and therefore their requirement for uptake falls. To represent this, the development stage of the parent plant is re-evaluated and reduced if the plant does not have the stored resource required by its current development stage.

This model is an effective framework for studying the effects of individual traits on community dynamics, since the simulated communities can be understood in terms of individual physiological parameters. The individual physiological traits can be parameterised using experimental data. The model was designed with a framework flexible enough to allow many plant strategies. The need for defining the competitive effect of plants on each other (which is difficult) is avoided by introducing explicit competition for resource and space. Environmental heterogeneity can be easily introduced, since the resource level is defined separately for each cell. Community diversity is also convenient to simulate, since each plant has its own set of parameters associated with it.

3.3 Model parameterisation

> 'The intrinsic rate of increase of crop plants has been known since Biblical times to be between 30-fold and 100-fold per generation (St. Matthew 13).'
>
> Crawley (1990), p. 127.

3.3.1 Physiological data

The model was parameterised using physiological data for the plant species *Rumex acetosa*. Data derived from 20 plants were used, with 10 plants taken from each of two sites. The first site was a lowland grassland site near Cleish in Fife, Scotland, OS map location NT082934. The other site was a hillside grassland site in Kirkton near Crianlarich in the west Perthshire, Scotland, OS map location NT360284. The collected plants were cloned for use in nutrient labelling experiments in a glasshouse. During the experiment, the plants were allowed to take up ^{15}N before winter, then grown on ^{14}N next year. The contributions of N translocated from storage and N taken up during growth of various tissues was then assessed. This information was collected at 7 different times from January to September 1997: January 29, March 20, April 17, May 6, May 26, June 16, and September 9. For each of the plant organs listed in Table 3.2, the following measurements were taken: dry weight, content of C, N, and the proportions of N translocated from storage or taken up. Full details of the sites and the experiment are given in Bausenwein *et al.* (2001).

Table 3.2 Plant parts about which information was collected. H1 – harvest 1; H2 – harvest 2, etc.

Leaves	Dead leaves Old leaves at H1 New leaves between H1 and H2 New leaves between H2 and H3 New leaves between H3 and H4 New leaves between H4 and H5 New leaves between H1 and H5 New leaves between H6 and H7 Total new leaves
Reproduction	Stem (flower stock) Flowers (and forming seeds for females)
Roots	Fine root Tap root

3.3.2 Parameterisation

Most of the parameters describing plants were estimated using the experimental data for *R. acetosa* plants described above. In a few cases where the experimental data were lacking, evidence from existing literature along with general biological considerations were used. Diversity in communities was represented by allowing variation in the parameters described by experimental data. This was accomplished by defining the parameters in terms of probability distributions of possible values. Normal distributions were defined in terms of the means and standard deviations derived from the observed distribution of parameter values for the 20 plants. The observed probability distributions were tested for normality with the Shapiro-Wilk and Anderson-Darling tests. In all but one case, the hypothesis that the distributions do not differ from normal could not be rejected at the 5% significance level. Two exceptions were the distribution of values for the time of reproduction and the y_o parameter of the essential uptake curve. Due to the lack of information to the contrary, their distributions were assumed to be normal also. Some exploration of the behaviour of the model was conducted when other distributions (uniform, lognormal) were used, but no difference in the behaviour of the model was noted. In cases when the model parameter distributions included values not physiologically possible, truncated distributions were used (as described below). The experimental data used to parameterise the model were collected for plants in close to optimal conditions. The constraints on plant growth and development in the model arose as a consequence of limitation in resource availability and competition. If parameters were not defined using experimental data, they were defined by an estimated value. The plant parameter values are listed in Table 3.1, and the estimation procedures are described below. Plants development was divided into 50 development stages. This number was chosen to represent the plant life cycle on a scale sufficiently small to capture the essential plant functions. According to the parameterisation, a development stage corresponds to 4.46 days of plant growth in perfect conditions.

The essential uptake $U_e(s)$ was approximated by the amount of N used by plants as a function of the development stage s. This was done since N is considered to be the main limiting resource in Scottish grasslands. $U_e(s)$ was estimated by adding the amount of N uptake to the amount of N moved from the storage (if any) at each harvest time. This defined a lower limit for $U_e(s)$, since the amount of N moved from an experimental plant's storage may have been limited by the release rate of the storage. This estimation of $U_e(s)$ was, therefore, less than or equal to the actual value. The parameters for $U_e(s)$ were obtained by fitting a sigmoidal function to the values of used N (Figure 3.4):

$$y = y_0 + \alpha / (1 + e^{-\beta(s - s_0)})$$

where y is the estimated used N, s is the development stage of the plant, and s_0, y_0, α and β are parameters. The choice of the function is explained in Appendix C. Parameters y_0 and β were described by distributions since they can be used to define the main properties of the curve: the height (defined by y_0) and the steepness of the rise of the curve (defined by β). The values of s_0 and α were defined by mean values. The values of s_0, y_0, α and β were scaled so that $U_e(s)$ was defined for s in the range 0 to 50 (the development stage range) and, for average values of the parameters, was 10 at the last development stage. The value of 10 was arbitrarily chosen as the maximum uptake value. The distribution of y_0 was truncated at 0, since the initial uptake cannot be negative.

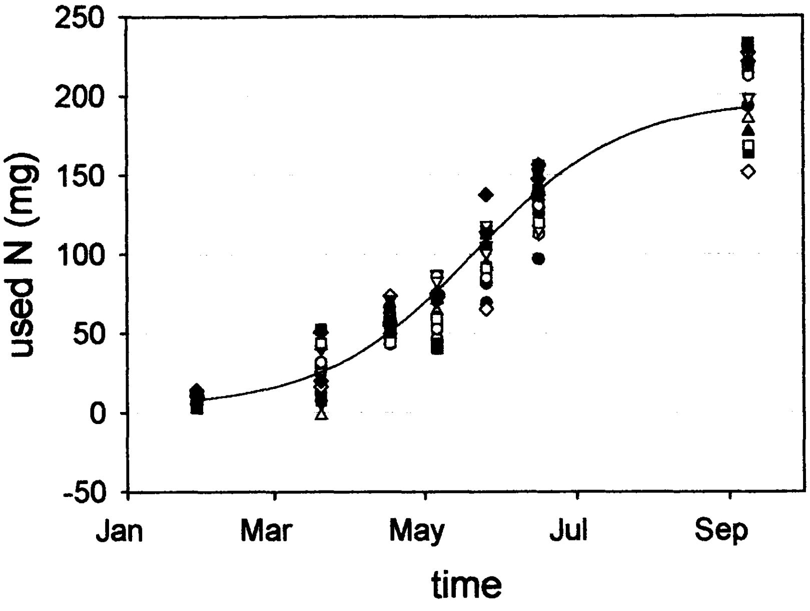


Fig. 3.4 a) Used N for *R. acetosa* plants at the seven harvests. Different symbols represent values of the used N for the experimental plants. Solid line - example of a sigmoidal curve fitted to the values of used N for one of the plants. The parameters of fitted curves, such as the curve shown, were used to define required uptake curves for plants in the model.

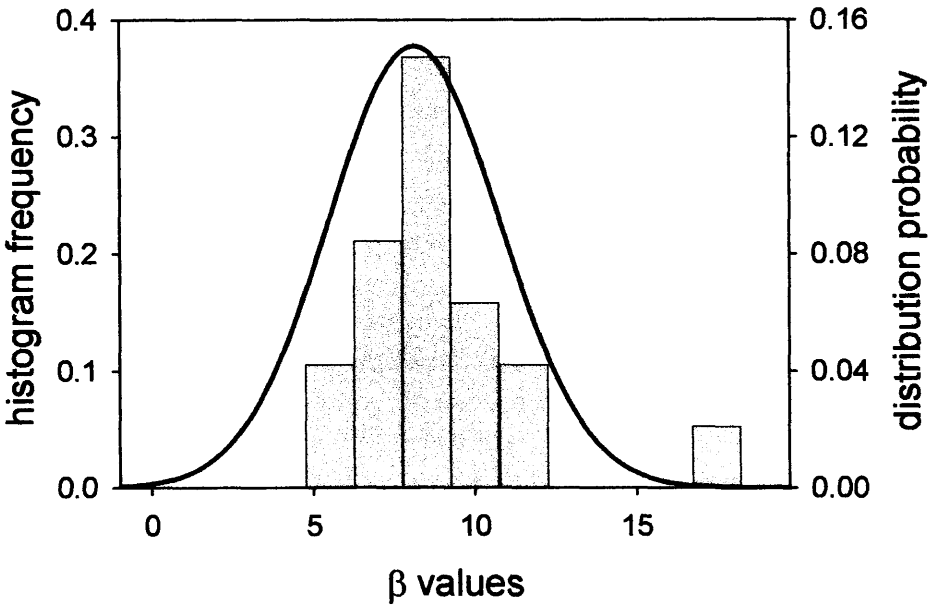


Fig. 3.4 b) The distribution of values of the parameter β, and the fitted normal distribution. The frequency of the observed values is plotted along the y-axis on the left. The distribution probability of the normalised normal distribution is plotted along the y-axis on the right.

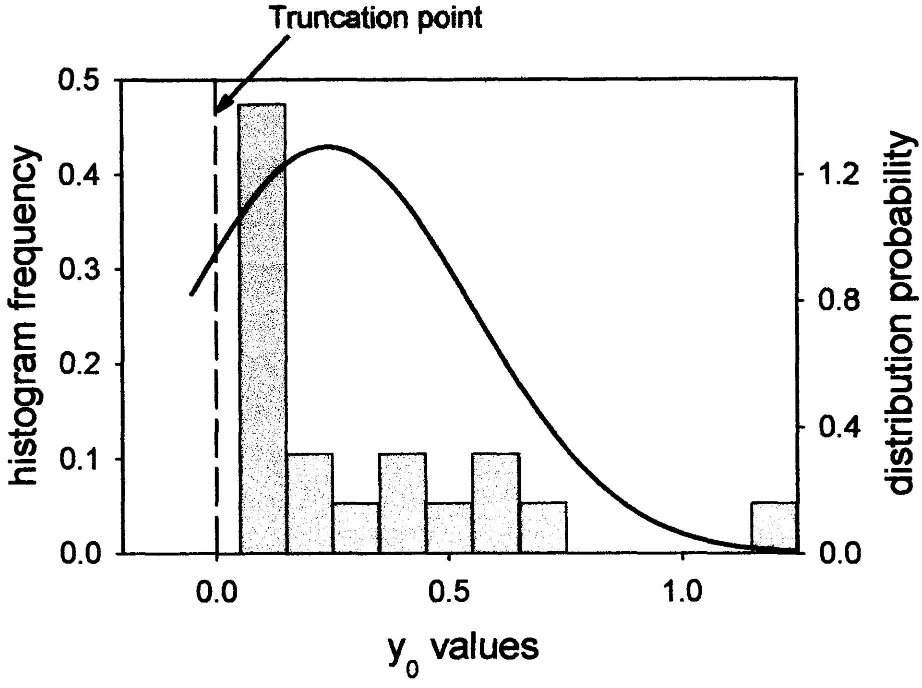


Fig. 3.4 c) The distribution of values of the parameter y_0, and the fitted normal distribution. Values of y_0 below the truncation point are rounded up to 0. The truncation is at 0 since y_0 describes the height of the plant uptake curve, and it cannot be less than 0. The frequency of the observed values is plotted along the y-axis on the left. The distribution probability of the normalised normal distribution is plotted along the y-axis on the right.

Figure 3.4 Experimental data and parameter distributions for plant uptake.

The relationship between the requested uptake U_r and $U_e(s)$ was estimated from the set of proportions that the uptake N was larger than the 'used N':

$$\frac{N_{up}(i,j)}{N_u(i,j)} \text{ if } N_{up}(i,j) > N_u(i,j) \text{ and } n \le ij .$$

where n is the number of times when $N_{up}(i,j) > N_u(i,j)$, $N_{up}(i,j)$ is the uptake of N and $N_u(i,j)$ is the 'used N' for plant i at harvest j. The values of these proportions as a function of the harvest time are shown in Figure 3.5. The dependence of the relationship between U_r and $U_e(s)$ on harvest time was unclear. Hence, U_r was assumed to be proportional to $U_e(s)$, *i.e.* $U_r = r_u U_e(s)$, where r_u was a constant and defined by the distribution with the mean and the standard deviation of the set of the above defined proportions. The distribution was truncated at 1, since the requested uptake should be more than the required uptake.

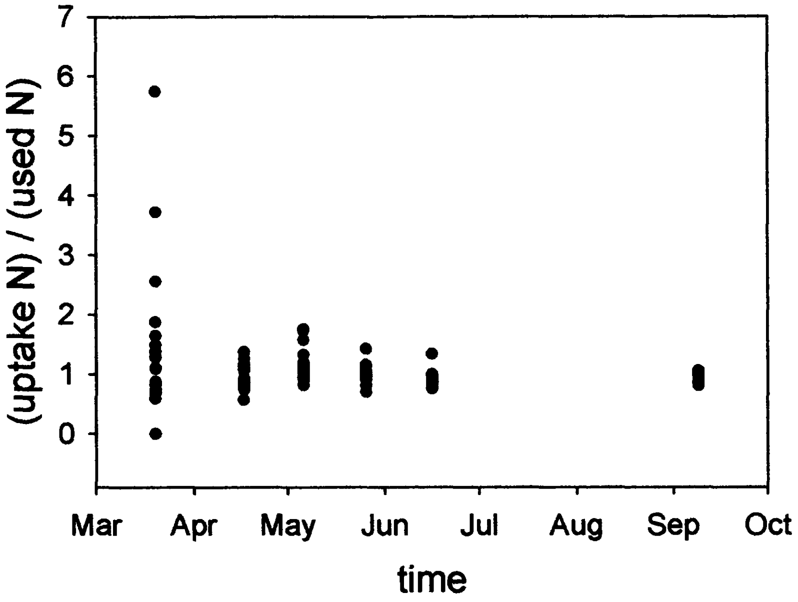


Figure 3.5 (uptake N/used N) determines whether plants absorbed more or less N than they required for growth. Dots represent values for different plants at different harvests.

The resource capture system was approximated by the root structure of *R. acetosa*. In the experimental system, competition for soil nutrients dominated, and therefore most of the competition for resource occurred in soil. Information on the actual dimensions and spatial distribution of the root structure of *R. acetosa* is lacking. Generally, however, *R. acetosa* has a cone-like root structure with a tap root more developed than the fine roots. This suggests that the resource capture area is relatively small, and its spread is generally slow and concentrated in the centre. These properties were used to define the resource capture system. It was represented in two configurations, one of which spread more slowly than the other (Table 3.3). One of the two configurations was assigned to plants with equal probability.

Table 3.3 Two types of resource capture distributions possible for *R. acetosa* in the model. B_i – band of lattice cells around location of the plant (Figure 3.3); *s* –development stage.

s	B_0	B_1
1-10	1	0
11-20	0.9	0.1
21-30	0.8	0.2
31-40	0.7	0.3
41-50	0.6	0.4

a) Type 1 resource capture distribution

s	B_0	B_1
1-10	1	0
11-20	0.8	0.2
21-30	0.6	0.4
31-40	0.4	0.6
41-50	0.2	0.8

b) Type 2 resource capture distribution

The distribution of the resource storage partition trait P_s was estimated by the proportions of the stored N that could be used between successive harvests. The distribution was defined in terms of the mean and the standard deviation of the set of proportions by which stored N in a given harvest was smaller than in the previous

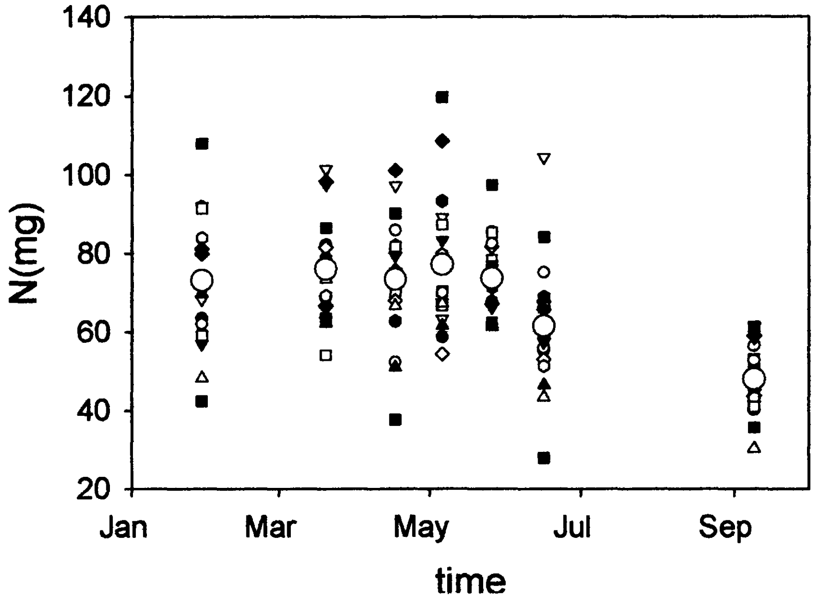


Fig. 3.6 a) Total stored N for *R. acetosa* plants at seven harvests. Different symbols represent values for different plants. Large circles are the average values for each harvest. The average proportion of stored N that remained when plants used stored N was used to approximate the resource storage partition trait P_s.

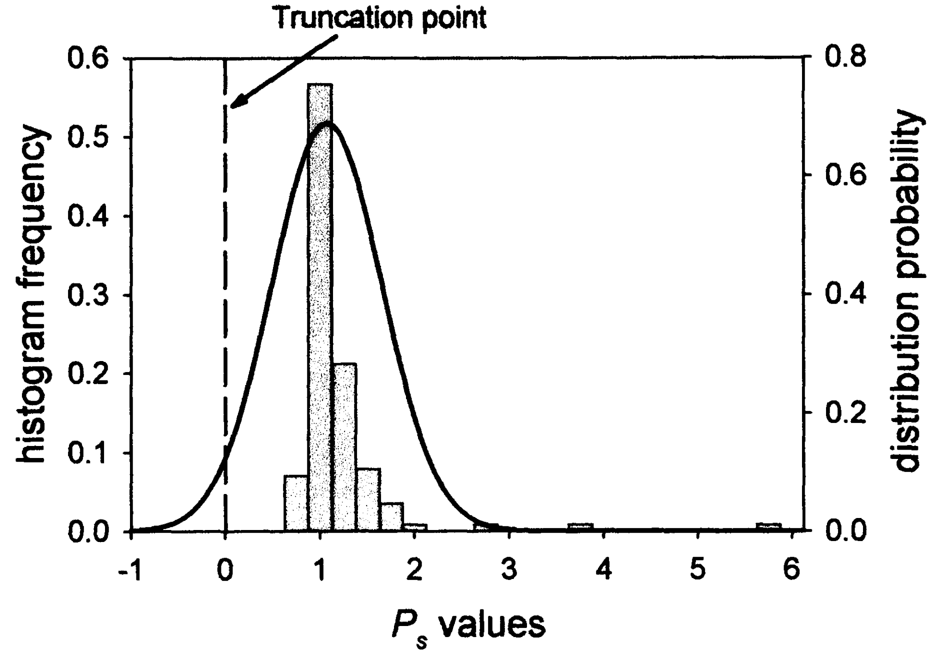


Fig. 3.6 b) The distribution of values of the parameter P_s, and the fitted normal distribution. Values of P_s below the truncation point are rounded up to 0. The truncation is at 0 since P_s is the resource storage partition trait, and it cannot be less than 0. The frequency of the observed values is plotted along the y-axis on the left. The distribution probability of the normalised normal distribution is plotted along the y-axis on the right.

Figure 3.6 Total stored N and the obtained distribution of the parameter P_s.

harvest:

$$\frac{N_s(i,j+1)}{N_s(i,j)} \text{ if } N_s(i,j) > N_s(i,j+1) \text{ and } n \le ij$$

where n is the number of times that $N_s(i,j) > N_s(i,j+1)$, N_s is the stored N that a plant i used between harvests j and $j+1$ (Figure 3.6).

The distribution of the general storage release proportion r_g was defined in terms of the mean and the standard deviation of the set of the proportions, N_l, of N lost by a plant in new leaves and fine root during reproduction. The amount of N in new leaves and fine root at different harvests is shown in Figure 3.7. For each plant, N_l was found by calculating the proportion by which the N content in leaves and fine roots at the harvest with maximum N was larger than the corresponding value at the harvest when N was minimum. In other words

$$N_l = \frac{\max\{N_{lf}(j)\} - \min\{N_{lf}(j)\}}{\max\{N_{lf}(j)\}}$$

where $N_{lf}(j)$ is the proportion of N lost from the new leaves and fine roots at harvest j, $1 \le j \le 7$. The distribution was truncated at 1 and 0, since the release proportion cannot be greater than 1 or less than 0.

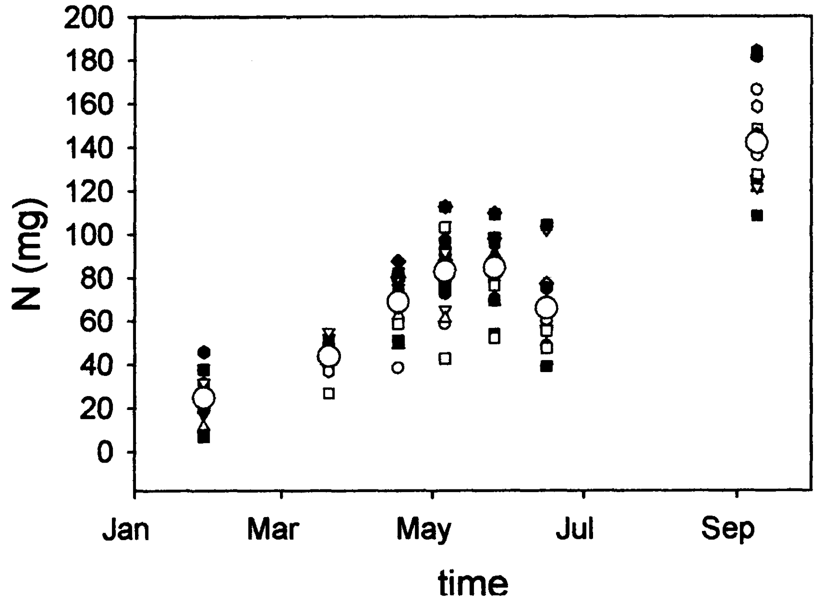


Fig. 3.7 a) N content in new leaves and fine roots in the *R. acetosa* plants. Different symbols represent values for different plants. Large circles are the average values for each harvest. The loss of N during reproduction was used to approximate the general storage release rate, r_g.

Since the main location of the surplus storage in *R. acetosa* is in the tap root, it was assumed that the surplus release proportion r_s may be estimated from the N content in the tap root. The distribution of r_s was defined in terms of the mean and the standard deviation of the set of proportional losses of N from the tap root N_{lt}. For each plant N_{lt} was found by calculating the proportion that the N content in the tap root at the harvest with maximum N was greater than the corresponding value at the harvest

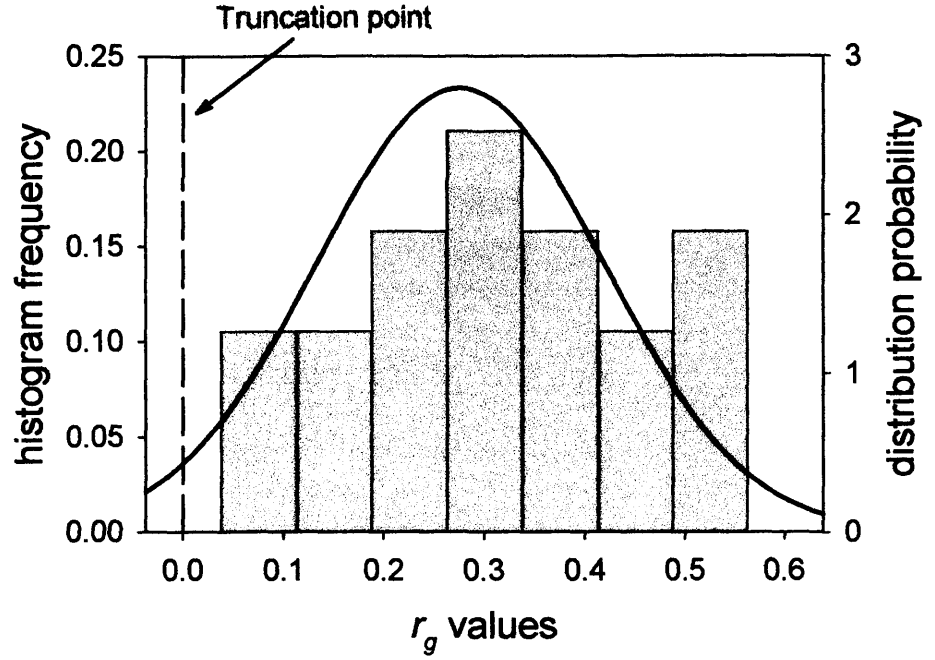


Fig. 3.7 b) The distribution of values of the parameter r_g, and the fitted normal distribution. Values of r_g below the truncation point are rounded up to 0. The truncation is at 0 since r_g is the general store release proportion, and it cannot be less than 0. The frequency of the observed values is plotted along the y-axis on the left. The distribution probability of the normalised normal distribution is plotted along the y-axis on the right.

Figure 3.7 N content in new leaves and fine roots and the obtained distribution for the parameter r_g.

when N was minimum. In other words

$$N_{lt} = \frac{\max\{N_{tap}(j)\} - \min\{N_{tap}(j)\}}{\max\{N_{tap}(j)\}}$$

where $N_{tap}(j)$ is the proportion of N lost from the tap root at harvest j, $1 \le j \le 7$. The distribution was truncated at 1 and 0, since the release proportion cannot be greater than 1 or less than 0.

The time dependent reproduction relation R_t was derived by fitting an inverted parabola to the measured dry weights of the reproductive parts:

$$y = -a(s - s_0)^2 + y_0$$

where s is time, and s_0, y_0, and a are the fitted parameters. The time when a plant started to lose weight in the reproduction parts was used to represent the time of reproduction. This time corresponded to the value of s when the parabola is at the maximum value, *i.e.* at s_0. The values of s_0, y_0, α_2 and β_2 were scaled so that *s* ranges from 0 to 50, in the same way as before. The distribution of R_t was defined in terms of a mean and a standard deviation of the s_0 values.

The dispersal of *R. acetosa* is determined by several factors, such as wind, cattle, and human activity (Grime *et al.* 1988). The dispersal of *R. acetosa* in the model was assumed to be random within a distance of 5 cells away from the reproducing plant. This corresponds to an area of 11 x 11 lattice cells centred at the plant location, or approximately 1 m^2. This area is approximately the smallest lattice size simulated (which was 10 x 10 lattice cells). An area smaller than that would contain an unrealistically small number of sites in which offspring could land given the nature of seed dispersal.

Data for the survival threshold V_t and the survival assessment period V_p were unavailable. These quantities were estimated from general biological considerations: V_t was assumed to be 1/10 of $U_e(s)$ at current development stage *s*; V_p was set to be 5 time steps (G. Squire, personal communication). The value for random death probability P_d was assumed be 0.001. P_d represents the disturbance in the system. Disturbance, in the intermediate range, was shown to promote diversity in communities (Rosenzweig 1995). Hence, the value of P_d was chosen to be in the intermediate range - higher and lower values of P_d reduced diversity in the simulated communities.

The parameter values were assumed to be independent from each other, *i.e.* when a plant was created in the model, any combination of parameter values was possible. Some of these may not be physiologically feasible (*e.g.* low uptake rate and frequent reproduction, etc.). Nevertheless, the relationships between parameters were not included in order to allow relationships between parameter values to evolve in the simulations.

Chapter 4. Origins and patterns of diversity of the communities in the individual-based simulation model

4.1 Introduction

Ecologists have puzzled over diversity patterns for over a century: the same patterns are observed in various communities and across a wide range of scales, but the mechanisms responsible for these patterns are still unclear (as has been mentioned in Ch. 1, Section 1.3). Two of the most prominent diversity patterns are the species-area relationship and the species-abundance distribution. This chapter explores diversity and these diversity patterns in simulated communities. Further, the mechanisms generating diversity patterns in the model are identified, and this knowledge is used to manipulate diversity by composing communities in which different numbers of plant types can coexist.

4.2 General design of the simulation experiments

The simulations were run for 50,000 time steps. This corresponds to about 1,110 generations (where a generation corresponds to R_t) depending on the actual values of R_t of the plants in a simulation. Simulations were started with 75 plants, unless stated otherwise, which were randomly distributed on the lattice. In simulations with individual variation, plants were randomly assigned parameter values from the parameter distributions. Plants' offspring inherited the parent plant's set of parameter values. Thus, after the initial 75 individuals reproduced, groups of individuals with the same set of parameter values formed. These groups are referred to as 'plant types'. The number of plant types represented the number of distinct sets of parameter values that existed in the community. Therefore, the number of plant types was used to characterise the community diversity. When communities of identical plants were simulated, parameter values were set to the mean values of the associated distributions. Where truncated distributions were used, the mean of the truncated distribution was used.

Since the model incorporated stochastic elements, an unchanging stable state of the system could not be achieved. In fact, all plant types in the model could eventually go extinct, since there was no influx of new types into the community, and there was a (very small) probability for each plant to die at each time step. However, the timeframe for random extinction was much longer than the timeframe of the processes studied in the model. Equilibrium is defined in this work as the state in which a constant number of plant types coexisted for a considerable amount of time (about 120 generations).

4.3 Diversity in the simulated communities

In the model, a set of plant types coexisted at equilibrium, if the resource level allowed survival. The initial diversity dropped in the beginning of the simulations, and subsequently settled to a steady number of individual types (Figure 4.1). This number was unchanged, except for some cases when individual types went extinct. The diversity in the model ranged from 1 to 22 plant types, depending on environmental conditions, lattice size, and chance.

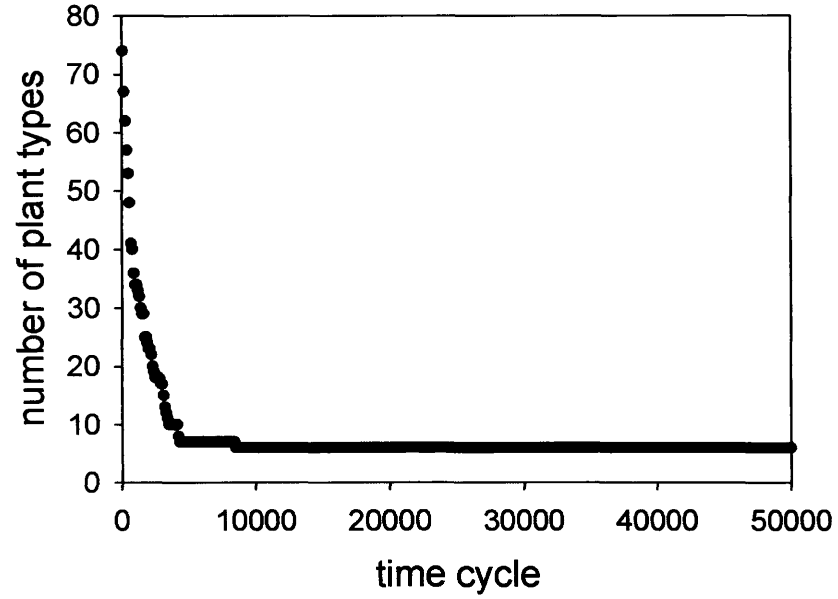


Figure 4.1 The number of plant types as a function of time for a typical simulation. Diversity drops and quickly settles to a steady number of coexisting plant types.

4.3.1 The species-area relationship

To explore the relationship between diversity and area in the model, simulations were performed on four different lattice sizes: 10 x 10, 20 x 20, 30 x 30 and 50 x 50. In the context of the present parameterisation, this corresponds to areas from 1 to 25 m^2. Ten simulations were performed on each lattice size. At the end of each simulation, the number of coexisting plant types was recorded. A plant type is a collection of plants with identical set of traits. In the model, it is akin to the notion of the species since the species represent a group of individuals with very similar traits. The plot of the number of coexisting plant types *vs.* the lattice area is shown in Figure 4.2. It shows a linear relationship on the log-log scale between plant types and lattice area (R^2=0.979 for the linear fit) – the same relationship is observed in natural communities (Rosenzweig 1995). Moreover, the slope of the fitted line was 0.343 with a standard error of 0.036, which lies within the range of slopes observed for communities on these scales of area – 0.2-0.5 (Crawley and Harral 2001). The ANOVA with lack-of-fit is presented inTable 4.1. The normality of residuals was visually examined and tested using Shapiro-Wilk test, and it was found that the hypothesis of normality could not be rejected at 5% level.

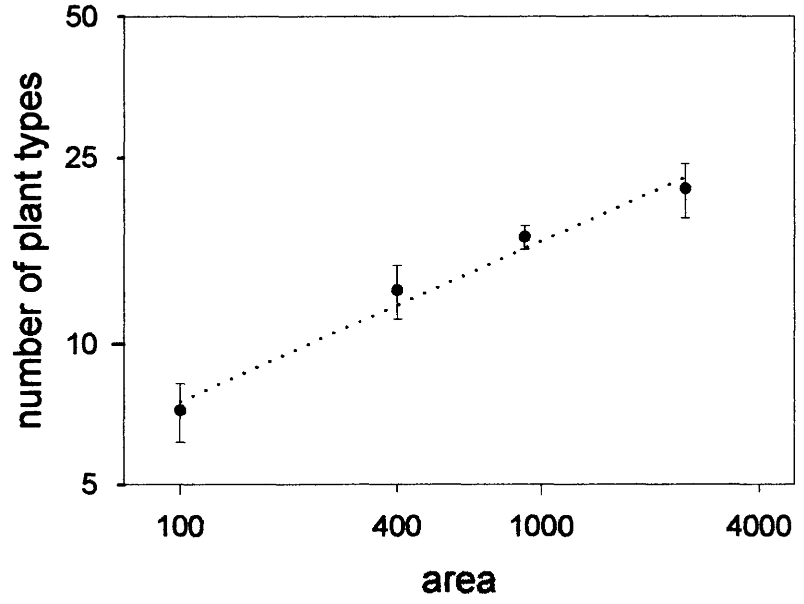


Figure 4.2 Relationship between the number of coexisting plant types and the lattice area. This is an analogue of the species-area curve in the model, with plant types replacing species. The area is the number of cells on the simulated lattice; the number of plant types is given at the end of the simulation. Average values and standard deviations for 10 replicates are shown. The dotted line is the linear fit to the data.

Table 4.1 Parameters and ANOVA for species-area curve with lack-of-fit analysis.

Parameter	**Standard Error**	**t**	**p**	
y_0	0.1916	0.0538	0.0011	
a	0.3432	0.0193	0.0001	
Source	**df**	**SS**	**MS**	**F ratio**
Regression	1	1.3502	1.3502	409.1515
Residual	38	1.1239	0.0033	(significant at 0.01 level)
Lack-of-fit	3	0.0266	0.0089	3.2963
Pure error	36	0.0973	0.0027	(significant at 0.01 level)
Total, corrected	39			

4.3.2 Structure in species hierarchy

The coexisting species in a community are often ranked by the number of individuals of each species. Analogously, in the model, plant types can be ranked by the number of individuals of each type. The model permitted observation of the evolution of plant type abundances in time. Recording the species present in a community and their abundances is one of the important ways in which an ecological community can be described (*e.g.* this is the basis for vegetation classification, see Rodwell, 1992). However, few ecological studies measure how stable this species ranking is in ecological communities, as it requires extensive long-term monitoring (a rare case in ecological studies). Observations on ecological communities are most often conducted at a relatively few points in time. Two studies examined the ranks of species over a short term (three to five years), in communities of beetles and plankton (Loreau 1992 and Pearson *et al.* 1982). These studies showed that species ranks were not constant, and could vary dramatically.

In the simulated communities, the ranks of coexisting plant types were observed over long periods of time. Figures 4.3 a) and b) are plots of the abundances of coexisting plant types as they change in time. The plots show a time period towards the end of the simulation when the number of coexisting plant types did not change anymore. Figure 4.3 a) shows a general stratification of plant type abundances, *i.e.* plant type abundances remain within certain bounds. This was often the case. However, in both plots the abundance of most plant types (and therefore their rank) varied in time. Plot 4.3 b) shows one plant type whose abundance changed drastically from rare to abundant. The factors governing the plant type population in the model gave rise to regular as well as stochastic-like behaviour. The regular behaviour appeared to be governed by factors that include general environmental conditions (such as substrate richness) and the plant physiological processes (determined by the parameter values assigned to plant types at the beginning of simulations). The stochastic-like behaviour could have arisen from factors that include the location of the plant (which determines the plant's competitors), the dispersal process (since the plants disperse their offspring randomly), and random death.

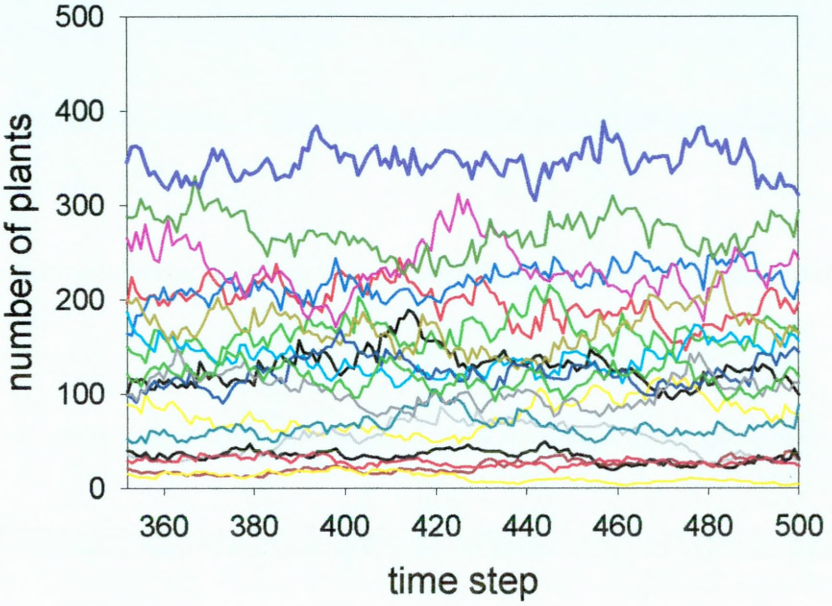


Fig. 4.3 a) Stratification of different plant types into rank groups in the final stage of a simulation on a 50 x 50 lattice, with 19 coexisting plant types. The most abundant type dominates, several types are consistently rare, and other types range across the intermediate abundances.

4.3.3 The species abundance distribution

For any given time step, a plot of ranked abundances shows how species abundances are distributed in a simulated community. Figure 4.4 shows an example of a ranked plot of plant types as a simulation progresses. In the beginning (time 0), the plot is flat (as each plant type constitutes just one individual). This shape changes to become roughly linear on log scale by time step 10,000. Then the shape of the curve changes, and a flat area emerges in the middle. This shape was observed in the ranked plot at the end of all simulations. When, in such a ranked plot, the histogram of plant types by abundance was constructed, it was of log-normal shape. The ranked plot with linear shape (observed in the beginning of the simulation) corresponds to a geometric distribution.

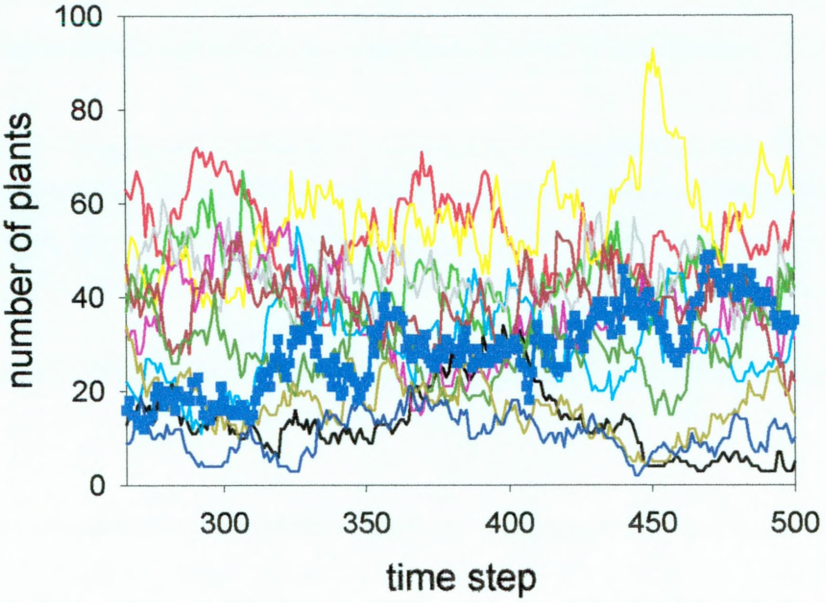


Fig. 4.3 b) The final stage of a simulation on a 20 x 20 lattice, with 12 coexisting plant types. There is not one most abundant type, and low-ranking types time can become high ranking, *e.g.* the one in blue.

Figure 4.3 Abundances of coexisting plant types.

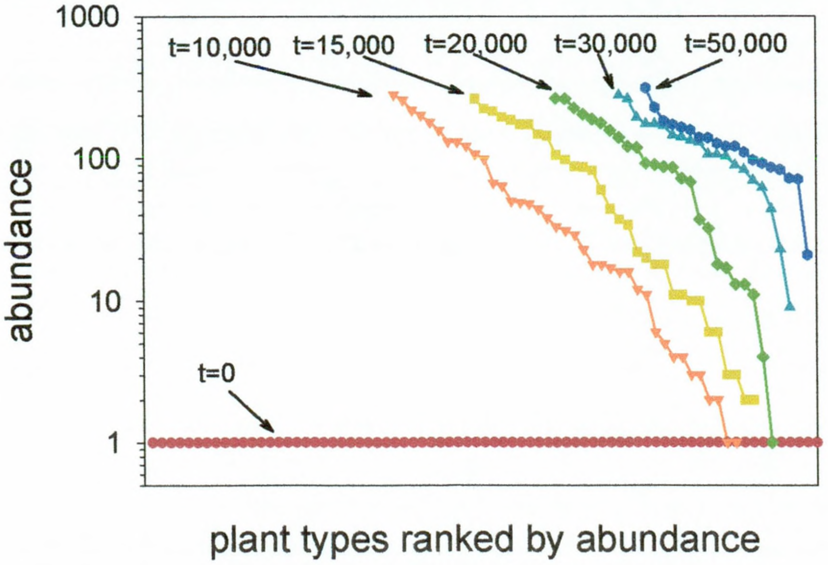


Figure 4.4 Change in the ranked plant type abundances over time for a simulation on a 50 x 50 lattice.

To confirm that the end distributions in the model were log-normal, they were analysed at the end of ten simulations (time step 50,000) each on lattices of sizes 20 x 20, 30 x 30, and 50 x 50. Simulations on the 10 x 10 lattices were not tested for log-normality, as there was an insufficient number of coexisting plant types for meaningful statistics (the number ranged from 6 to 9). For the simulations where the number of plant types was sufficient, the plant types distribution was plotted with number of individuals transformed on $\log_2$ (which has become the standard transformation following Preston, 1948). Inspection of the abundances of plant types during simulations showed that when plant types abundance approached low values (less than 10), these plant types soon went extinct. Therefore, to select simulations that could be considered to be in dynamic equilibrium at the end, those simulations that did not have any plant types with abundance less 10 were picked. There were 14 such simulations. The distributions in these simulations were checked for normality using Shapiro-Wilk and Anderson-Darling tests. Of the 14 distributions, the hypothesis that the distribution does not differ from the lognormal one could not be rejected at the 5% significance level in all but 2 cases. An example of abundance distribution on a 30 x 30 lattice is shown in Figure 4.5. In the four cases this hypothesis could be rejected. Inspection of plant type population levels for those four cases revealed that one or more plant types were close to extinction. This meant that the distribution was skewed towards the rarer types. To ensure that the distributions fitted a lognormal distribution better then a geometric one, the distributions were checked to find if they corresponded to a geometric distribution. If the plant type abundances were distributed according to a geometric distribution, then the histogram of abundances transformed on $\log_2$ scale would be uniformly distributed. The Kolmogorov-Smirnov test was again used to test whether the distributions were uniformly distributed. It was found that, for all cases, the test statistic was less significant in tests for a uniform distribution (geometric abundance) as compared to a normal distribution (lognormal abundance).

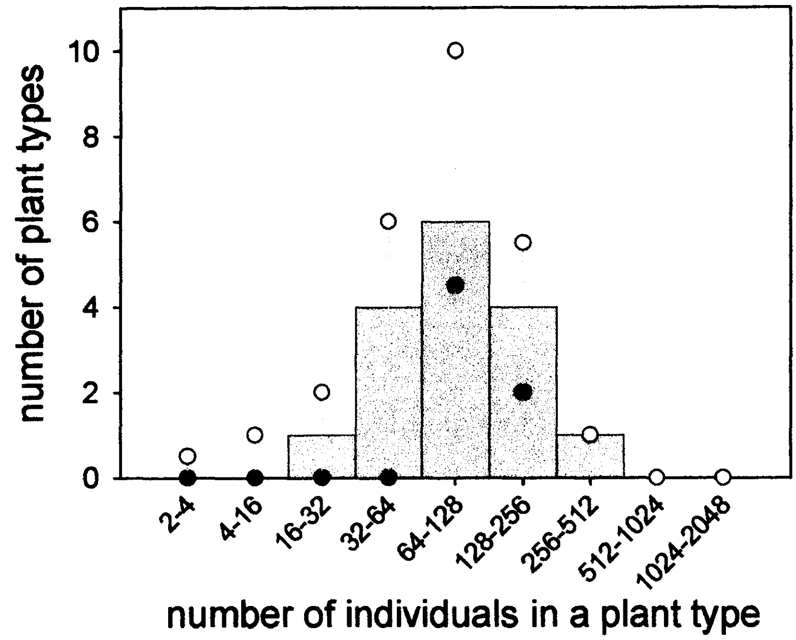


Figure 4.5 Plant type abundance distribution for a simulation on a 30 x 30 lattice. The distribution is plotted on a $\log_2$ scale, after Preston (1948). Circles indicate the maximum (white circles) and minimum values over the length of the simulation.

4.4 Origins of diversity in the simulated communities

4.4.1 Sensitivity analysis

To investigate the mechanisms allowing plant types to coexist, a sensitivity analysis was performed. It was done by systematically removing variation in all parameters but one. The variation was removed by assigning to parameters the mean values of the corresponding distributions. Five simulations were performed for each configuration, and at the end of each simulation the number of coexisting plant types was recorded as a measure of community diversity. Only one parameter in the model was responsible for allowing plant types to coexist – time to reproduction R_t. Without variation in R_t, only one plant type remained.

Since R_t determined the time of reproduction, it implicitly affected the number of offspring produced by plants, as follows. The number of offspring N_{off} was determined by dividing the storage used for reproduction by the amount of resources necessary for the offspring to progress to the first development stage, R_{min} (see Ch. 3, Table 3.1). If a plant reproduced more often, it had a smaller storage. Therefore, it produced a smaller number of offspring.

The relationship between time to reproduction R_t and number of offspring N_{off} was explored in simulations with variation in all parameters. For ten simulations on 20 x 20 lattices, the R_t of coexisting plant types was plotted *vs.* their N_{off}. A sample plot for one of the simulations is shown Figure 4.6. The plot does not show a clear relationship between the two, although the number of offspring is generally higher in survivors for the same values of R_t. However, in addition to R_t, the number of offspring produced by plants was also affected by R_{min}, the amount of resources necessary for the offspring to progress to the first development stage. The value of R_{min} is determined by parameters y_o and β which describe the shape of the uptake curve (which, in turn, describes the plant uptake necessary for progressing along development stages). To remove the effect of these parameters, N_{off} was multiplied by R_{min} to obtain the reproductive biomass R_b. The reproductive biomass was plotted *vs.* R_t (Figure 4.7), and a positive correlation was observed. A line was fitted to the data corresponding to each of the ten simulations. The parameters of the lines ($R_b = mR_t + b$) are presented in Figure 4.8 as a plot of the slope m *vs.* the y-intercept b. A linear relationship between m and b was observed. The statistical estimation of the fit is described in Table 4.2. In addition, the normality of the residuals was visually examined and tested using Shapiro-Wilk test, and it was found that the hypothesis of normality could not be rejected on 5% level.

Table 4.2 Parameters and ANOVA for linear relationship between *m* and *b*.

Parameter	**Standard Error**	**t**	**p**	
yo	0.5279	0.0083	<0.0001	
a	-0.0249	0.0010	<0.0001	
Source	**df**	**SS**	**MS**	**F ratio**
Regression	1	0.3562	0.3562	679.0904
Residual	8	0.0042	0.0005	(significant at 1% level)
Total, corrected	9	0.3604	0.0400	

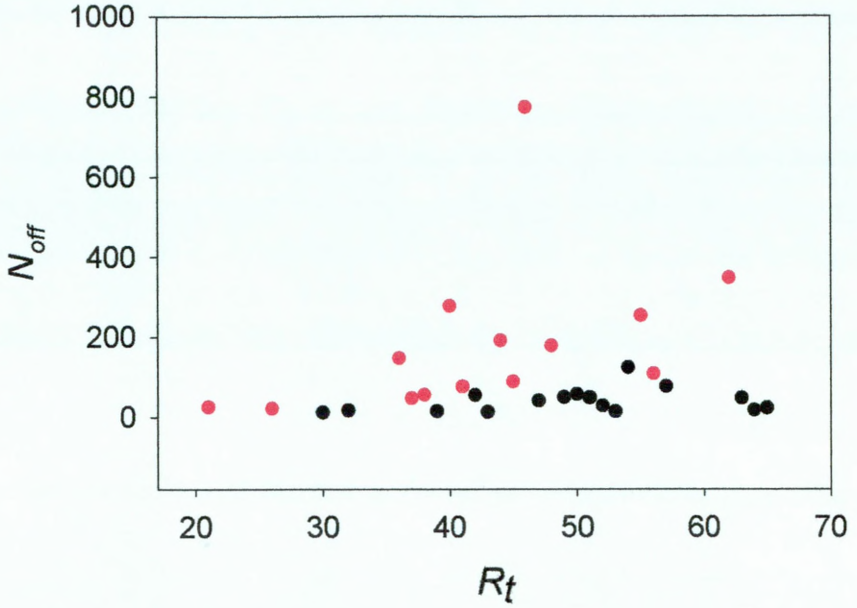


Figure 4.6 Plot of average number of offspring produced N_{off} *vs.* time to reproduction R_t. Red dots correspond to plant types that survived until the end of the simulation, and black dots to those that did not.

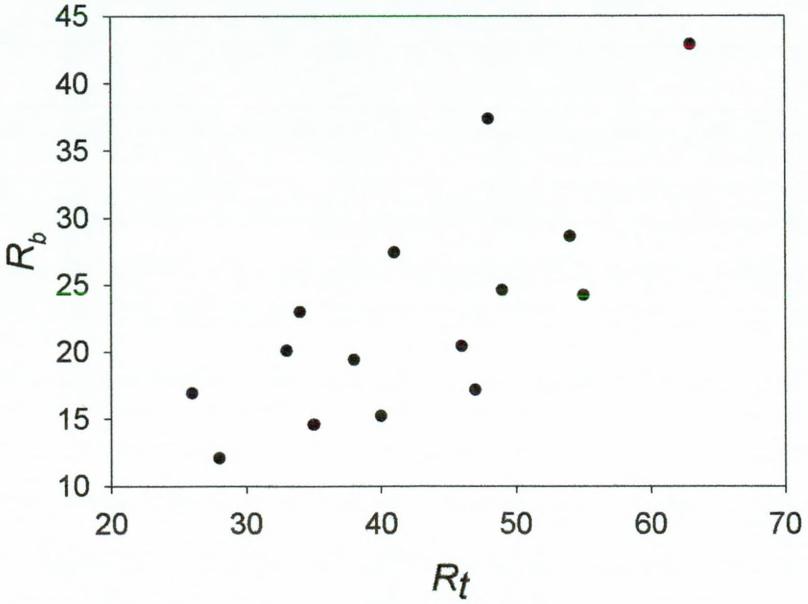


Figure 4.7 The positive correlation between the time to reproduction R_t and the reproductive biomass R_b of coexisting plant types for a simulation in a 20 x 20 lattice.

4.4.2 The simplified model

A simplified model was then defined. It incorporated only time to reproduction R_t with variation (*i.e.* defined by a distribution), the linear trade-off between R_t and reproductive biomass R_b, and a random death factor. Resource, resource uptake, storage, and survival were not explicitly incorporated into this version of the model, but were implicit in the trade-off. The trade-off was modelled by the line $R_b = mR_t + b$ with slope m=0.42 and constant b=4.19. These values for m and b were obtained by taking the average slope and constant observed in simulations with full variation (Figure 4.8).

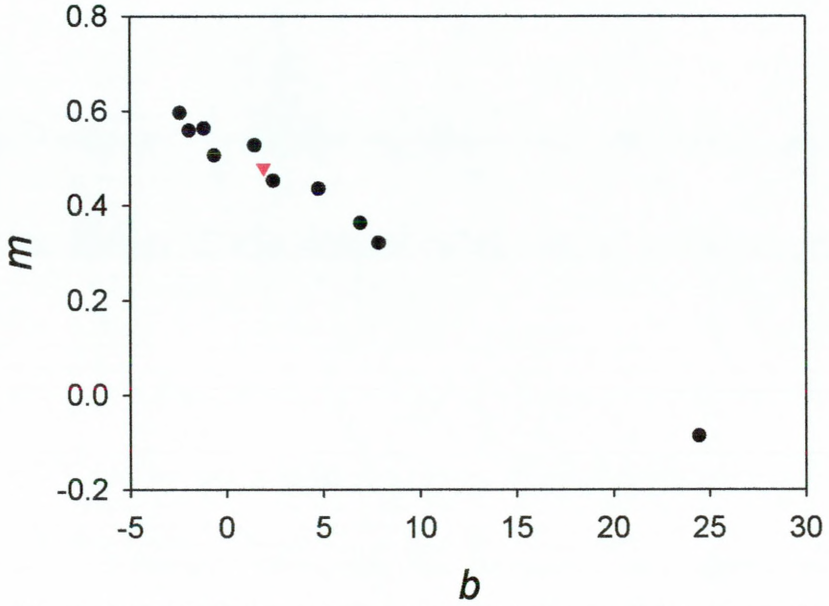


Figure 4.8 The relationship between the slope m and the constant b of the lines fitted to the reproductive biomass *vs.* R_t. Dots correspond to the values obtained from fitting the lines for 10 simulations on a 20 x 20 lattice, and the triangle is the average.

The model simulated a lattice with only one plant possible at each lattice site. The parameters of the model were the following: the probability distribution of R_t, a random death factor, and m and b -- the parameters of the line describing the trade-off between R_t and reproduction biomass R_b. The distribution of R_t and the random death probability were assigned the same values as in the full version of the model. The simulations were started with 75 plants randomly placed on the lattice. For each plant, R_t was randomly assigned according to its probability distribution. During simulations, plants reproduced at intervals of R_t. At each reproduction, R_b was found according to the trade-off. The number of offspring was calculated by dividing R_b by R_{min} for an average plant in the full model (with R_{min}= 0.56 calculated using parameters for the full model).

4.4.3 Diversity patterns in the simplified model

4.4.3.1 The species-area relationship

For each of the lattice sizes 10 x 10, 20 x 20, 30 x 30, and 50 x 50, ten simulations were performed. At the end of each simulation, the number of surviving plant types was recorded. The plot of the number of surviving plant types and the area simulated showed a linear relationship on log-log scale, as in simulations of the full model. The slope of a line fitted to this plot was close to that obtained from simulations of the full model. The slope was 0.416 with standard error of 0.0864 (compared to a slope of 0.3425 with standard error of 0.0357 in the full model).

4.4.3.2 The species abundance distribution

The species abundance distributions were analysed for ten simulations each on 20 x 20, 30 x 30, and 50 x 50 lattices, as was done for the full model. Here again, the distributions on the lattice size 10 x 10 were not used, as the number of coexisting plant types (ranging from 5 to 7) was too small to give statistically meaningful results. For higher lattice sizes, the distribution of plant types as a function of abundance was plotted, as was done for the full model. A sample abundance distribution in a simulation on a 20 x 20 lattice is shown in Figure 4.9. The distribution is close to normal plotted on $\log_2$ scale. Inspection of the abundances of plant types during simulations showed that when plant types abundance approached low values (less than 10), these plant types soon went extinct. Therefore, to select simulations that could be considered to be in dynamic equilibrium at the end, those simulations that did not have any plant types with abundance less 10 were picked. As compared to the full model, there were fewer simulations that did not have plant types with abundances less than 10. There were 8 such simulations. The distributions in these simulations were checked for normality using Shapiro-Wilk and Anderson-Darling tests. Of the 8 distributions, the hypothesis that the distribution does not differ from the lognormal one could not be rejected at the 5% significance level in all but 1 case. As before, to ensure that the distributions fitted a lognormal distribution better than geometric, the Kolmogorov-

Smirnov test was again used to test whether the histograms of abundances transformed on $\log_2$ scale were uniformly distributed. It was found that, for all cases but one, the test statistic was less significant in a test for a uniform distribution (geometric abundance) as compared to the normal distribution (lognormal abundance).

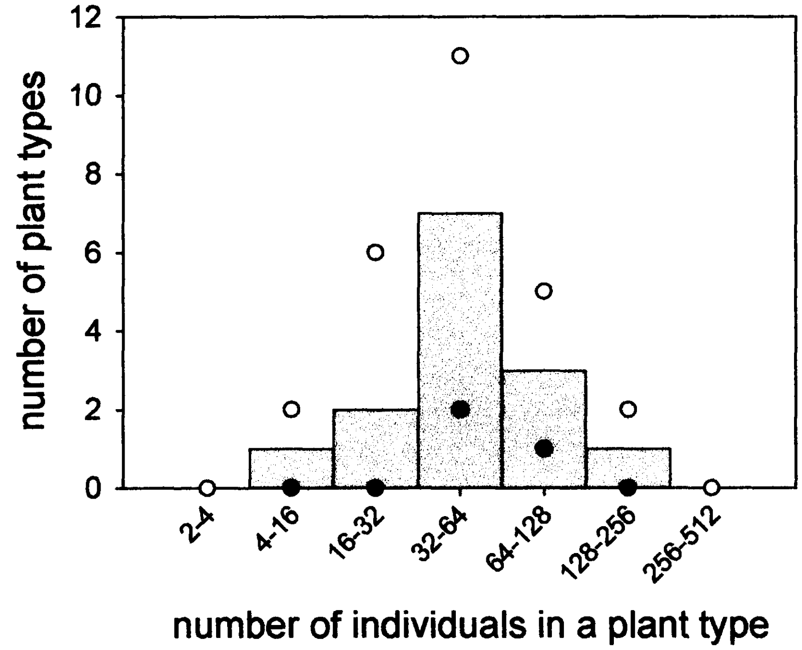


Figure 4.9 The plant type abundance distribution on a 20 x 20 lattice in a simulation with the simplified model. Circles indicate the maximum (white circles) and minimum values over the length of the simulation.

A relationship between the surviving plant types' R_t and their abundance was observed. The earlier reproducing plants were more abundant (Figure 4.10). For simulations on the 20 x 20 lattice, the correlation coefficients were calculated between the surviving plant types' R_t and abundance at the last time cycle, and it was found that R_t and abundance were negatively correlated. The results were significant at the 0.01 level. This means that the plants that reproduced more often were more abundant in simulations with the simplified model. This may be because frequent reproduction gave offspring a better chance to find a free space on the lattice. To compare these results to the full model, the correlation between the surviving plant types' R_t and abundance at the last time cycle for the simulations on the 20 x 20 lattice was calculated. For the full model, a negative correlation was observed in 6 out of 10 cases. A weaker correlation in the full model can be explained by the fact that competition in the full model occurred for resource as well as for space. Hence, abundance was a result of the plant's ability to compete for resources as well as its time to reproduction. In addition, the full model incorporated variation in the resource uptake parameters of plants. This variation generated a scattered relationship between the number of seeds produced and the time of reproduction, as described before (Figure 4.6). This in turn affected the ability of plant types to compete for space, since the plants which produced more seeds had a higher probability of finding an empty site.

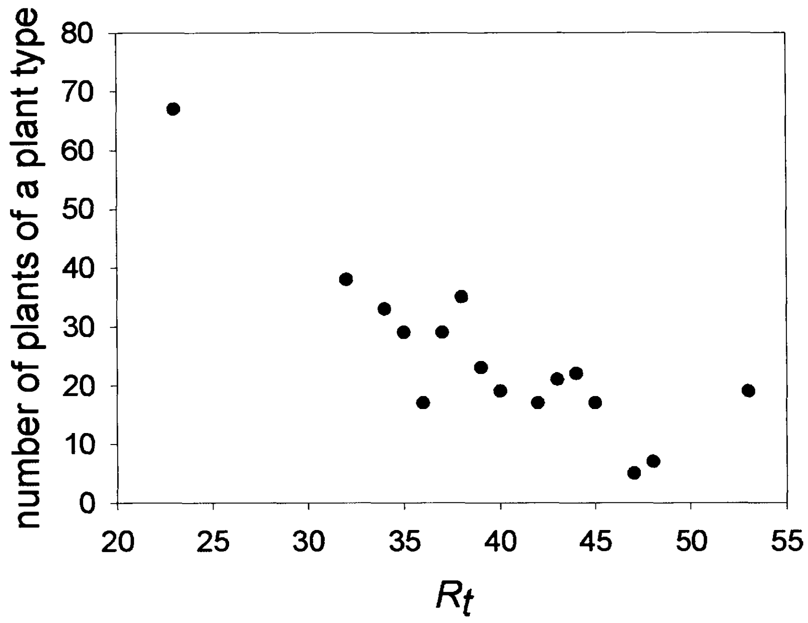


Figure 4.10 The relationship between R_t and abundance for each plant type at the last time cycle in a simulation on a 20 x 20 lattice.

4.4.4 Effects of trade-off manipulation on diversity

To explore the effect of the trade-off between reproductive biomass R_b and time to reproduction R_t on diversity, the response of the model to changes in parameter values of the linear trade-off was examined. The slope was varied while keeping the constant at its previous value, and vice versa. The slope *m* was set to 0.01, 0.1, 10, and 100 (as compared to the value of 0.42 which was used in the simulations discussed in section 4.6), and the constant *b* was set to 0 and 100 (as compared to 4.19). For each configuration, ten simulations were performed. The number of plant types coexisting at the end of the simulations was recorded. The medians were compared using the Mann-Whitney test (Tables 4.1 and 4.2, which are discussed below).

Variation in both the slope *m* and the constant *b* of the linear trade-off had an impact on community diversity. The community diversity increased as the slope changed from flat to steep (Figure 4.11). Table 4.3 shows that the difference was statistically significant between samples with a) m=0.01 and 0.1, b) m=0.1 and 0.42, and c) m=0.42 and 10. There was no significant difference between samples with m=10 and 100. The community diversity also increased as the value of b increased (Figure 4.12).

Table 4.3 Comparison of numbers of plant types for different values of the slope m in the trade-off $R_b = mR_t + b$ where R_b is the reproductive biomass and R_t is the time to reproduction. The value of b here is 4.2 (as estimated from full model simulations). The medians of distributions were compared using the Mann-Whitney test. **p** is the probability that the median values are the same.

Comparison of two samples with different values of m	Mann-Whitney U statistic	p
m=0.01 and 0.1	83	0.0115
m=0.1 and 0.42	100	<0.0001
m=0.42 and 10	98.5	<0.0001
m=10 and 100	71.5	0.1230

Table 4.4 The results of comparing samples of the number of coexisting plant types for different values of the constant b in the trade-off $R_b = mR_t + b$ where R_b is the reproductive biomass and R_t is the time to reproduction. The value of m here is 0.42 (as estimated from full model simulations). The medians of distributions were compared using the Mann-Whitney test. **p** is the probability that the median values are the same.

Comparison of two samples with different values of b	Mann-Whitney U statistic	p
b=0 and 4.2	65	0.2799
b=4.2 and 100	84	0.0084

However, Table 4.4 shows that this difference was only found between samples with b=4.2 and 100. No significant difference was found between samples with b=0 and 4.2. The positive slope of the trade-off indicated that plants that reproduced less frequently produced more offspring. This gave them a chance to compete with more frequently reproducing plants. Variation in slope revealed that, for higher slopes of the trade-off, community diversity increased, whereas for flatter slopes the diversity decreased. If the slope was steep then the plants that reproduced less frequently produced relatively more offspring relative to the case with flatter slopes. This gave them an advantage in competing with plants that reproduced more frequently. Hence more slow-reproducing types could survive. The shape of the abundance distributions changed as well. The ranked plant type abundances were plotted for simulations with different values of *m* (Figure 4.13). With increasing slope, the resulting communities were more diverse. The shape of the plant type abundance distribution changed from close to linear (on log scale) for small numbers of plant types to a shape flattened in the middle for larger numbers of coexisting plant types.

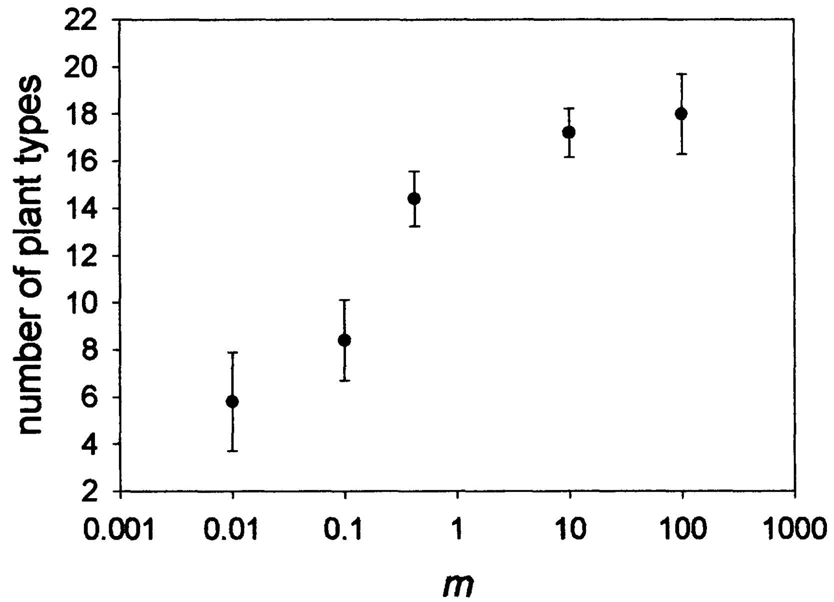


Figure 4.11 The effect of varying the slope *m* of the linear trade-off in the simplified model. The dots are the number of coexisting plant types averaged over ten simulations, with standard deviations denoted by bars.

4.5 Discussion

The species abundance distribution is a well known community characteristic in ecology. The exact shape of this distribution and its origin has been much debated. However, the general consensus is that the log-normal shape of the species abundance distribution is observed in communities at equilibrium in stable environmental

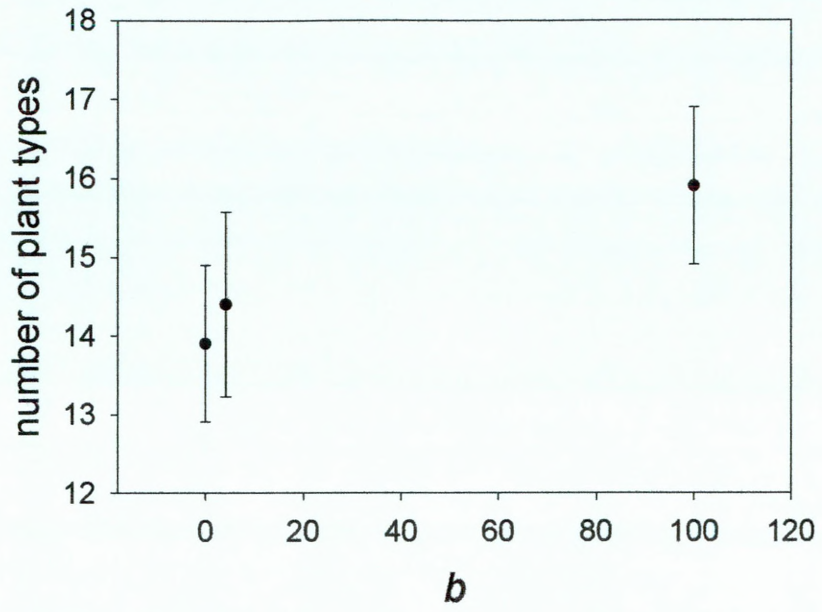


Figure 4.12 The effect of varying the constant value *b* of the linear trade-off in the simplified model. The dots are the number of coexisting plant types averaged over ten simulations, with standard deviations denoted by bars.

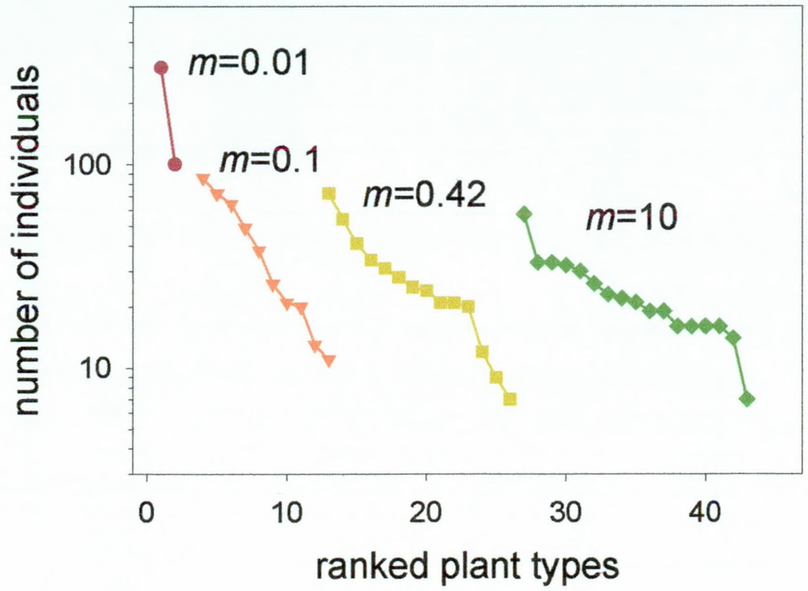


Figure 4.13 The change in the species abundance distribution as a function of the trade-off slope *m*.

conditions (Putman 1994). The lognormal distribution corresponds to a situation when there are few species with high and low abundances, and many species with intermediate abundances. The geometric species (*i.e.* power-law) abundance distribution is observed in communities that are under disturbance or stress, or in the process of succession (when new sites are colonised by plants). Such a distribution means that the species abundances are distributed evenly on log scale.

Diversity in the full model was found to exhibit the same patterns as those observed in natural communities. In the model, the linear ranked plot (corresponding to the geometric distribution) is characteristic of the early stages of a simulation, when the community is adjusting to the initial conditions. This plot evolves to one with a flattened middle (corresponding to the log-normal distribution) toward the end of the simulation when the community is approaching a dynamical equilibrium.

To investigate the origins of these patterns, the mechanisms generating diversity were found and were shown to be sufficient to give rise to diverse communities. The model was simplified to include only the individual traits and the processes specifically responsible for generating diversity were isolated. These were found to be variation in the time to reproduction, a trade-off between time to reproduction and reproductive biomass, and a random death factor. Other trade-offs have been shown to lead to diversity, for example the competitive ability/dispersal/longevity trade-off (Tilman, 1994), dispersal/germination strategy (Lavorel and Chesson 1995), and seed size/number strategy (Rees and Westoby 1997 and Geritz *et al.* 1999). The time to reproduction *vs.* reproductive biomass trade-off has not been explored. This trade-off leads to temporal separation of reproductive events for different plant types. This reduces competition for space, and allows coexistence of types. However, the abundance of the plant types depends on how often they reproduce. The plant types that reproduce often, but in smaller numbers are able to get a larger proportion of space than other plant types.

The simplified model produced similar diversity patterns. The factors affecting the plant type abundance were local dispersal and competition for space. These factors may be responsible for the diversity patterns observed in ecological communities. The simplified model was used to explore the effects of changes in the trade-off between individual traits on community diversity. The shape of the species abundance curve changed as the slope and the constant of the trade-off were varied. For small slopes, the diversity was low and the resulting distribution was close to linear (on a log scale), which corresponds to a geometric distribution. Small slopes correspond to a situation when the competitive differences in the plant types are large (*i.e.* plant types that reproduce more often have a relatively big advantage over plants that reproduce less often). For larger slopes, the diversity was higher and the shape of the species abundance curve was more flattened in the middle, which corresponds to a log-normal distribution. Large slopes correspond to a situation when the competitive differences between plant types are small (*i.e.* plant types that reproduce more often have a relatively small advantage over plants that reproduce less often). Variation in the trade-off constant resulted in the same effects. This shows that the species abundance distribution depends on the trade-off responsible for diversity in the system. The trade-off affects the relationship between the individuals in the community and leads to a different diversity distribution. Changes in the trade-off give an indication of how diversity in communities may be manipulated.

4.6 Connection to the mean-field model

The results of this chapter relate the properties of an individual to community diversity. It was shown that a trade-off between time to reproduction and reproductive biomass was necessary for diverse communities to exist. Moreover, the form of the trade-off defined the relative abundance of individuals with different R_t values. These results are consistent with conclusions of Chapter 2. In both the mean-field and the simulation models, a trade-off in individual properties was required for diverse communities to exist. It is the trade-off between death, birth and germination rates in the mean-field model, and it is the trade-off between time to reproduction and reproductive biomass in the simulation model.

The mean-field model gave indication that community diversity can be defined in terms of individual traits. It showed the importance of individual characteristics and also interactions between individuals in a community. The interactions, expressed as the integral term, strongly affected the stability and diversity of the system. Informed by the results of the mean-field model, the simulation model was then defined and explored for possible trade-offs. The simulation model gave an opportunity for the trade-off to evolve, as it was not defined explicitly. In addition, the simulation model, by virtue of being more realistic, produced diversity patterns quite similar to those in real communities. Thus, the two modelling approaches complemented each other. The mean-field approach provided general results. With these in mind, a simulation model was defined with more realistic features. The simulation model shed some light on possible origins and patterns of diversity in ecological communities.

The complementary use of simulation and analytical approaches is a developing technique in ecological modelling. Several other works have connected analytical and simulation approaches. Winkler *et al.* (1999) used an individual-based simulation model and a difference-equation model to analyse diversity mechanisms in plant communities. Sumpter and Broomhead (2001) used complementary individual-based simulation model and mean-field model to represent the lifecycle of a honeybee parasite. Fahse *et al.* (1998) extracted the growth rate of nomadic birds from a simulation individual-based model to define a differential equation model of the population growth.

Chapter 5. Effects of diversity on the productivity and stability of communities

5.1 Introduction

The previous chapter explored how diverse individuals organise themselves and why they can coexist in simulated communities. It is now appropriate to ask: what are the consequences of diversity for a community? This question has been much deliberated in ecology, particularly in the context of the connection between diversity and community productivity and community stability (Loreau 2000, Schwartz *et al.* 2000, Hector *et al.* 1999, Tilman 1999, Tilman and Downing 1994, Naeem *et al.* 1994, Schulze and Mooney 1994). Out of the debate evolved an understanding that there are no simple relationships between diversity and either productivity or stability. Under various environmental conditions, different factors in community dynamics can dominate (Tilman 1999), *e.g.* diversity may promote productivity in a heterogeneous environment but not in a homogeneous one. Another element contributing to the effects of diversity on population dynamics is the range of diversity (Nijs and Roy 2000), *e.g.* a community of species similar to each other may not respond to disturbance in the same way as a more varied community with an equal number of species. However, it is not understood precisely which environmental conditions together with diversity lead to a particular effect in population dynamics (Loreau 2000).

In this chapter the model is applied to explore the effects of diversity on community productivity in different levels of substrate richness. The factors driving these effects are examined by comparing the composition of diverse communities on different substrate levels. Further, in the poor substrate, the effects of environmental heterogeneity on the productivity of diverse and homogeneous communities are explored. Finally, the effects of initial community diversity on evolving productivity are examined, shedding light on possible effects of the community composition on productivity.

5.2 Design of simulation experiments

The same general simulation design was used as in the previous chapter. The parameterisation of the model for *R. acetosa* described in chapter 3 was used. Homogenous populations were composed of individuals with mean parameter values. Diverse populations were composed of individuals with parameter values drawn randomly from the corresponding statistical distributions. Simulations began with 75 plants distributed randomly on the lattice (unless stated otherwise). The state of the lattice was recorded every 100 time steps. The simulations were run for 50,000 time steps (approximately 1,100 generations). Simulations were performed on a 20 x 20 lattice, which corresponds to about 4 m^2 populated with *R. acetosa*.

5.3 Survival threshold

The survival threshold was defined as the minimum value of resource level in which a community could survive. The survival threshold of diverse and homogeneous communities was used to estimate the effect of diversity on a community's ability to survive on a poor substrate. The survival threshold was found by progressively reducing substrate levels in simulations until communities could not survive. For homogeneous communities, the survival threshold was estimated by performing ten simulations on substrate levels of 0.021 and 0.022 for 1,000 time steps on a 20 x 20 lattice and observing whether the community survived. On a substrate of 0.021, none of the communities in the ten simulations survived for 1,000 time steps. The substrate level of 0.022 defined a definite survival threshold for homogeneous communities, below which survival was impossible. Heterogeneous communities survived on a much lower substrate. Heterogeneous communities were able to persist 5 out of 10 times on a substrate of 0.001; 2 out of 10 times on a substrate of 0.0001; and 1 out of 10 times on a substrate of 0.00001. In contrast to the sharp threshold for homogeneous communities, the survival threshold for diverse communities was a gradual one.

5.4 Effects of substrate richness on productivity in diverse and homogeneous communities

5.4.1 Simulations

To estimate the effects of substrate richness on productivity, simulations were conducted on four levels of resource: 0.03, 0.3, 3 and 30. On each substrate, ten simulations were performed. The substrate level 0.03 was chosen to represent poor environmental conditions because it was close to 0.022, the survival threshold of homogeneous communities. The substrate level 30 was chosen by evaluating the amount of resource that can be requested from a cell, supposing that the cell and the neighbourhood around it are occupied by fast growing plants. The fast growing plants were defined as plants whose essential uptake parameter values were two standard deviations away in the direction of increasing the essential uptake. This amount was 15.9. A value approximately twice that, 30, was used to represent the richest level of substrate.

5.4.2 Measures of community productivity

Community productivity at a time step was estimated by summing the resource uptake of the plants present on the lattice. Resource uptake was used as a measure of plant productivity since plant uptake is closely related to plant biomass (Crawley, 1997). Plant uptake and population levels were assessed starting at time step 5,000, to allow the community to settle. For each of the ten simulations, the cumulative uptake P_c was calculated for each substrate level from time steps 5,000 to 50,000, as:

$$P_c = \sum_{i=5,000}^{50,000} P_{tot}(i)$$

where $P_{tot}(i)$ is the plant uptake summed over all plants present on the lattice at time i. The average uptake over time, which would be another convenient measure, could not be used, because the time series of plant productivity in simulations were autocorrelated. For autocorrelated time series, the statistical analysis for their comparison is involved and is outside the scope of this work. Hence, the cumulative measure of productivity was used instead. The comparison of productivity was conducted by comparing samples of the cumulative uptake obtained at different substrate levels. Each sample was tested for normality using the Shapiro-Wilk and Anderson-Darling tests that showed that the hypothesis that the samples were normal could not be rejected at the 5% significance level for all samples. The means of the samples were compared using independent t-tests, and variances of the samples were compared using Levene's test (Table 5.1).

Table 5.1 Comparison of the cumulative productivity samples of homogeneous and heterogeneous communities on different substrate levels. Means were compared using the independent t-test, and Levene's test was used to compare the variances of the samples. The **p** value is the probability that the means or variances of the two samples are the same.

		Substrate level			
		0.03	0.3	3	30
Comparing samples from homogeneous and heterogeneous communities	Mean	**p=0.001,** t(8.009)= -5.017	**p=0.001,** t(8.071)= 4.926	**p=0.001,** t(8.036)= -5.480	**p<0.001,** t(8.009)= -6.882
	Variance	**p <0.001,** F=22.361	**p=0.001,** F=16.905	**p<0.001,** F=36.202	**p=0.003,** F=12.076

5.4.3 Results

The difference in productivity of homogeneous *vs*. diverse communities was found to depend on environmental conditions. Table 5.2 presents the cumulative productivity for homogeneous and diverse communities on different substrate levels. The productivity of diverse communities was higher in very poor (0.03) and very high substrate levels (3 and 30). However, for the intermediate substrate level (0.3), diverse communities were less productive. The difference between homogeneous and heterogeneous communities was in the parameter values of the surviving plants. Therefore, the differences between plant parameter values should explain why the change in community productivity depended on the substrate level.

Table 5.2 Cumulative uptake for homogeneous and heterogeneous communities on different substrate levels. Mean values for the ten simulations are shown with standard deviations in parentheses.

	Substrate level			
	0.03	0.3	3	30
Productivity in homogeneous communities (×10^4), $\mathbf{H_0}$	18.51 (0.02)	128.1 (0.3)	1.9 (0.10)	190.03 (0.07)
Productivity in heterogeneous communities (×10^4), $\mathbf{H_1}$	20.21 (0.9)	122.5 (4.9)	188.4 (2.2)	196.2 (2.6)
	$\mathbf{H_0 < H_1}$	$\mathbf{H_0 > H_1}$	$\mathbf{H_0 < H_1}$	$\mathbf{H_0 < H_1}$

5.4.4 Differences in parameter values of homogeneous *vs.* diverse communities

In homogeneous communities, all plants had parameter values equal to the parameter distribution means. In heterogeneous communities, the parameter values of surviving plant types were recorded for each simulation. For each substrate level, these were collected in one sample and compared to the parameter values from homogeneous populations.

Significant differences between the parameter values in diverse and homogeneous communities were found for the following parameters: resource uptake parameters y_0 and β, time to reproduction R_t, and requested/essential uptake ratio r_u. These changes depended on the substrate level. The normality of the distribution of parameters R_t, and β was tested using the Shapiro-Wilk and Anderson-Darling tests that showed that the hypothesis that distributions were normal could not be rejected at the 5% significance level. For these parameters, one-sample *t*-tests (at the 5% significance level) were used to determine whether the distributions could have the same mean as the value in homogeneous communities. For parameters y_0 and r_u the Shapiro-Wilk and Anderson-Darling tests showed that the hypothesis could be rejected at the 5% significance level. Hence, the Mann-Whitney test was used to determine whether the sample median could be equal to the y_0 and r_u of plants in homogeneous communities.

Increase in the median y_0 value of coexisting plant types was observed with increase in substrate level. Figure 5.1 shows the median value of y_0 in surviving plant types for different substrate levels. In the poorer substrates of 0.03, 0.3 and 3, the surviving plants had a lower median y_0 than average. The difference was statistically significant. The parameter y_0 determined the height of the plant uptake curve. The results suggest that plants that persisted on the low substrate were those that needed less resource to survive and grow. As the substrate level increased, the pressure to have a low uptake curve disappeared, and on the rich substrate, the height of the uptake curve did not differ between diverse and homogeneous communities. Figure 5.2 shows the mean value of parameter β in surviving plant types for different substrate levels. Similar to y_0, the mean value of parameter β was significantly less than the average for all substrates, but it increased for richer substrates. The mean value for substrate 30 was significantly higher than that of substrate 3; and the mean for substrate 3 was significantly higher than that of substrate 0.3. The means for substrates 0.3 and 0.03 were not significantly different. Parameter β determined the steepness of the uptake curve, and therefore the time that the uptake curve began to increase. The lower the value of β, the later the curve rose. Therefore, similarly to the effect of decreasing y_0, lower values of β facilitated survival on lower substrates.

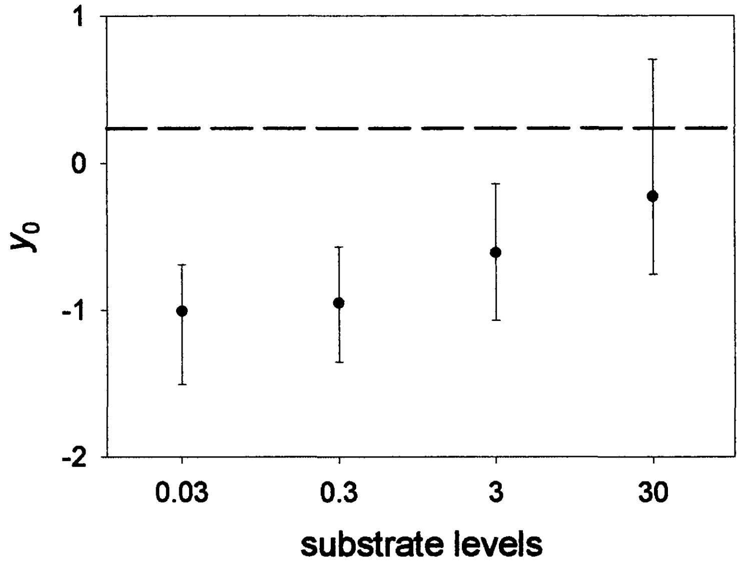


Figure 5.1 The median ± a quartile of the values of parameter y_0 in different substrate levels. The dashed line represents the value of the parameter for the plants in a homogeneous population.

The opposite trend was observed in the values of parameter R_t, time to reproduction. Figure 5.3 shows the mean value of R_t in surviving plant types for different substrate levels. On lower substrates (0.03 and 0.3), the distribution mean of R_t was not significantly different from that of homogeneous communities. On the other hand the mean shifted towards smaller values on higher substrates (3 and 30). This change was statistically significant.

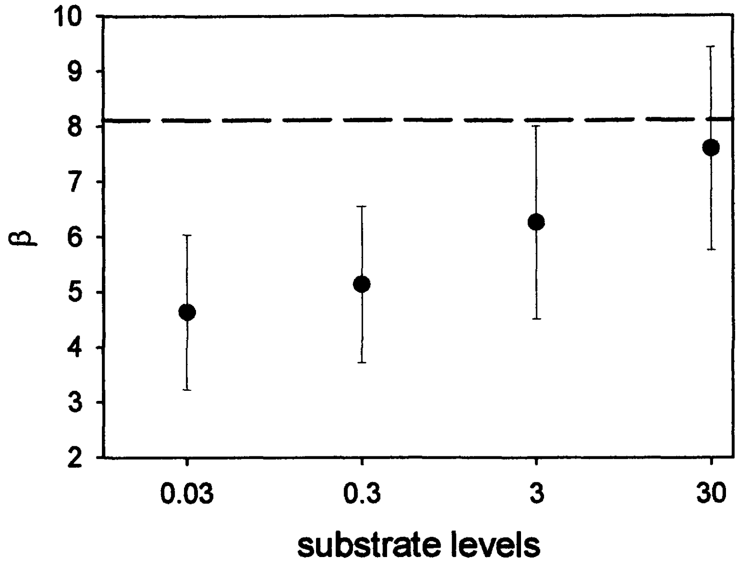


Figure 5.2 The means and the standard deviations of the values of parameter β in different substrate levels. The dashed line represents the value of the parameter for the plants in a homogeneous population.

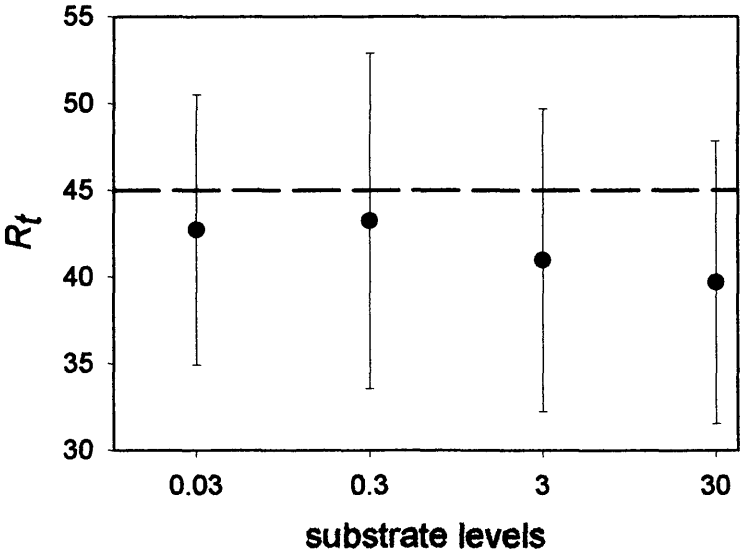


Figure 5.3 The means and the standard deviations of the values of parameter R_t in different substrate levels. The dashed line represents the value of the parameter for the plants in a homogeneous population.

The range of population levels observed on different substrates is presented in Table 5.3. The population levels were positively related to the substrate levels. This increased the importance of competition for space. Therefore, time to reproduction R_t came into play on higher substrates because competition for space became important, and dispersing seeds at higher frequencies but in smaller numbers raises the chance of finding an empty cell for the offspring.

Table 5.3 Ranges of population levels observed in communities for different substrate levels. The maximum and minimum values observed in ten simulations performed on each substrate are shown.

Substrate level	0.03	0.3	3	30
Population range	252-400	386-400	388-400	392-400

Finally, the mean values of r_u, the ratio of the requested to the essential uptake, were found to be significantly higher for all substrates, except the poorest one. The proportion that the requested uptake was bigger than the required uptake was determined by r_u. The higher values of the requested uptake, the higher the proportion of resources allotted to the plant in the case of competition. Therefore, higher values of r_u aided in competition between plants. When the lattice was full (on higher substrates), higher values of r_u were more important than on the lowest substrate when the lattice was not as full.

5.5 Effects of environmental heterogeneity on productivity in diverse and homogeneous communities

Environmental heterogeneity can have strong effects on community dynamics (Tilman and Kareiva 1997). In this section, the effect of spatial environmental heterogeneity on productivity is examined as it manifests itself in diverse and homogeneous communities. Environmental heterogeneity has the most effect on low substrates, when a small change in the substrate level plays an important role in plant survival. Therefore, the effect of environmental heterogeneity was examined on a poor substrate.

5.5.1 Simulations

Four scenarios were simulated: 1) communities of identical individuals (homogeneous communities) in a homogeneous substrate, 2) diverse communities in a homogeneous substrate, 3) homogeneous communities in heterogeneous substrates, and 4) diverse communities in heterogeneous substrates. As previously, a diverse community was composed of individuals with parameter values randomly chosen from the corresponding distribution. In a homogeneous community, individuals were assigned the average parameter values. For each scenario, ten simulations were performed. For each of ten cases, a separate heterogeneous substrate lattice was created. This was done by randomly assigning each lattice cell a resource level from 0.01 to 0.05 according to a uniform distribution. The average level for lattices ranged from 0.029244 to 0.030845. For each heterogeneous lattice, a corresponding homogeneous lattice was created with all cells having the substrate level equal to the average obtained from the corresponding heterogeneous lattice.

The four samples for each scenario (with and without diversity/heterogeneity) were tested for normality using the Shapiro-Wilk and Anderson-Darling tests. The test showed that the probability that samples were normal could not be rejected at the 5% significance level. Independent t-tests were used to compare the means of the samples, and Levene's test was used to compare the variances of the samples (Table 5.4).

Table 5.4 Results of a comparison of the cumulative productivity samples in homogeneous (μ_1) and heterogeneous (μ_2) environments of homogeneous and heterogeneous populations. Means were compared using the independent t-test, and Levene's test was used to compare variances of the samples. The **p** value is the probability that the means or variances of the two samples are the same.

		Homogeneous population	Heterogeneous population
Heterogeneous and homogeneous environments	Mean	**p<0.001,** t(18)=-7.357	**p=0.285,** t(9.976)=-1.130
	Variance	**p=0.443,** F=0.642	**p=0.002,** F=13.853

5.5.2 Results

Homogeneous communities were significantly more productive in a homogeneous environment than in a heterogeneous one. Comparison of the productivity of communities in the two environments is presented in Table 5.5. The variance among simulations was significantly lower in homogeneous environments (the statistics are shown in Table 5.4). These effects can be explained by the spatial variation in resource distribution. Heterogeneity in the resource levels led to some plants being unable to survive or develop normally in some locations on the lattice. Productivity in heterogeneous environments depended on the distribution of resources in the substrate and on where the plants landed by chance. This increased variation amongst simulations.

Table 5.5 Cumulative uptake for homogeneous and diverse communities on homogeneous and heterogeneous substrate. Mean values for the ten simulations are presented with standard deviations in parentheses.

	Productivity of homogeneous population ($\times 10^4$)	Productivity of heterogeneous population ($\times 10^4$)
Homogeneous environment	18.51 (0.30)	21.03 (1.70)
Heterogeneous environment	17.40 (0.39)	19.51 (0.39)

Heterogeneous communities, on the other hand, were not significantly affected by environmental heterogeneity (Table 5.5). Plants that survived in heterogeneous populations were better adapted to the poor substrate (as shown in previous section). Therefore, heterogeneous populations were able to deal with environmental heterogeneity without significantly affecting community productivity. The different responses of diverse and homogeneous populations to environmental heterogeneity shows the importance that diversity can play in population dynamics. Because plants in diverse communities were adapted to the low level of substrate, they were able to deal with the heterogeneity much better than plants in homogeneous communities.

5.6 Effects of initial diversity on the resulting productivity

5.6.1 Simulations

To explore the effects of initial community diversity on productivity, simulations were performed with the initial population reduced from 75 (as it was for all aforementioned simulations) to 15 plants. The same heterogeneous substrates were used, as for previous simulations. This led to a poorer sampling of the parameter space. Simulations with reduced initial diversity were done for each of the heterogeneous lattices. Normality of the sample was checked using the Shapiro-Wilk and Anderson-Darling tests that showed that the hypothesis that the samples were normal was rejected at the 5% significance level for the sample of productivity in simulations with reduced initial diversity. Therefore, the cumulative productivity samples of simulations with 75 and 15 initial plants were compared using the Mann-Whitney test to compare the medians ($p=0.089$, $U= 27$ that the medians were equal).

5.6.2 Results

The cumulative productivity for the simulations with reduced initial diversity of 15 had a mean of 1.185E+05 and standard deviation of 1.404E+04. In case of initial diversity of 75, the cumulative productivity sample had a mean of 1.951E+05 and a standard deviation of 0.3969E+04. Simulations with higher initial diversity did not have significantly different productivity than simulations with lower initial diversity. However, the probability that the values were the same was very low (0.053) suggesting that communities with higher initial diversity might be more productive. There was a significant difference in the variances of the two samples (the probability that they were the same was $p=0.001$). The productivity of communities with lower initial diversity varied much more amongst simulations than the productivity of populations with higher initial diversity.

5.7 Discussion

Results show that community diversity can significantly affect population dynamics. In particular, differences were noted in the ability to survive on poor substrates, community productivity in different substrate levels, and response to environmental heterogeneity. The reason for these differences lay in the ability of diverse communities to adapt to the environment. This adaptation meant changes in the community composition and, therefore, in community productivity and ability to survive.

The survival threshold for diverse communities was found to be about 20 times lower than that of homogeneous communities. This was possible because, in the presence of diversity, some plants were better at surviving on a poor substrate than the average plants (which constituted a homogeneous community). This occurred due to the variability of the physiological traits relating to the plant's ability to survive such as the required uptake, the release rates of the storage compartment and allocation to reproduction. In a variable community, it was possible that some plants had combinations of the trait values that allowed them to persist on lower substrate levels. The difference in the survival threshold between homogeneous and diverse communities is quite marked, particularly considering that the model incorporated the variation present in a single species. The results indicate that considering a species as a collection of identical individuals (characterised by mean parameter values) may give misleading estimates of population properties.

Diverse communities were observed to have a markedly different productivity than homogeneous communities. The ability of diverse communities to adapt to their environment was responsible for these differences. The adaptations had consequences which affected community productivity. At the lowest substrate level, diverse communities were much better at surviving in poor conditions. Thus, although resource uptake of plants in diverse communities was lower than in homogeneous communities, higher population levels led to higher productivity in diverse communities. At the intermediate substrate level (0.3), population levels of both types of communities were similar, and therefore resource uptake in diverse communities was lower than in homogeneous communities. This resulted in a lower productivity in diverse communities than in homogeneous communities. At high substrate levels, plants in diverse communities had the same uptake as plants in homogeneous communities, but were better at taking advantage of gaps on the lattice. This resulted in higher productivity of diverse communities than that of homogeneous communities. The changes in parameter values show that, under different environmental conditions, different mechanisms at the individual level becme important, and may have affected community dynamics in varying ways. Therefore, community productivity was shown to be a result of both diversity and the environmental conditions in which the community existed. The interplay of these factors created a complex relationship between community productivity and diversity, which has been noted to occur in communities (Loreau 2000, Pugnaire and Luque 2001).

The initial diversity in the system was shown to greatly increase the variability in community productivity among simulations. This shows that the diversity composition may play an important role in determining the productivity of a system. This point was raised by Nijs and Roy (2000), who stressed that the extent of differences between species in a community can play an important role in community dynamics.

Chapter 6. Individual interactions and community diversity

6.1 Introduction

The results discussed in Chapter 4 showed that competition for space over time can be important for community diversity. However, competition is only one example of the interactions between individual that occur in communities. Mutualism and predation are other interactions among individuals widely observed in ecological communities. With respect to predation, both observations and mathematical studies show that predator-prey interactions can support diversity in some systems (Ricklefs and Miller 1999). Mutualistic relationships in social communities (*e. g.* cooperation) have been widely studied (Pepper and Smuts 2000). However, existing research has been mainly focused on the mechanisms that may generate such relationships (*e.g.* group selection). Less is known about mutualistic relationships in ecological communities. In particular, the effect that mutualistic relationships may have on community diversity is not clear, as these relationships have been shown to influence diversity both negatively and positively (Stachnowicz 2001, Kiers *et al.* 2000, Wilkinson and Parker 1996, Bronstein 1994). A model of organism interactions was formulated to explore the potential effect of mutualistic relationships on community diversity and its evolution in time (Pachepsky and Taylor 2002).

6.2 Model of organism interactions

The basis for the model of organism interactions is the plant individual-based model described in Chapter 3. However, several changes have been made: a) the model no longer simulates plants, but generic organisms; b) there are several types of resources on the lattice instead of one, and they consist of discrete units, as opposed to the continuous distribution of one resource used in the previous version of the model; c) the physiology of organisms is simplified; d) organisms modify the resources that they digest, and can mutually benefit each other by digesting resources from the same area; e) mutation is introduced in the reproduction process.

In the model, organisms compete for space and resources but can also form mutualistic relationships. A biological system corresponding to the model is one where one type of organism produces something useful to another organism and vice versa, for example the mycorrhizal relationships, *i.e.* mutualistic relationships observed in roots (Read 1996). The physiological details of the life cycle of organisms were simplified so that only processes relevant to development of mutualistic interactions were included. In particular, the details of resource allocation and storage were removed from the model. Reproduction occurs when organisms accumulate a certain amount of resources, and this amount is the same for all organisms. Mutation is introduced in the model to increase the possibility that mutualistic relationships develop. This was necessary since mutualistic relationships can only develop between particular types of individuals, and mutation increases the chance that these complementary types can develop (Rosenzweig 1995).

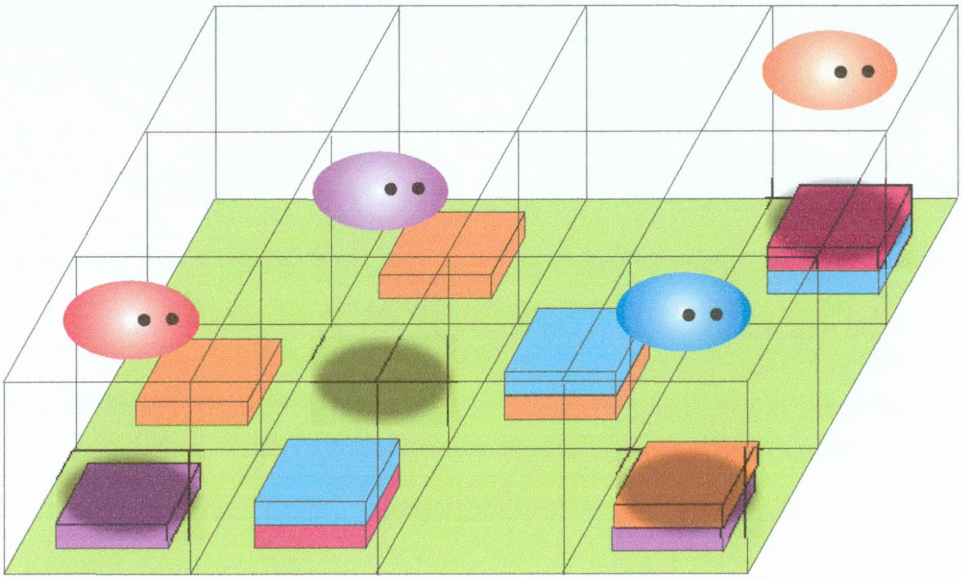


Figure 6.1 The representation of the part of the lattice. The ovals represent the different types of organisms. The bricks represent the different types of resources.

6.2.1 Substrate

There are 8 types of resources available on the lattice. The resources are distributed in packets, with each packet potentially able to contain all 8 types of resources. A resource packet is represented by an ordered string of 8 ones and zeros. A one in the nth position corresponds to the presence of the nth resource in the packet, and a zero corresponds to its absence. For example a resource packet '0011 1100' contains resource types 3, 4, 5 and 6 and does not contain resource types 1, 2, 7 and 8. Since there are 8 resource types possible, there are 256 possible resource packets. The number of resource packets at a single lattice cell can vary from 0 to the maximum number of resources per cell R_{cell} (a model parameter). A representation of a section of the lattice of the model is shown in Figure 6.1.

The model is initialised with resource packets randomly distributed on the lattice. The number of resource packets is defined by $R_{init}X$ where R_{init} is the initial proportion of resources placed on the lattice, and X is the size of the lattice. At each time step a proportion R_{re} of resource packets present on the lattice is randomly removed, and the same number is distributed randomly over the lattice. This represents a resource flow through the system and a disturbance in the environment (which can be important for maintaining diversity).

The type of the resource packet placed in the environment is a random string of zeros and ones with probability (1-P_{br}) or is a particular type of resource packet with probability P_{br}. The latter is the 'basic' resource packet, towards which the environment is biased. This ensures that a population of organisms on the lattice is under some pressure to adapt to this combination of resource packets. This drives the system to a state of low diversity since organism types best adapted to digesting the basic resource packet will outcompete other types. Therefore, if mutualistic interactions increase diversity, the effect will be stronger. The basic resource packet in simulations (unless specified otherwise) was arbitrarily set to '1111 1111'.

6.2.2 Organisms

The organisms distributed on lattice cells, take up resources, digest and metabolise them, produce waste, reproduce, and die. These processes are characterised in the following manner.

6.2.2.1 Uptake of resources

An organism can obtain resource packets from its lattice cell and the cells around it in a square area. This area is the organism's resource capture area A_r with radius described by the parameter A_n with

$$A_r = (2A_n + 1)^2 .$$

The A_r represents the area over which an organism can collect resources. At each time step, organisms place a request for a number of resource packets defined by the parameter O_r. Each organism randomly chooses locations within its capture area from which to request resources. The resource packets are then allocated to the organisms according to availability.

When demand for resource packets at a particular cell exceeds the number available, competition occurs in the following way. Let x be the total number of resources demanded, and k the total number of resources available, at the cell. At each time step, the resources at a given cell are distributed among the organisms requesting resources from it using 'roulette wheel' selection, as follows: each organism is assigned an area of the wheel that is proportional to its demand from that cell relative to x. The roulette wheel is then spun k times, and after each spin one resource packet is transferred from the cell to the organism selected.

However, if one of the organisms requesting resources for a particular cell resides in that cell, it gets all of the resources it requests (or however many there are available). The rest of the resources are then distributed among the remaining organisms using the roulette wheel selection as described above. This allows organisms with small resource capture areas to compete with those with larger resource capture areas. It also represents a situation in which the organism physically located in a particular space has access to all of the resources there, *e.g.* if it is a plant, it may have an extensive root structure in that location.

6.2.2.2 Resource digestion

Each organism has a 'template' associated with it. The template, like the resource packet, is an ordered 8-bit string of zeroes and ones (*e.g.* '1110 0111'). In an organism, the template represents the organism's preference for different types of resources. The digestion of a resource consists of matching the template to the resource bit by bit, and counting the number of matched bits (*i.e.* '1' in the template and '1' in the resource, or '0' in the template and '0' in the resource). In other words, an organisms gets a match for each time its preferred resource type is present in the resource packet. Depending on the number of matches, the organism is assigned utility points which are used by organism for metabolism and reproduction. The correspondence of matches to utility points is shown in Table 6.1. In an environment with random resource packets, organisms will get 1 utility point on average (which is spent on metabolism as explained below). Each organism is initially assigned a number of utility points, defined by the parameter U_{init}.

Table 6.1. Correspondence of the number of matches -- between an organism's template and a resource -- to the number of the utility points obtained.

Number of matches	0	1	2	3	4	5	6	7	8
Utility points	-3	-2	-1	0	+1	+2	+3	+4	+5

The product of digestion, 'waste', is then deposited in place of the digested resource packet. Waste is the logical NOT of the template (*i.e.* for template '1111 0000', the waste is '0000 1111'). This means that after digesting a resource packet, the organism removed from the resource packet the resource types that it preferred and output the resource types that it did not prefer. This matching scheme gives rise to the possibility of mutualistic relationships between organisms developing. For example, two organism with templates '1100 0011' and '0011 1100', respectively, get 8 matches from digesting each other's waste, giving them the maximum possible utility points (Figure 6.2). Of course, this can only occur if by chance one of the organisms is in a position to take up a resource which is the 'waste' of the other.

The utility points obtained from digesting resources are 'spent' on metabolism and reproduction. Metabolic processes cost organisms a given number of utility points per time step, defined by the parameter M. Reproduction occurs when a number of utility points T_{rep} is achieved, where

$$T_{rep} = 2NU_{init}$$

and N is the number of offspring that organisms must produce at each reproduction. This means that an organism has to accumulate twice the amount of utility points necessary to produce offspring, half of which is spent on reproduction and half of which stays with the organism.

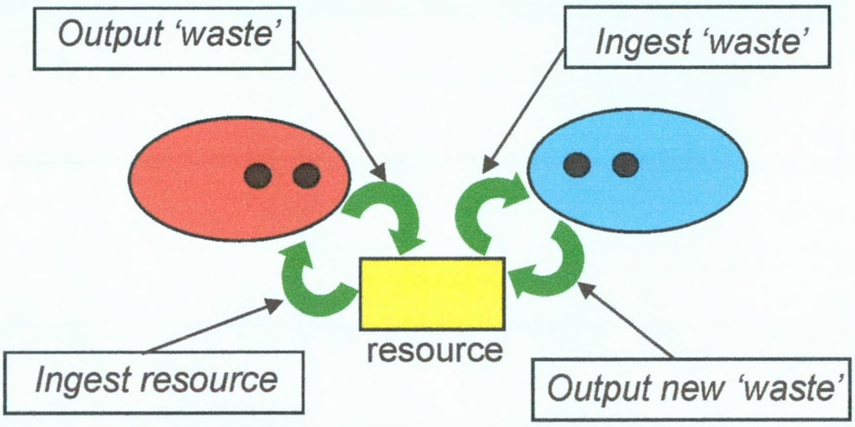


Figure 6.2 Interactions between organisms through resources. One individual can digest a resource and output a 'waste', which can be ingested by another organism. If the 'waste' of one organism is beneficial to another organism, then mutualistic interactions can occur.

6.2.2.3 Reproduction and death

When an organism reproduces, its offspring are dispersed randomly over a distance D from the location of the parent. At each time step, the organisms reproduce in random order. The parent-organism gives each of its offspring a number of utility points defined by U_{init}. If the cell on which the offspring lands is occupied, the offspring dies. When created, each offspring can mutate with some probability P_m in which case its template and resource capture area may change values in the following manner. The catchment area and each bit of the template have an equal probability to mutate. The number of mutations (from 0 to 9 --8 bits and 1 resource capture area) is chosen randomly. The bit in the template is changed from '0' to '1' or visa versa, and the radius of the resource capture area mutates to a random value between 1 and A_n.

At each time step there is a probability, P_d, that each organism may die.

6.3 Experimental design

For all simulations, the initial population size was set to $X/2 = 450$ organisms where X is the environment size (Table 6.2), which were randomly distributed on the lattice. The state of each organism (template and resource capture area) and locations were recorded every 100 time steps throughout the simulation. The simulation length was based on the number of generations it spanned, where a generation was defined to be the mean across all organisms of the time between reproductive events.

6.4 Measures of community dynamics

In order to quantify and compare the community dynamics under different conditions, the following four measures were used. The cumulative number of individuals, C_{ind}, during a simulation was used to estimate the abundance of the community. The value of C_{ind} was calculated by adding the number of individuals present on the lattice at each time step. In other words, C_{ind} at time i was found by

$$C_{ind} = \sum_{t=0}^{t=i} N_{tot}(t)$$

where $N_{tot}(t)$ is the total number of individual present on a lattice at time t. The cumulative measures were used instead of average measures for the same reason as explained in Chapter 5: the time series of the number of individuals present on a lattice were autocorrelated, in which case an average of the series is not a proper measure. The statistical analysis for comparison of autocorrelated time series is involved and is outside the scope of this work. The same reasoning was behind the use of other cumulative measures.

The cumulative number of types C_{type} and number of persisting types were used to estimate the diversity in the system. The value of C_{type} was calculated in the similar manner to the cumulative number of individual. In particular, C_{type} was calculated by adding the number of organism types present on the lattice at each time step. This measure is problematic because it is dependent on the mutation rate, and it does not give an idea about the persistence of some types *vs.* others (*e.g.* this measure can be the same if different types arose throughout the simulation and if some types persisted consistently through time). Therefore, an additional measure of diversity, the number of persisting types T_p, was used.

The number of persisting types T_p was defined to be the number of types that persist on the lattice for a time equal to, or greater than, 10,000 time cycles (which corresponds to about 63 generations on average). The number of persisting types and the time period of their persistence contains information about whether new persistent types arise in the system continually. A potential problem with using this measure is that the state of the system was only recorded once every 100 time steps. This means that some of the types may have disappeared and returned between the two points when the state of the lattice was recorded. To assess the importance of this problem, the state of the system was recorded every time step for two simulations. In these simulations, the same number of persisting types was obtained either based on records for each time step or every 100 time steps. This suggests that recording the state of the lattice every 100 time steps does not affect the counted number of persisting individual types.

The average number of 1's in the templates of the persisting types T_{ones} was used as a characterisation of the composition of the community. This gives a measure of how adapted the organisms are to the basic resource packet (which was arbitrarily picked to be all '1's). For example, if the average number of '1's is close to 8 then most of the surviving types are adapted to the basic resource packet.

6.5 Sensitivity analysis

The model parameters were selected so that the model exhibited diversity and mutualistic interactions. These values of the model parameters are listed in Table 6.2. Before obtaining results from the model, the sensitivity of the model to the parameter values was investigates in order to determine whether the results would be similar across a range of parameter values. This section describes the sensitivity analysis. The length of the simulations for the sensitivity analysis was set to 200,000 time steps, which corresponds to between 660 and 10,000 generations depending on the value of the number of offspring N, which largely determines the generation length (see section 6.3 Experimental Design for definition of a 'generation').

6.5.1 Sensitivity to the parameter values of organism properties

The sensitivity analysis was performed for the following parameters: the dispersal distance D, the number of offspring N, and the total resource request per organism O_r. These were chosen since they were interrelated, and the effect of simultaneously varying them was not obvious. The two parameters that were held constant were U_{init} and M. These had a straightforward effect on the dynamics. Initial utility points controlled the ability of an organism to persist in unfavourable conditions. Metabolic rate raised the pressure on organisms to find better suited resource packets (*i.e.* it increased competition).

The sensitivity analysis was performed as follows. The dispersal distance D was set to 3, 10, and 30 cells away from the location of the parent. The number of offspring produced at a reproduction N was set to 1, 3, and 5 offspring. The total resource request per organism at each time step O_r was set to 4, 7, and 81 requests. The upper limit of 81 requests was chosen to correspond to the largest capture area possible. One simulation for each configuration was conducted, giving a total of 27 simulations.

Table 6.2. The basic set of values for the model parameters.

Environment	
environment size, X	30 x 30
Resources	
maximum number of resources per cell, R_{cell}	7
initial resource distribution proportion, R_{init}	0.5
resource renewal proportion, R_{re}	0.3
basic resource probability, P_{br}	0.05
Organisms	
total resource request per organism, O_r	7
catchment area number, A_n	1 - 5
initial utility points, U_{init}	10
metabolic rate, M	1
dispersal distance, D	10
number of offspring, N	3
random death probability, P_d	0.001
mutation probability, P_m	0.025 (or 0.0 for no-mutation simulations)

For each configuration the following were recorded: cumulative number of individuals C_{ind}, cumulative number of types C_{type}, and number of persisting types T_p. The results are summarised in Figures 6.3, 6.4 and 6.5. Variation in the number of offspring and the dispersal distance did not have an effect on the measured quantities, while variation in the number of requested resources had a substantial effect. The minimum number of requested resources that was necessary for community survival is presented in Table 6.3. C_{ind} responded to an increase of the number of requested resources by increasing towards a maximum value. On the other hand, T_p and C_{type} increased towards the maximum when the number of requested resources was 7 (Figures 6.4 and 6.5). This may be due to the fact that high numbers of requested resources reinforced the persistence of dominant types in the model in the following way. When two organisms were in a mutualistic relationship with each other, they benefited from digesting the 'waste' products of each other. The higher the number of the resource packets that organisms requested, the more 'waste' they produced and the more beneficial resource packets they could digest. Therefore, if a mutualistic relationship became established in the model, it was stronger when the number of requested resource packets was higher.

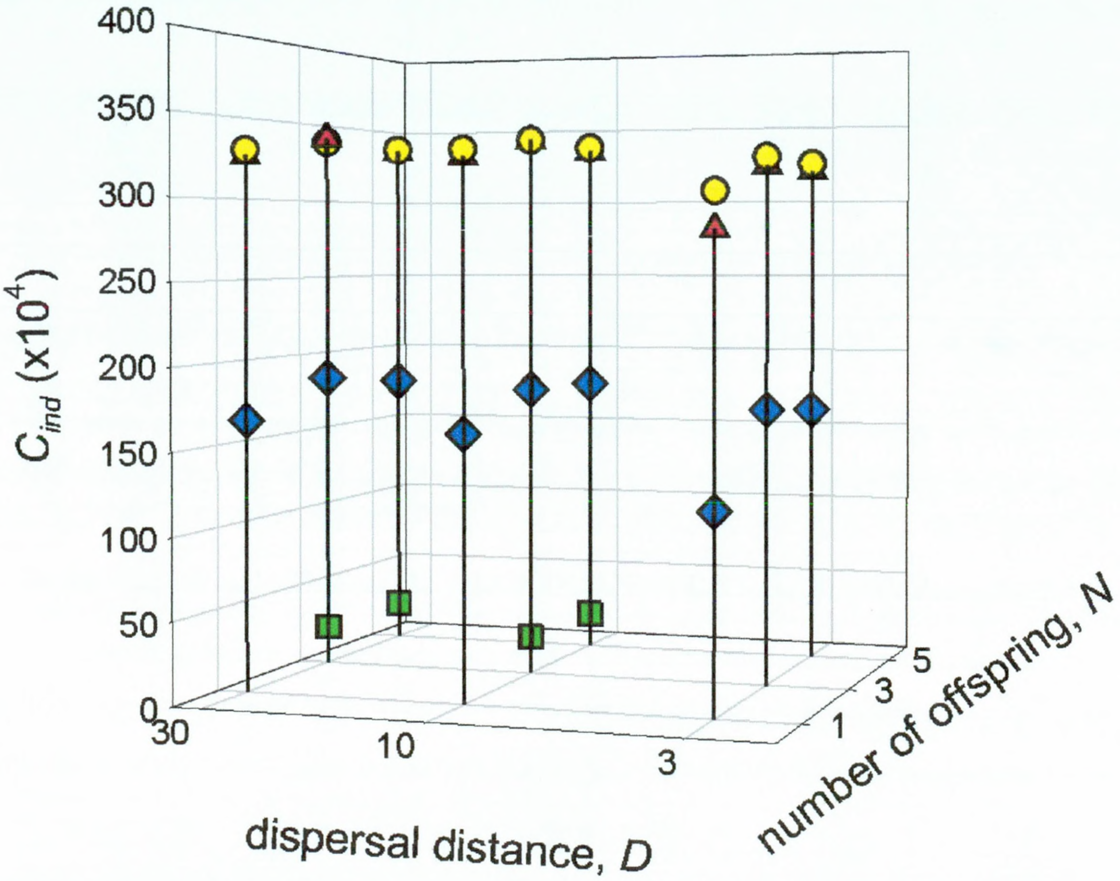


Figure 6.3 Cumulative number of individuals C_{ind} for the range of values of D, N, and O_r. Green square symbol corresponds to $O_r = 3$; blue diamond - $O_r = 4$; red triangle - $O_r = 7$; yellow circle - $O_r = 81$.

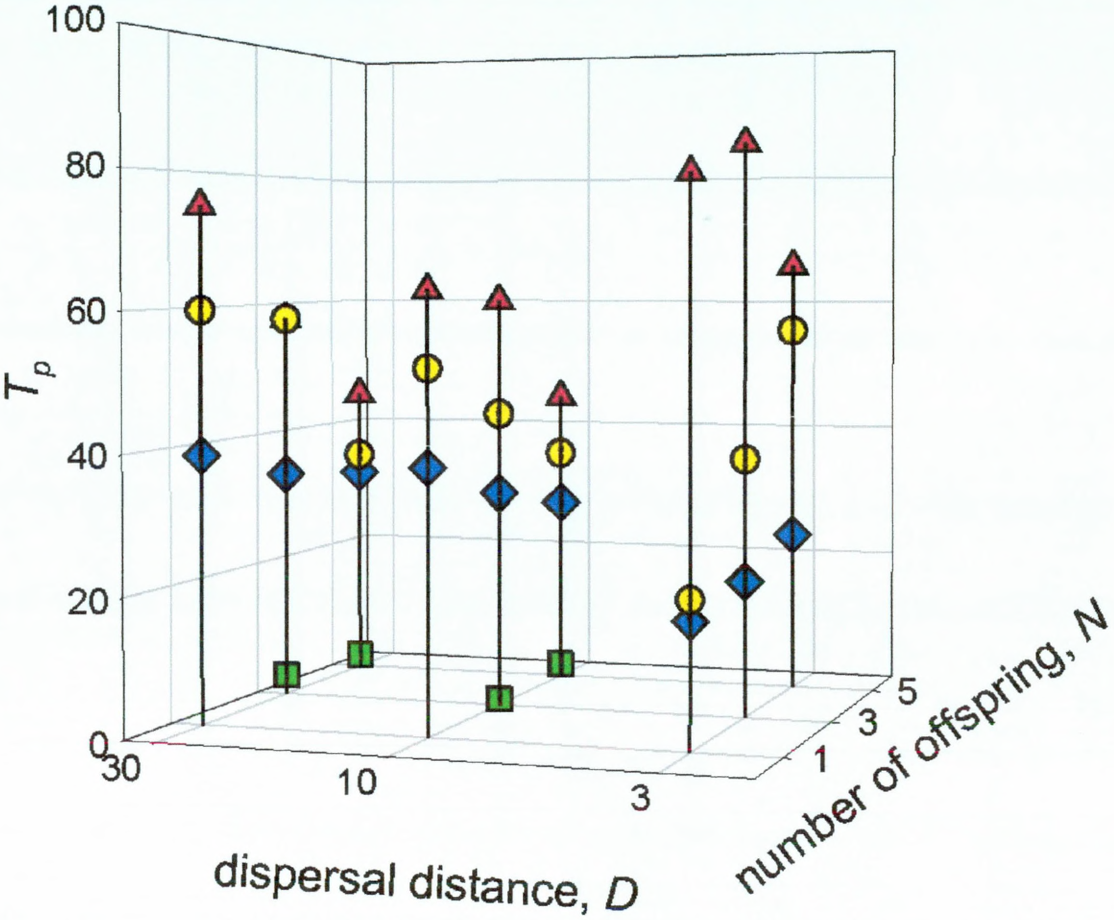


Figure 6.4 Number of persisting types T_p for the range of values D, N, and O_r. Green square symbol corresponds to $O_r = 3$; blue diamond - $O_r = 4$; red triangle - $O_r = 7$; yellow circle - $O_r = 81$.

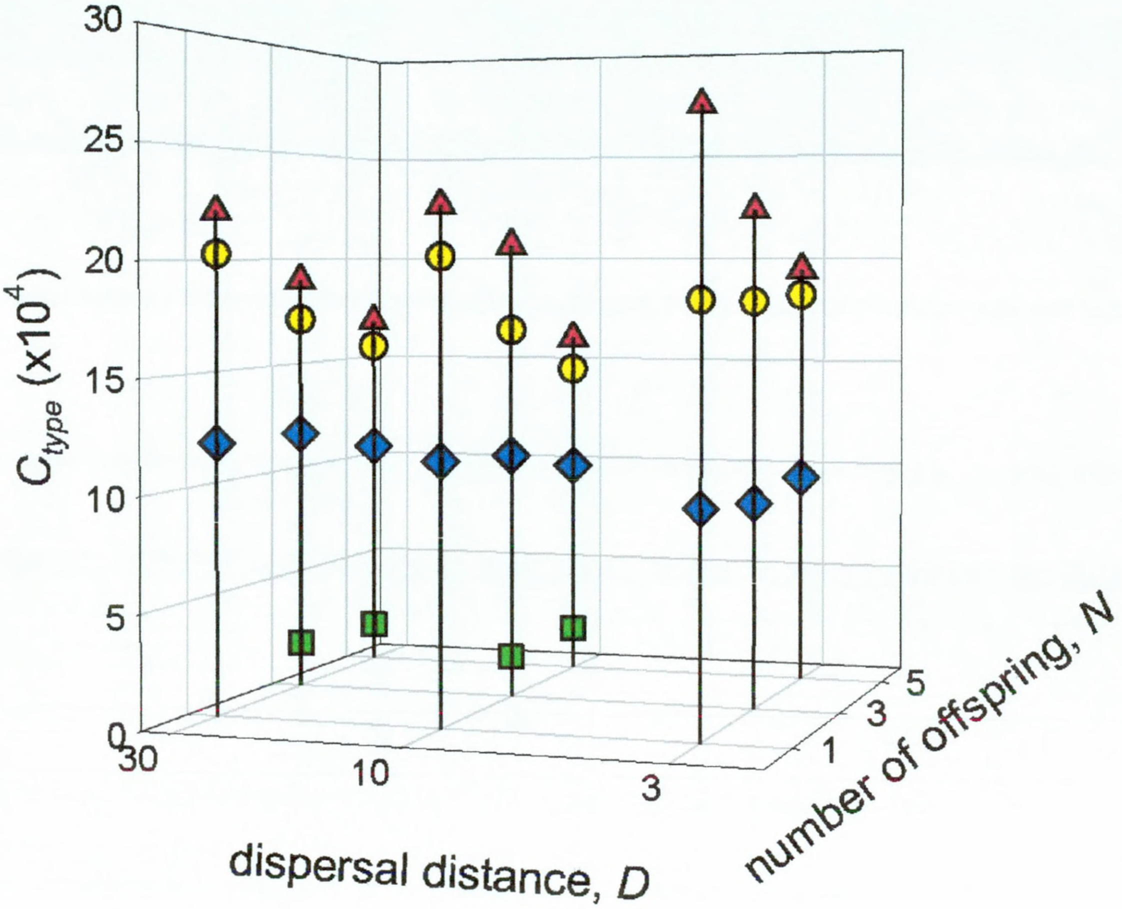


Figure 6.5 Cumulative number of types C_{type} across the range of values of D, N, and O_r. Green square symbol corresponds to $O_r = 3$; blue diamond - $O_r = 4$; red triangle - $O_r = 7$; yellow circle - $O_r = 81$.

Table 6.3 The minimum value of total resource request per organism O_r necessary for survival of the population for a range of values of dispersal distance D and the number of offspring N.

		D		
		3	10	30
N	1	4	3	3
	3	4	3	3
	5	4	4	4

6.5.2 Sensitivity to mutation rates

To estimate the effect of mutation on community dynamics, the mutation rate P_m was varied. P_m was assigned values of 0.0014, 0.025 and 0.5. Table 6.4 shows the response of diversity both in terms of the cumulative and persisting number of types. In both cases, the number of types increased with increasing mutation rate. This is not surprising, as higher mutation increases the rate of new types created in a community.

Table 6.4 The response of the number of persisting types T_p, cumulative number of individuals C_{ind}, and cumulative number of types C_{type} to changes in the mutation rate P_m.

P_m	T_p	C_{ind} ($\times 10^4$)	C_{type} ($\times 10^4$)
0.0014	17	338.8	7.9
0.025	61	336.8	20.7
0.5	117	333.6	146.4

6.5.3 Sensitivity to resource composition

For one selected configuration, $(D, N, O_r)=(10, 3, 7)$, three resource properties were varied: the proportion of the lattice initially filled with resources R_{init}; the basic resource bias P_{br}; and the substrate renewal rate R_{re}. The parameter R_{init} was set to 0.3, 0.5 and 0.7; P_{br} was set to 0.5, 0.1, 0.05, and 0.01; and R_{re} was set to 0.1, 0.3, and 0.7. Each parameter was varied individually, with the other two being set to the values of $(R_{init}, P_{br}, R_{re})=(0.5, 0.05, 0.3)$.

The response of the model to variation in R_{init} is shown in Table 6.5. The value of R_{init} was directly proportional to the cumulative number of individuals and both diversity measures. A larger initial proportion of resources on the lattice predictably led to a larger population size. The positive effect of R_{init} on diversity implies that, within the range of values explored, increasing substrate richness improved conditions for diversity.

Table 6.5 The effect of variation in the initial resource distribution proportion R_{init}.

R_{init}	T_p	C_{ind} ($\times 10^4$)	C_{type} ($\times 10^4$)
0.3	5	233.7	5.6
0.5	61	336.8	20.7
0.7	146	671.7	40.0

The results of varying R_{re}, the proportion of resources renewed every time step, are presented in Table 6.6. The cumulative number of individuals was directly proportional to the replenishment rate. The diversity measures, on the other hand, peaked at the intermediate value (R_{re}=0.3). This can be explained by the fact that for high values of the renewal rate, mutualistic relationships failed to establish themselves, since increase in replenishment rate increased the probability that the 'waste' of organisms will be renewed to a random resource packet. This led to the domination of types with templates consisting predominantly of '1's. This, in turn, led to higher population levels, since those types utilised the basic substrate '1111 1111' most effectively (see the description of the matching process).

Table 6.6 The effect of variation in the resource renewal proportion R_{re}.

R_{re}	T_p	C_{ind} ($\times 10^4$)	C_{type} ($\times 10^4$)
0.1	26	322.1	15.3
0.3	61	336.8	20.7
0.7	8	653.5	8.4

The results of varying P_{br} are presented in Table 6.7. Varying P_{br} did not seem to affect the cumulative number of individuals. Nor did it have a drastic effect on diversity, although a general unimodal (humped) relationship was observed, with higher values of diversity measures observed for intermediate values of P_{br} (0.1 and 0.05). However, a clear trend was observed in the average number of '1's in the templates of persisting types T_{ones}; T_{ones} approached 8 with an increasing bias towards the basic resource packet P_{br}. For the intermediate values of the resource bias, T_{ones} was close to 4 (which means that the templates were, on average, half '1's and half '0's). This shows how the composition of a community responds to the level of bias towards a particular basic resource packet.

Table 6.7 The effect of variation in the basic resource probability P_{br}.

P_b	T_p	T_{ones}	C_{ind} ($\times 10^4$)	C_{type} ($\times 10^4$)
0.5	50	6.4	334.4	15.8
0.1	60	4.9	337.7	19
0.05	61	4.1	336.8	20.7
0.01	51	3.7	337.6	19.3

6.6 Results

6.6.1 Effects of organism interactions and mutation on diversity and speciation

The possibility of interactions between organisms in the model was introduced by allowing the waste of an organism to be a potential resource to other organisms. To explore the effects of organism interactions on diversity, the model was run with and without waste production with parameter values listed in Table 6.2. To investigate the effects of waste production and mutation in combination, simulations were performed with the following configurations: mutation and waste production, mutation and no waste production, no mutation and waste production, and finally, no mutation and no waste production. For each scenario, ten simulations were performed. For simulations without waste production, the organism's 'waste' was a random resource. In order to investigate the long-term evolutionary dynamics of the system, the simulations were run for 1,000,000 time cycles which corresponds to about 6,250 generations (see section 6.3, Experimental design, for the definition of a 'generation'). For each configuration, each sample of 10 simulations was tested for normality using the Shapiro-Wilk and Anderson-Darling tests that showed that the hypothesis that the samples were normal was rejected at the 5% significance level for some of the samples. Therefore, to compare simulations with different configurations, the samples were subjected to Mann-Whitney test. All differences mentioned in the text were significant at 5% level.

The results of the simulations are summarised in Table 6.8. With no mutation, community diversity was much lower. For simulations without waste production, simulations with mutation had a higher cumulative number of individuals than in those without mutation. In the presence of waste production, the cumulative number of individuals with and without mutation were not significantly different. Mutation was important when no waste was produced because it allowed better suited types to evolve in the course of a simulation. In the simulations with waste production, however, evolution promoted not only the best suited type but also mutualistic pairs which were not as good at extracting value from the substrate as the best suited type. Therefore, the number of individuals on a lattice was not as high.

Table 6.8 Comparison of simulations with and without waste production and with and without mutation. The values shown are means (with standard deviations in parentheses) of 10 simulations.

		T_p	T_{ones}	C_{ind} (×10⁴)	C_{type} (×10⁴)	Average A_r of persisting types
with mutation	with waste	226.3 (17.0)	4.3 (0.2)	338.2 (0.6)	17.8 (0.5)	66.3 (0.7)
	no waste	14 (4.2)	7.1 (0.1)	463.2 (0.1)	6.7 (0.1)	9.2 (0.6)
no mutation	with waste	13.5 (1.7)	4.3 (0.2)	339.1 (2.1)	5.7 (1.1)	68.1 (2.8)
	no waste	1.7 (0.7)	7 (0.4)	442.1 (10.6)	1.3 (0.1)	9.8 (2.5)

There were significant differences between simulations with and without waste production. In simulations without waste production, one or a few types soon established themselves and dominated the community dynamics. In simulations with waste production, the overall picture is dynamic – many types persisted for a significant length of time, the dominant types changed – and this process did not seem to end. To visualise the evolution of diversity in the model, a cumulative evolutionary activity measure was used. The cumulative evolutionary activity of an individual type j at a time t_i is given by $\sum_{t=0}^{t=t_i} N_j(t)$ where $N_j(t)$ is the number of individuals of type j at a time t (Bedau *et al.* 1998). Figure 6.6 a) shows the development of diversity in a simulation without waste production, and Figure 6.6 b) in a simulation with waste production. Among persisting types, each type could be matched up to other types with which mutualistic relationships were possible. For example, during a simulation one of the dominant types had a template '1111 1010'. During the same time, its exact opposite '0000 0101' (*i.e.* the best partner for mutualism) existed on the lattice in similar abundance, and 4 of its close opposites, with only one defective bit, existed on the lattice as well. This situation was typical for all persisting types.

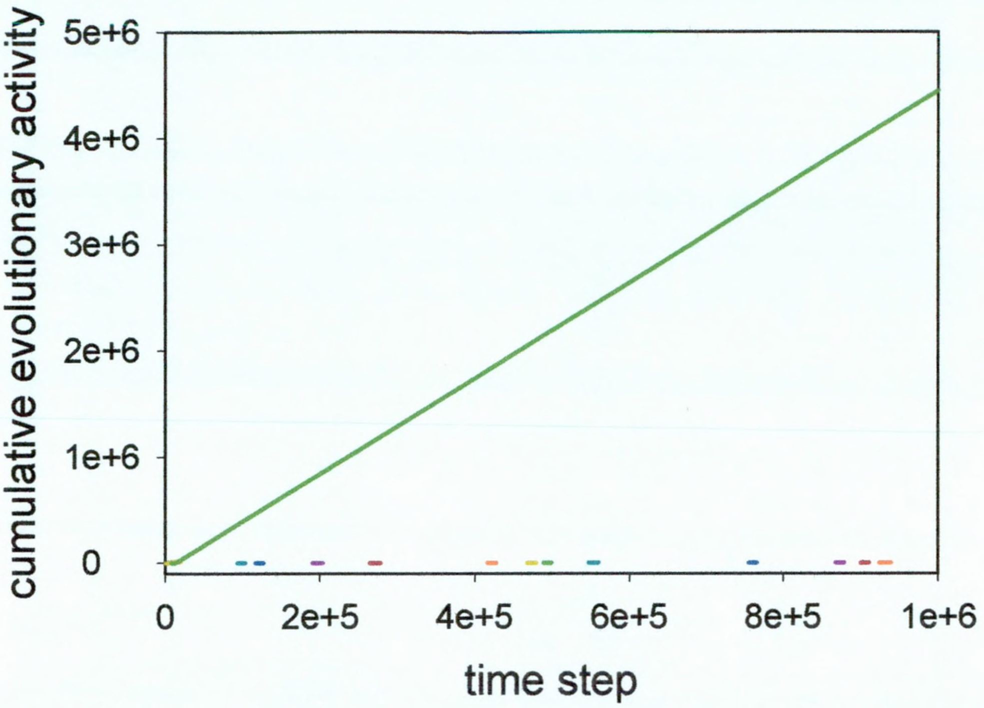


Fig. 6.6 a) Example of a cumulative evolutionary activity plot for a simulation without waste production. One type (with template of '1111 1111') dominates, with a few closely related types arising in small numbers.

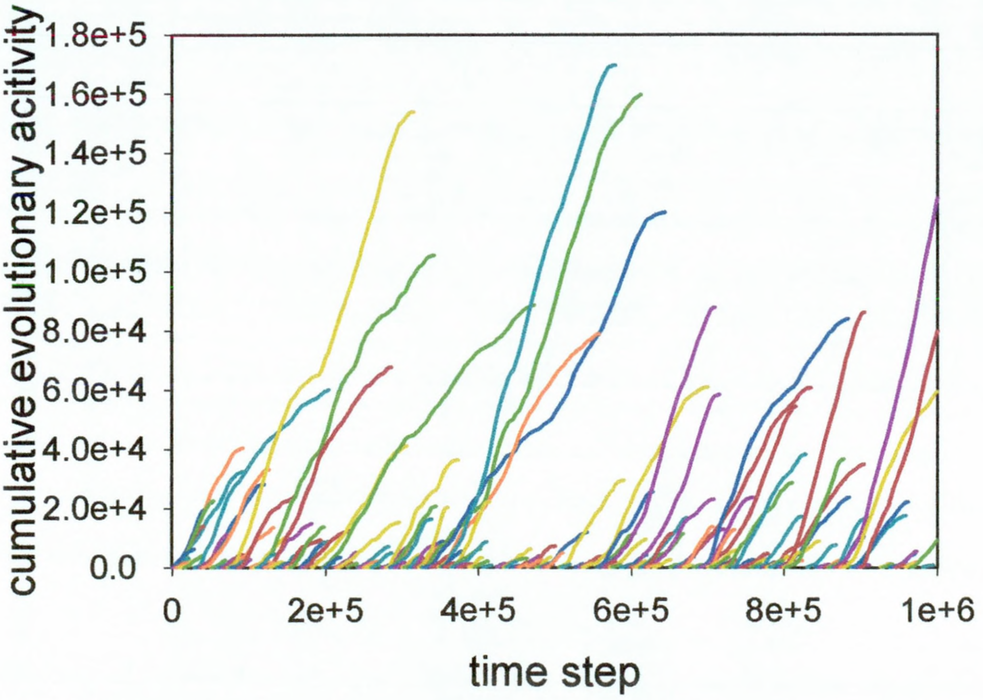


Fig. 6.6 b) Cumulative evolutionary activity plot in a simulation with waste production.

Figure 6.6 Comparison of simulation output with and without waste production (both with mutation). The simulations with waste production is much more dynamic.

Comparison of community characteristics in the cases with and without waste production is shown in Table 6.8. Both cumulative number of types and number of persisting types are higher in the case with waste production. This indicates that waste production promoted community diversity. Both with and without mutation, the number of '1's in templates of persisting types T_{ones} was lower with waste production than without. This means that with waste production, the persisting templates were not as adapted to the basic resource, as they could 'adapt' to each other. That is, with waste production, the range of diversity in a community was wider. The cumulative number of individuals, however, was lower with waste production. This was because the types that persisted due to mutualistic relationships were not as good at exploiting the basic resource. Moreover, these types produced waste which was detrimental to themselves (see the description of the matching scheme).

The average resource capture area of organisms tended to be large in cases with waste production, and small in cases without. The large resource capture area was advantageous when mutualistic relationships were possible, as this increased the chance of acquiring resource packets which were the 'waste' of another organism. Without waste production, no such pressure existed. In this case, the advantage of having a small resource capture area was that an organism had a high chance of requesting a resource packet from its own cell, thus avoiding competition.

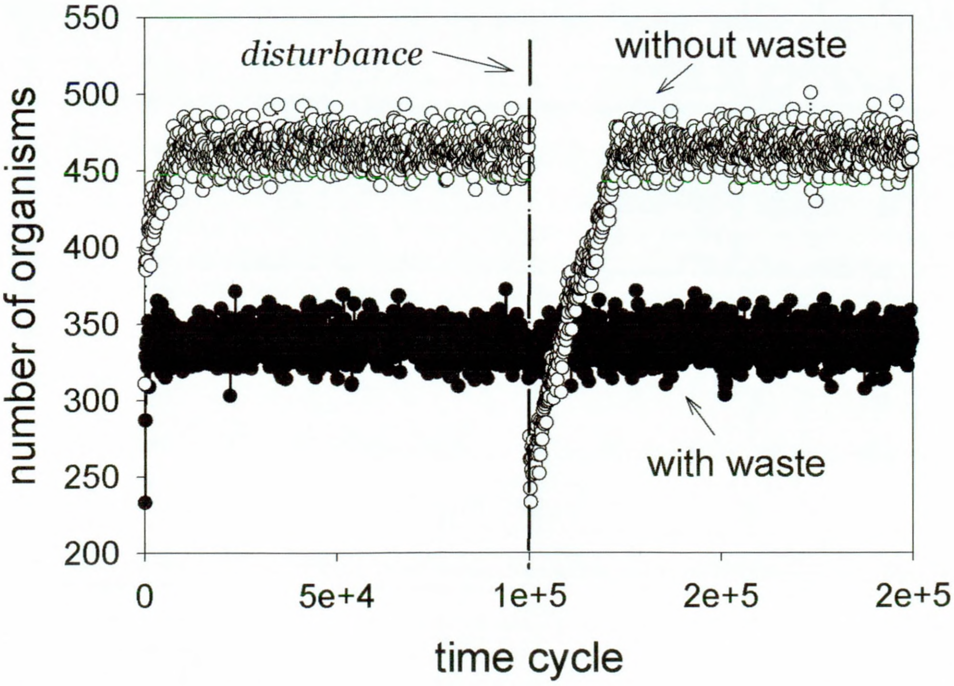


Figure 6.7 Response of communities to a change in the basic resource bias in the middle of a simulation.

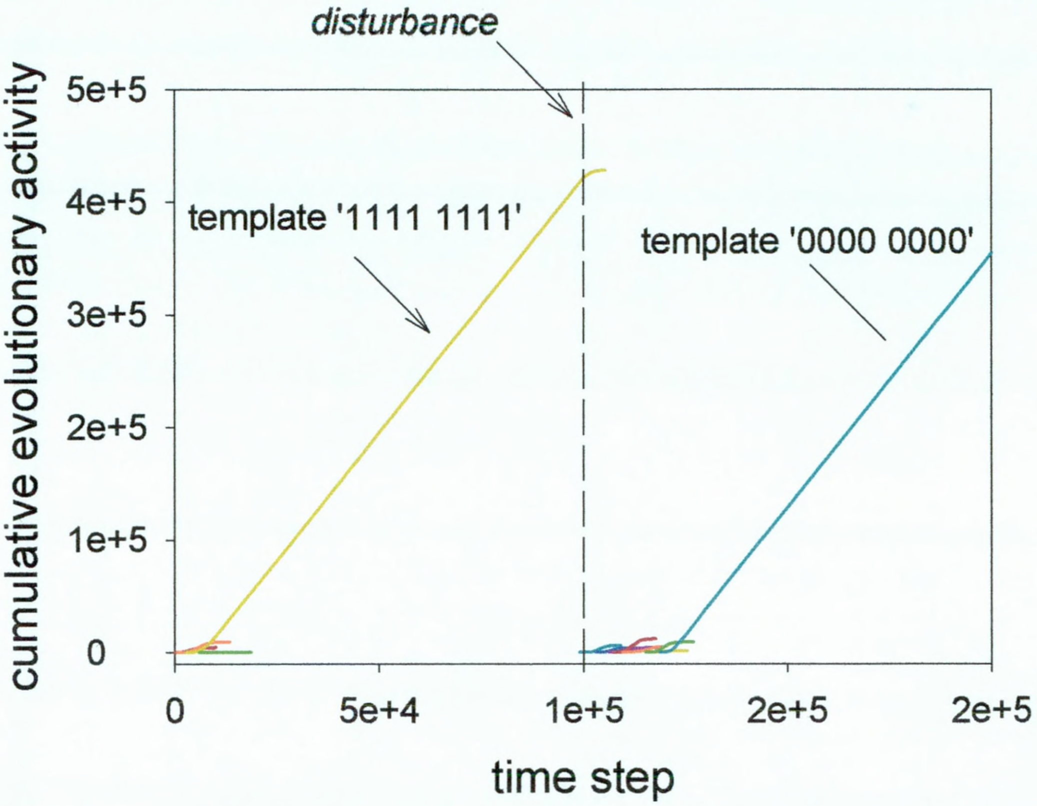


Fig. 6.8 a) Cumulative evolutionary activity plot in a simulation with disturbance of communities without waste production. In the first half of the simulation the basic resource packet is '1111 1111', and therefore the dominant type has a template '1111 1111'. In the second half of the simulation the basic resource packet is changed to '0000 0000', and the dominant type emerges with template '0000 0000'.

6.6.2 Effects of mutualistic relationships on community stability

The previous results show that mutualistic relationships in the model expanded the range of individual types able to persist in a community. In order to investigate whether such an expansion had any effect on the stability of the system, the system was subjected to an environmental disturbance. This was achieved by switching the basic resource packet from '1111 1111' to '0000 0000' in the middle of a simulation. Five simulations were performed for each of two configurations: with waste production, and without waste production (with mutation in both cases). The simulations were run for 200,000 time steps. Figure 6.7 shows the number of individuals on the lattice over time. In both cases communities survived the disturbance, but communities with waste production were less affected by the change. Figure 6.8 shows the cumulative

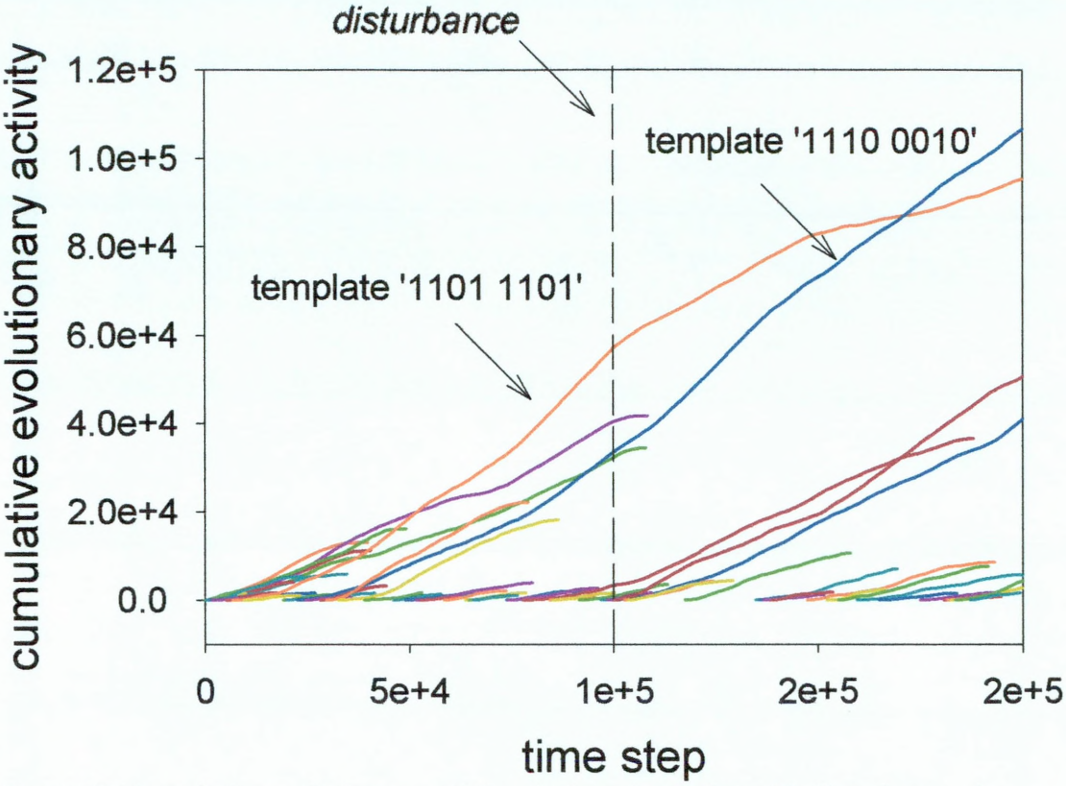


Fig. 6.8 b) Cumulative evolutionary activity plot in a simulation with disturbance of communities with waste production. In the first half of the simulation the basic resource packet is '1111 1111', and in the second half of the simulation the basic resource packet is changed to '0000 0000'. While some types go extinct after the disturbance, some of the types persist (*e.g.* two types with templates '1101 1101' and '1110 0010').

Figure 6.8 Cumulative evolutionary activity in simulations with disturbance of communities with and without waste production.

evolutionary activity plots in two cases. Figure 6.8 a) shows that in case without waste production, one dominant type changes to another once the bias in the type of basic resource packet is changed. On the other hand, Figure 6.8 b) shows that, in a case with waste production, activity is not as affected by the change in the resource bias. Some of the types do go extinct when the disturbance is introduced, but some do not. Since the types in mutualistic relationships do not rely on the basic resource packet to the same extent, the type composition does not change as drastically with the change in the basic resource packet.

6.7 Discussion

A model with the possibility of simple mutualistic interactions among individuals was presented. The mutualistic interactions occurred through resource interactions. Individuals digested resources and deposited 'waste', which could be used by other individuals (Figure 6.2). In some cases, the 'waste' of one organism was beneficial for another organism and vice versa. This allowed mutualistic interactions to occur. However, since the organisms took up resources locally and at random, it was not obvious whether the mutualistic relationships could be established. The fact that they were shows that individuals did not need sensory perceptions or mobility (although organism types 'move' when organisms disperse seed) to form relationships. It was enough to have a sufficient area over which the individuals could look for resources.

Mutualistic relationships formed within a wide range of parameter values, and affected population size, community diversity, and community composition. The dynamics of communities was explored when an environmental pressure on a community was imposed: a certain type of resource was more abundant than others. In a situation without mutualistic interactions, the community diversity quickly disappeared and the type most adapted to the environment survived. The possibility of mutualistic relationships broadened the range of types of organisms that survived in a particular environment. This occurred because the organisms in mutualistic relationships could compete with organisms of the type that was most adapted to the environment. This had an interesting effect on population. In particular, the size of the populations was smaller when the mutualistic relationships formed. The population size in the model depended on the number of offspring produced. This, in turn, depended on the amount of utility points gained by organisms. The individuals in mutualistic relationships, while they were able to compete with the most adapted type, were not able to produce as many offspring as the individuals that were best adapted to the environment. This resembles the situation in the previous chapter, in which the productivity and population levels in diverse communities were lower than in homogeneous communities.

In the presence of mutualistic interactions, the community was continually evolving. Instead of some relationships establishing and remaining dominant, many types became dominant and then went extinct, and this process did not seem to end (Figure 6.6 b). Since the dominance of the mutualistic relationships depended on organisms finding the 'waste' of their counterpart, there was a stochastic element in the process. This was sufficient to generate instabilities that allowed other dominant types to arise.

Early works in artificial life modelling have designed systems where mutualistic relationships were possible (Barricelli 1962, 1963, Conrad and Patee 1970) with the aim to evolve complex organism behaviours. In that they were not successful. Later artificial life system such as Tierra designed by Ray (Ray 1991) and Echo developed by Holland (Holland 1995, Hraber *et al.* 1997), explored evolution of trophic interactions. However, the key ingredient to developing of complex interactions in systems is still unknown. Two avenues of research may provide the answer: increasing the complexity of the environment and individual capabilities, and designing a system which incorporates the potential for the evolution of complexity. The aim of this model was to approach a question of evolution of behaviour with increasing complexity by allowing evolution of relationships, instead of pre-defining them.

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

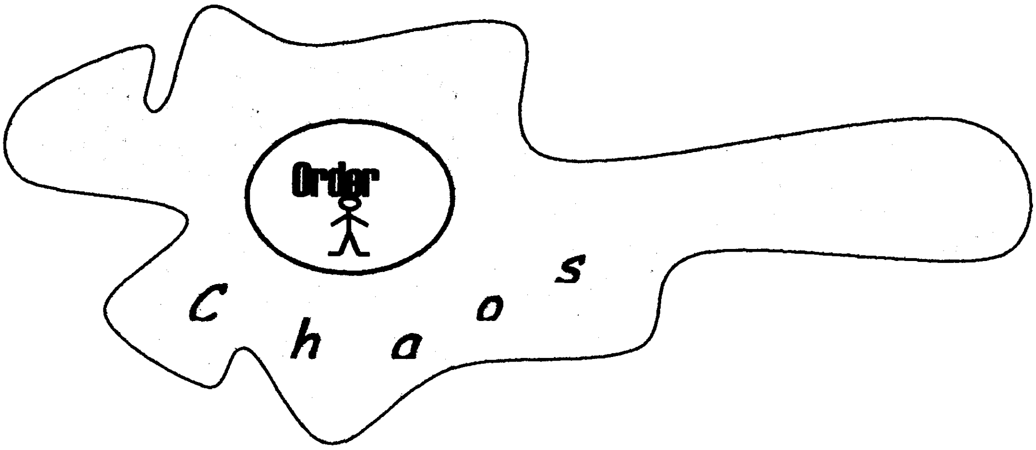


Figure 7.1 World as a sphere of order surrounding humans, and 'chaos' around.

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^2 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

Appendix A. Linear stability analysis

The system in question is

$$\begin{cases} \dfrac{\partial F}{\partial \tau} = -\lambda \dfrac{\partial H}{\partial \lambda} \dfrac{1}{H(\lambda,\tau)} - F(\lambda,\tau) \\ -\dfrac{\partial^2 H}{\partial \tau \partial \lambda} = P(\lambda)F(\lambda,\tau) + C\lambda \dfrac{\partial H}{\partial \lambda} \end{cases} \qquad \text{(A.1)}$$

Put $H(\lambda,\tau)=h(\lambda)+\tilde{h}(\lambda,\tau)$ and $F(\lambda,\tau)=f(\lambda)+\tilde{f}(\lambda,\tau)$ where (0, 1) and (*f*, *h*) are steady states.

Expanding (A.1) about the steady state gives

$$\begin{cases} \dfrac{\partial \tilde{f}}{\partial \tau} = -\lambda \dfrac{\partial}{\partial \lambda}\left(h(\lambda)+\tilde{h}(\lambda,\tau)\right) \dfrac{1}{h(\lambda)+\tilde{h}(\lambda)} - \left(f(\lambda)+\tilde{f}(\lambda,\tau)\right) \\ -\dfrac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda} = P\left(f(\lambda)+\tilde{f}(\lambda,\tau)\right) + C\lambda \dfrac{\partial}{\partial \lambda}\left(h(\lambda)+\tilde{h}(\lambda,\tau)\right) \end{cases} \qquad \text{(A.2)}$$

A.1 Steady state (0, 1)

In this case, (A.2) becomes

$$\frac{\partial \tilde{f}}{\partial \tau} = -\lambda \frac{\partial \tilde{h}(\lambda,\tau)}{\partial \lambda} \frac{1}{1+\tilde{h}(\lambda,\tau)} - \tilde{f}(\lambda,\tau)$$

$$-\frac{\partial^2 \tilde{h}}{\partial \lambda \partial \tau} = P\tilde{f}(\lambda,\tau) + C\lambda \frac{\partial \tilde{h}}{\partial \lambda}$$

This can be expressed as

$$\left[1+\tilde{h}(\lambda,\tau)\right]\frac{\partial \tilde{f}}{\partial \tau} = -\lambda \frac{\partial \tilde{h}(\lambda,\tau)}{\partial \lambda} - \left(1+\tilde{h}(\lambda,\tau)\right)\tilde{f}(\lambda,\tau)$$

$$-\frac{\partial^2 \tilde{h}}{\partial\tau\partial\lambda} = P\tilde{f}(\lambda,\tau)+C\lambda\frac{\partial \tilde{h}}{\partial\lambda}$$

and retaining terms to $O(\tilde{h})$ and $O(\tilde{f})$

$$\begin{cases} \dfrac{\partial \tilde{f}}{\partial\tau} = -\lambda\dfrac{\partial \tilde{h}}{\partial\lambda} - f(\tilde{\lambda},\tau) \\ -\dfrac{\partial^2 \tilde{h}}{\partial\tau\lambda} = P\tilde{f}(\lambda,\tau)+C\lambda\dfrac{\partial \tilde{h}}{\partial\lambda} \end{cases} \qquad \text{(A.3)}$$

Substituting $h' = \frac{\partial \tilde{h}}{\partial\lambda}$ into (A.3)

$$\frac{\partial \tilde{f}}{\partial\tau} = -\lambda h' - \tilde{f}(\lambda,\tau) \qquad \text{(A.4)}$$

$$\frac{\partial h'}{\partial\tau} = -P\tilde{f}(\lambda,\tau) - C\lambda h' \qquad \text{(A.5)}$$

Differentiating (A.5) with respect to time,

$$\frac{\partial^2 \tilde{h}}{\partial\tau^2} = -P\frac{\partial \tilde{f}}{\partial\tau} - C\lambda\frac{\partial h'}{\partial\tau}$$

and substituting (A.4),

$$\frac{\partial^2 h'}{\partial\tau^2} = -P\left[-\lambda h' - \tilde{f}(\lambda,\tau)\right] - C\lambda\frac{\partial h'}{\partial\tau}$$

or

$$\frac{\partial^2 h'}{\partial\tau^2} + P\left[-\lambda h' - \tilde{f}(\lambda,\tau)\right] + C\lambda\frac{\partial h'}{\partial\tau} = 0 \qquad \text{(A.6)}$$

where

$$-\tilde{f} = \frac{1}{P}\frac{\partial h'}{\partial\tau} + \frac{C}{P}\lambda h'$$

then (A.6) becomes

$$\frac{\partial^2 h'}{\partial \tau^2}+P\left[-\lambda h'+\frac{1}{P}\frac{\partial h'}{\partial \tau}+\frac{C}{P}\lambda h'\right]+C\lambda\frac{\partial h'}{\partial \tau}=0$$

or

$$\frac{\partial^2 h'}{\partial \tau^2}-\lambda h'P+C\lambda h'+\frac{\partial h'}{\partial \tau}+C\lambda\frac{\partial h'}{\partial \tau}=0$$

and therefore,

$$\frac{\partial^2 h'}{\partial \tau^2}+\left(1+C\lambda\right)\frac{\partial h'}{\partial \tau}+\left(C-P\right)\lambda h'=0 \qquad \text{(A.7)}$$

Similarly, differentiating (A.4) with respect to time

$$\frac{\partial^2 \tilde{f}}{\partial \tau^2}=-\lambda\frac{\partial h'}{\partial \tau}-\frac{\partial \tilde{f}}{\partial \tau}$$

and substituting (A.5) gives

$$\frac{\partial^2 \tilde{f}}{\partial \tau^2}=-\lambda\left[-P\tilde{f}-C\lambda h'\right]-\frac{\partial \tilde{f}}{\partial \tau}$$

From (A.4)

$$-\lambda h'=\frac{\partial \tilde{f}}{\partial \tau}+\tilde{f}\left(\lambda,\tau\right)$$

Therefore,

$$\frac{\partial^2 f}{\partial \tau^2}=-\lambda\left[-P\tilde{f}+C\frac{\partial \tilde{f}}{\partial \tau}+C\tilde{f}\left(\lambda,\tau\right)\right]-\frac{\partial \tilde{f}}{\partial \tau}$$

or

$$\frac{\partial^2 \tilde{f}}{\partial \tau^2}+\lambda\tilde{f}\left(C-P\right)+\frac{\partial \tilde{f}}{\partial \tau}+\lambda C\frac{\partial \tilde{f}}{\partial \tau}=0$$

and therefore,

$$\frac{\partial^2 \tilde{f}}{\partial \tau^2}+\left(1+C\lambda\right)\frac{\partial \tilde{f}}{\partial \tau}+\left(C-P\right)\lambda\tilde{f}=0 \qquad \text{(A.8)}$$

The characteristic polynomial for (A.7) and (A.8) is

$$m^2+(1+C\lambda)m+\lambda(C-P)=0$$

When

with roots given by

$$m=\frac{1}{2}\left[-(1+C\lambda)\pm\sqrt{(1+C\lambda)^2-4\lambda(C-P)}\right]$$

Now the radical is

$$(1+C\lambda)^2-4\lambda(C-P)$$

$$=1+2C\lambda+C^2\lambda^2-4C\lambda+4\lambda P$$

$$=1-2C\lambda+C^2\lambda^2+4\lambda P$$

With with $=(1-C\lambda)^2+4\lambda P>0$

Therefore, roots are real.

Roots are negative definite iff

$1+C\lambda>0$ (true)

and $C-P>0$

Therefore, the system is linearly stable (exponentially) provided $P/C<1$.

Therefore, (0, 1) is a stable node if $P/C<1$. It is sufficient to show that *f*=0 is stable, since if there are no flowers, the seeds cannot be produced.

Note that even is we prove stability for *h*', *e.g.* suppose $h'=e^{-m\tau}g(\lambda)$ then

$\tilde{h}=\int h'd\lambda=e^{-m\tau}\int g(\lambda)d\lambda+q(\lambda)$ where $q(\lambda)$ is arbitrary so $\tilde{h}$ does not necessarily tend to zero if *h*' does. However, since *f*=0 implies that *s*=0 we must have $q(\lambda)=0$.

A.2 Steady state *(f, h)*

In this case P/C is a function of λ, otherwise *f=0.*

From equation (A.2),

$$\left(h+\tilde{h}\right)\frac{\partial \tilde{f}}{\partial \tau}=-\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right)-\left(h+\tilde{h}\right)\left(f+\tilde{f}\right)$$

and

$$-\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=P\left(f+\tilde{f}\right)+C\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right)$$

Linearise the system to get

$$h\frac{\partial \tilde{f}}{\partial \tau}=-\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right)-hf-\tilde{h}f-\tilde{f}h \tag{A.9}$$

$$-\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=P\left(f+\tilde{f}\right)+C\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right) \tag{A.10}$$

Dividing (A.10) by C gives

$$-\frac{1}{C}\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=\frac{P}{C}\left(f+\tilde{f}\right)+\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right)$$

and setting

$$p(\lambda)=\frac{P}{C},$$

$$-\frac{1}{C}\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=p\left(f+\tilde{f}\right)+\lambda\frac{\partial}{\partial \lambda}\left(h+\tilde{h}\right) \tag{A.11}$$

In the steady state, $h=p$ and $f=-\frac{\lambda}{p}\frac{dp}{d\lambda}$.

Using these results in (A.9) and (A.11) gives

$$\begin{cases} p\dfrac{\partial \tilde{f}}{\partial \tau}=-\lambda\dfrac{\partial}{\partial \lambda}\left(p+\tilde{h}\right)-p\left(-\dfrac{\lambda}{p}\dfrac{dp}{d\lambda}\right)-\tilde{h}\left(-\dfrac{\lambda}{p}\dfrac{dp}{d\lambda}\right)-\tilde{f}p \\ -\dfrac{1}{C}\dfrac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=p\left(-\dfrac{\lambda}{p}\dfrac{dp}{d\lambda}+\tilde{f}\right)+\lambda\dfrac{\partial}{\partial \lambda}\left(p+\tilde{h}\right) \end{cases}$$

Simplifying

$$\begin{cases} p\dfrac{\partial \tilde{f}}{\partial \tau}=-\lambda\left(\dfrac{dp}{d\lambda}+\dfrac{\partial \tilde{h}}{\partial \lambda}\right)+\lambda\dfrac{dp}{d\lambda}+\dfrac{\lambda}{p}\dfrac{dp}{d\lambda}\tilde{h}-p\tilde{f} \\ -\dfrac{1}{C}\dfrac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}=-\lambda\dfrac{dp}{d\lambda}+p\tilde{f}+\lambda\dfrac{dp}{d\lambda}+\lambda\dfrac{\partial \tilde{h}}{\partial \lambda} \end{cases}$$

$$\begin{cases} p\dfrac{\partial \tilde{f}}{\partial \tau} = -\lambda\dfrac{\partial \tilde{h}}{\partial \lambda} + \dfrac{\lambda}{p}\dfrac{dp}{d\lambda}\tilde{h} - p\tilde{f} \\ -\dfrac{1}{C}\dfrac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda} = p\tilde{f} + \lambda\dfrac{\partial \tilde{h}}{\partial \lambda} \end{cases} \tag{A.12}$$

Substituting for $p\tilde{f}+\lambda\frac{\partial \tilde{h}}{\partial \lambda}$ in the first equation of (A.12) using the second equation gives

$$p\frac{\partial \tilde{f}}{\partial \tau} = \frac{1}{C}\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda} + \frac{\lambda}{p}\frac{dp}{d\lambda}\tilde{h} \tag{A.13}$$

Now, the second equation in (A.12) can be rewritten as

$$p\tilde{f} = -\frac{1}{C}\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda} - \lambda\frac{\partial \tilde{h}}{\partial \lambda}$$

and differentiating with respect to τ gives

$$p\frac{\partial \tilde{f}}{\partial \tau} = -\frac{1}{C}\frac{\partial^3 h}{\partial^2 \tau \partial \lambda} - \lambda\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda}$$

Using this in (A.13) gives

$$\frac{1}{C}\frac{\partial^3 \tilde{h}}{\partial^2 \tau \partial \lambda} + \lambda\frac{\partial^2 \tilde{h}}{\partial \lambda \partial \tau} + \frac{1}{C}\frac{\partial^2 \tilde{h}}{\partial \tau \partial \lambda} + \frac{\lambda}{p}\frac{dp}{d\lambda}\tilde{h} = 0$$

First equation in (A.12) can be rewritten as

$$\frac{\partial \tilde{f}}{\partial \tau} = -\frac{\lambda}{p}\frac{\partial \tilde{h}}{\partial \lambda} + \frac{\lambda}{p^2}\frac{dp}{d\lambda}\tilde{h} - \tilde{f}$$

i.e.

$$\frac{\partial \tilde{f}}{\partial \tau} = -\lambda\left[\frac{1}{p}\frac{\partial \tilde{h}}{\partial \lambda} - \frac{1}{p^2}\frac{dp}{d\lambda}\tilde{h}\right] - \tilde{f}$$

i.e.

$$\frac{\partial \tilde{f}}{\partial \tau} = -\lambda\frac{\partial}{\partial \lambda}\left[\frac{\tilde{h}}{p}\right] - \tilde{f}$$

and finally,

$$\frac{\partial \tilde{f}}{\partial \tau} + \tilde{f} = -\lambda\frac{\partial}{\partial \lambda}\left[\frac{\tilde{h}}{p}\right] \tag{A.14}$$

Look for separable solutions to (A.14) of the form $\tilde{h} = e^{\delta\tau}L(\lambda)$, then (A.14) can be rewritten as

$$\frac{\partial \tilde{f}}{\partial \tau} + \tilde{f} = -\lambda \frac{\partial}{\partial \lambda}\left[\frac{e^{\delta\tau}L}{p}\right]$$

i.e.

$$\frac{\partial \tilde{f}}{\partial \tau} + \tilde{f} = u(\lambda)e^{\delta\tau} \qquad \text{(A.15)}$$

where

$$u(\lambda) = -\lambda \frac{d}{d\lambda}\left(\frac{L}{p}\right)$$

with solution

Toward

for *v* some arbitrary function of λ and $\delta \neq -1$.

If $\delta = -1$ then (A.15) is

$$\frac{\partial \tilde{f}}{\partial \tau} + \tilde{f} = u(\lambda)e^{-\tau}$$

with solution

$$\tilde{f} = \tau e^{-\tau}u(\lambda) + v(\lambda)e^{-\tau}$$

i.e. $\tilde{f}$ and $\tilde{h}$ → 0 when $\tau \to \infty$ which implies stability of $\tilde{f}$ and $\tilde{h}$ for $\delta = -1$.

Now, consider the consequences for *F* and *H*.

Note that

$$H = p + \tilde{h} = p + e^{-\tau}L(\lambda) = 1 + \int_{\lambda}^{1} s(l,\tau)\,dl$$

Differentiating with respect to λ

$$\frac{dp}{d\lambda} + e^{-\tau}\frac{dL}{d\lambda} = -s(\lambda,\tau)$$

and in the limit $\tau \to \infty$, we have

$$\frac{dp}{d\lambda} = -s(\lambda,\tau_\infty)$$

Since $s(\lambda,\tau_\infty) > 0 \forall \lambda \Rightarrow \frac{dp}{d\lambda} < 0$. (A.16)

If $\delta \neq 1$, then

$$\tilde{f} = \frac{e^{\delta\tau}}{\delta + 1}u(\lambda) + v(\lambda)e^{-\tau}$$

where $u(\lambda) = -\lambda\frac{d}{d\lambda}\left(\frac{L}{p}\right)$

and

$$\tilde{h} = e^{\delta\tau}L(\lambda)$$

with arbitrary $v(\lambda)$.

Now, the second equation of (A.12) can be written as

$$-\frac{1}{C}\delta e^{\delta\tau}\frac{dL}{d\lambda} = -p\lambda\frac{d}{d\lambda}\left(\frac{L}{p}\right)\frac{e^{\delta\tau}}{\delta+1} + pv(\lambda)e^{\delta\tau} + \lambda e^{\delta\tau}\frac{dL}{d\lambda}$$

$$\frac{1}{C}\delta\frac{dL}{d\lambda} - p\lambda\frac{1}{\delta+1}\frac{d}{d\lambda}\left(\frac{L}{p}\right) + pv(\lambda) + \lambda\frac{dL}{d\lambda} = 0$$

$$\left(\frac{1}{C}\delta + \lambda\right)\frac{dL}{d\lambda} + pv(\lambda) - \frac{p\lambda}{\delta+1}\left[\frac{p\frac{dL}{d\lambda} - L\frac{dp}{d\lambda}}{p^2}\right] = 0$$

$$\left(\frac{\delta}{C} + \lambda\right)(\delta+1)\frac{dL}{d\lambda} + (\delta+1)pv(\lambda) - \frac{\lambda}{p}\left[p\frac{dL}{d\lambda} - L\frac{dp}{d\lambda}\right] = 0$$

$$\left[\left(\frac{\delta}{C} + \lambda\right)(\delta+1) - \lambda\right]\frac{dL}{d\lambda} + (\delta+1)pv(\lambda) + \frac{\lambda}{p}L\frac{dp}{d\lambda} = 0$$

$$\left[\frac{\delta^2}{C} + \delta\lambda + \frac{\delta}{C} + \lambda - \lambda\right]\frac{dL}{d\lambda} + (\delta+1)pv(\lambda) + \frac{\lambda}{p}L\frac{dp}{d\lambda} = 0$$

$$\left[\frac{1}{C}\delta^2 + \lambda\delta + \frac{1}{C}\delta\right]\frac{dL}{d\lambda} + (\delta+1)pv(\lambda) + \frac{\lambda}{p}L\frac{dp}{d\lambda} = 0$$

$$\left(\frac{1}{C}\delta^2 + \left(\lambda + \frac{1}{C}\right)\delta\right)\frac{1}{L}\frac{dL}{d\lambda} + \frac{(\delta+1)pv(\lambda)}{L(\lambda)} + \frac{\lambda}{p}\frac{dp}{d\lambda} = 0 \qquad \text{(A.17)}$$

Return to consider possible forms of $v(\lambda)$

$$\tilde{f} = \frac{e^{\delta\tau}}{\delta + 1}u(\lambda) + v(\lambda)e^{-\tau}$$

where $\delta \neq -1$

Now, since $\delta \neq -1$ => $\tilde{f} = \frac{e^{\delta\tau}}{\delta+1}u(\lambda)\left[1 + (\delta+1)\frac{v(\lambda)}{u(\lambda)}e^{-(1+\delta)\tau}\right]$

If $\delta > -1$ and $\tau \to \infty$, $\tilde{f} = \frac{e^{\delta\tau}}{\delta+1}u(\lambda)$

If $\delta < -1$ => $\tilde{f} = v(\lambda)e^{-\tau}$ as $\tau \to \infty$ and this is stable for $\frac{dp}{d\lambda} < 0$ from equation (A.16).

Therefore, $\delta \le -1$ gives rise to stable solutions.

Now consider $\delta > -1$.

Then $\tilde{f} = \frac{e^{\delta\tau}}{\delta+1}u(\lambda)$ for large τ.

Substituting this into the second equation of (A.12) gives a simple form of equation (A.17), *i.e.*

$$\delta\left[\frac{\delta}{C}+\lambda+\frac{1}{C}\right] = \frac{-\frac{\lambda}{p}\frac{dp}{d\lambda}}{\frac{1}{L}\frac{dL}{d\lambda}} = w(\lambda)$$

but *L*(*λ*) is still arbitrary since *w*(λ) can be positive or negative.

If $w(\lambda) > 0 \Rightarrow \delta > 0$ or $\delta < -c\lambda - 1$.

But $\delta > -1$ and therefore, $w(\lambda) > 0 \Rightarrow \delta > 0$.

If $w(\lambda) < 0 \Rightarrow -(c\lambda + 1) < \delta < 0$.

But $\delta < -1$ and therefore, $-1 < \delta < 0$.

Therefore, dependently on the form of *L*(*λ*), it is possible that $\delta > 0$, and therefore, the system may not be stable. Therefore, *L*(*λ*) needs to be constrained with additional boundary conditions. At present, it is not clear what these should be.

Appendix B. An extension of the discrete model with two populations

An extension of the analysis for two populations of the discrete system from Ch. 2, section 2.6.2 is presented in this appendix. Consider a system of n populations with values λ_1, λ_2, ..., λ_n with $\lambda_1 < \lambda_2 < ... < \lambda_n$ and evenly spaced with λ-step $\Delta\lambda$. Suppose these populations are affecting each other through competition and no other population are affecting them. The system is

$$\begin{cases} \dfrac{dF_i}{d\tau} = \dfrac{\lambda_i S_i(\tau)}{1+(\Delta\lambda)\sum\limits_{j=1}^{n} S_j(\tau)} - F_i(\tau) = g_i \\ \dfrac{dS_i}{d\tau} = P_i F_i(\tau) - C\lambda_i S_i(\tau) = h_i \end{cases}$$

where g_i is a function of F_1, ..., F_n, S_1, ..., S_n.

Let f_1, s_1, f_2, s_2, ..., f_n and s_n be the steady state solutions. Then, the possible steady states for this system are the trivial steady state $\{f_1, s_1, f_2, s_2, ..., f_n, s_n\} = \{0, ..., 0\}$ and

$$\{f_1, s_1, f_2, s_2, ..., f_n, s_n\} = \begin{cases} f_i \neq 0, s_i \neq 0, \text{ for } i = i_1, i_2, ..., i_k \text{ with } 1 \leq k \leq n, \\ f_j = 0, s_j = 0 \quad \forall\ j \neq i. \end{cases}$$

In the non-zero steady state

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_1}}{C}$$

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_2}}{C}$$

$$\vdots$$

$$1+(\Delta\lambda)(s_{i_1} + s_{i_2} + ... + s_{i_k}) = \frac{P_{i_k}}{C}$$

This is only possible if $P_{i_1} = P_{i_2} = \ldots = P_{i_k}$. Say $P_0 = P_{i_1} = P_{i_2} = \ldots = P_{i_k}$. In that case the populations can coexist, and their values are determined by the initial conditions and by the relationship

$$1 + (\Delta\lambda)(s_{i_1} + s_{i_2} + \ldots + s_{i_k}) = \frac{P_0}{C} \qquad \textbf{(B.1)}$$

and therefore

$s_{i_1} + s_{i_2} + \ldots + s_{i_k} = \dfrac{1}{(\Delta\lambda)}\left(\dfrac{P_0}{C} - 1\right)$. This is the only constraint, and having picked the values of s_i, f_i can be found by

$$f_i = \frac{C\lambda_i s_i}{P_0}.$$

For the linear stability analysis, first consider the case when $P_0 = P_1 = P_2 = \ldots = P_n$, *i.e.* all peaks have the same value of P_0, and they all survive. A short description of the linear stability analysis is presented in Appendix A, section A.0.

The Jacobian matrix is defined by

$$M = \begin{bmatrix} \frac{\partial g_1}{\partial f_1} & \frac{\partial g_1}{\partial f_2} & \cdots & \frac{\partial g_1}{\partial f_n} & \frac{\partial g_1}{\partial s_1} & \cdots & \frac{\partial g_1}{\partial s_n} \\ \vdots & \ddots & & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial g_n}{\partial f_1} & \frac{\partial g_n}{\partial f_2} & \cdots & \frac{\partial g_n}{\partial f_n} & \frac{\partial g_n}{\partial s_1} & \cdots & \frac{\partial g_n}{\partial s_n} \\ \frac{\partial h_1}{\partial f_1} & \cdots & & \frac{\partial h_1}{\partial f_n} & \frac{\partial h_1}{\partial s_1} & \cdots & \frac{\partial h_1}{\partial s_n} \\ \vdots & \ddots & & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial h_n}{\partial f_1} & \cdots & & \frac{\partial h_n}{\partial f_n} & \frac{\partial h_n}{\partial s_1} & \cdots & \frac{\partial h_n}{\partial s_n} \end{bmatrix}$$

where

$\dfrac{\partial h_i}{\partial f_i} = P_0$, $\dfrac{\partial h_i}{\partial f_j} = 0$ when $i \neq j$, $\dfrac{\partial h_i}{\partial s_i} = -C\lambda_i$, $\dfrac{\partial h_i}{\partial s_j} = 0$, when $i \neq j$,

$\dfrac{\partial g_i}{\partial f_i} = -1$, $\dfrac{\partial g_i}{\partial f_j} = 0$ when $i \neq j$.

On the other hand $\frac{\partial g_i}{\partial s_i}$ and $\frac{\partial g_i}{\partial s_j}$ (when $i \neq j$) are more complicated, so leave them as they are for now.

$$M = \begin{bmatrix} \overbrace{\begin{matrix} -1 & & 0 \\ & \ddots & \\ 0 & & -1 \end{matrix}}^{n\times n} & \begin{matrix} \frac{\partial g_1}{\partial s_1} & \cdots & \frac{\partial g_1}{\partial s_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial g_n}{\partial s_1} & \cdots & \frac{\partial g_n}{\partial s_n} \end{matrix} \\ \begin{matrix} P_0 & & 0 \\ & \ddots & \\ 0 & & P_0 \end{matrix} & \underbrace{\begin{matrix} -C\lambda_1 & & 0 \\ & \ddots & \\ 0 & & -C\lambda_n \end{matrix}}_{n\times n} \end{bmatrix}$$

This can be transformed into

$$M^* = \begin{bmatrix} -1 & & & 0 & \frac{\partial g_1}{\partial s_1} & \cdots & & \frac{\partial g_1}{\partial s_1} \\ & \ddots & & & \vdots & \ddots & & \vdots \\ 0 & & & -1 & \frac{\partial g_n}{\partial s_1} & \cdots & & \frac{\partial g_n}{\partial s_n} \\ 0 & \cdots & \cdots & 0 & -C\lambda_1 + P_0\frac{\partial g_1}{\partial s_1} & P_0\frac{\partial g_1}{\partial s_2} & \cdots & P_0\frac{\partial g_1}{\partial s_n} \\ \vdots & \ddots & & \vdots & P_0\frac{\partial g_2}{\partial s_1} & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \vdots & \vdots & \ddots & \ddots & P_0\frac{\partial g_{n-1}}{\partial s_n} \\ 0 & \cdots & \cdots & 0 & P_0\frac{\partial g_n}{\partial s_1} & \cdots & P_0\frac{\partial g_n}{\partial s_{n-1}} & P_0\frac{\partial g_n}{\partial s_n} \end{bmatrix}$$

This can be achieved by multiplying the first row of M by P_0, and subtract from row $(n+1)$, then multiply the second row by P_0 and subtract from row $(n+2)$, etc.

Now, $\det M = \det M^* = (\det B)(\det C)$ (B.2)

where

$$B = \begin{bmatrix} \underbrace{\begin{matrix} -1 & & 0 \\ & \ddots & \\ 0 & & -1 \end{matrix}}_{n\times n} \end{bmatrix} \text{ and } \det B = (-1)^n$$

and

$$C = \begin{bmatrix} -C\lambda_1 + P_0 \frac{\partial g_1}{\partial s_1} & P_0 \frac{\partial g_1}{\partial s_2} & \cdots & P_0 \frac{\partial g_1}{\partial s_n} \\ P_0 \frac{\partial g_2}{\partial s_1} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & P_0 \frac{\partial g_{n-1}}{\partial s_n} \\ P_0 \frac{\partial g_n}{\partial s_1} & \cdots & P_0 \frac{\partial g_n}{\partial s_{n-1}} & -C\lambda_n + P_0 \frac{\partial g_n}{\partial s_n} \end{bmatrix}$$

Consider the expressions in the matrix C

$$\frac{\partial g_i}{\partial s_i} = \frac{\left(1+(\Delta\lambda)\sum_{i=1}^{n} s_i\right)\lambda_i - s_i\lambda_i(\Delta\lambda)}{\left(1+(\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} = \lambda_i \frac{1+(\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)}{\left(1+(\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} \tag{B.3}$$

For *i≠j*

$$\frac{\partial g_i}{\partial s_j} = -\lambda_i \frac{(\Delta\lambda)s_i}{\left(1+(\Delta\lambda)\sum_{i=1}^{n} s_i\right)^2} \tag{B.4}$$

Using (B.1)

$$1+(\Delta\lambda)(\sum_{m=1}^{n} s_m) = \frac{P_0}{C} \tag{B.5}$$

(B.3) and (B.4) can be rewritten as

$$\frac{\partial g_i}{\partial s_i} = \lambda_i \frac{C^2}{P_0^2}\left(1+(\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)\right) \text{ and}$$

$$\frac{\partial g_i}{\partial s_j} = -\lambda_i \frac{C^2}{P_0^2}(\Delta\lambda)s_i .$$

From each term $C\lambda_i$ can be factored out.

Then $\det C = \left(\prod_{i=1}^{n} \lambda_i\right) \det C'$

where

$$C'_{ii} = -1 + \frac{C}{P_0}\left(1 + (\Delta\lambda)\left(\sum_{m=1}^{n} s_m - s_i\right)\right)$$

and

$$C'_{ij} = -\frac{C}{P_0}(\Delta\lambda)s_i$$

where $i \neq j$.

For convenience, let $C^* = \frac{C}{P_0}$ and $s_i^* = (\Delta\lambda)s_i$. **(B.6)**

Then

$$C'_{ii} = -1 + C^*\left(1 + \left(\sum_{m=1}^{n} s^*_m - s_i\right)\right)$$

and

$$C'_{ij} = -C^* s^*_i$$

For clarity of notation omit the subscripts *, and call the new matrix *E*.

$$E = \begin{bmatrix} -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_1\right)\right) & -Cs_1 & \cdots & -Cs_1 \\ -Cs_2 & -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_2\right)\right) & \ddots & \vdots \\ \vdots & \ddots & \ddots & -Cs_{n-1} \\ -Cs_n & \cdots & -Cs_n & -1 + C\left(1 + \left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

Subtract column 2 from column 1

$$\begin{bmatrix} -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_1\right)\right)+Cs_1 & -Cs_1 & \cdots & -Cs_1 \\ 1-C\left(1+\left(\sum_{m=1}^{n} s_m - s_2\right)\right)-Cs_2 & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_2\right)\right) & & \vdots \\ 0 & & \ddots & \\ \vdots & \vdots & \ddots & -Cs_{n-1} \\ 0 & -Cs_n & \cdots\ -Cs_n & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

or

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -Cs_1 & \cdots & -Cs_1 \\ 1-C\left(1+\sum_{m=1}^{n} s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_2\right)\right) & & \vdots \\ 0 & & \ddots & \\ \vdots & \vdots & \ddots & -Cs_{n-1} \\ 0 & -Cs_n & \cdots\ -Cs_n & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

Subtract column 3 from column 2, column 4 from column 3, ..., column *n* from column *n*-1.

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 1-C\left(1+\sum_{m=1}^{n} s_m\right) & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & \vdots \\ 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -Cs_{n-1} \\ 0 & 0 & 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

Diagonalise this matrix by adding row 1 to row 2,

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -Cs_{n-1} \\ 0 & 0 & 0 & 1-C\left(1+\sum_{m=1}^{n} s_m\right) & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - s_n\right)\right) \end{bmatrix}$$

then add row 2 to row 3, row 3 to row 4, etc.

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 0 & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -C\sum_{m=1}^{n-1} s_m \\ 0 & 0 & 0 & 0 & -1+C\left(1+\left(\sum_{m=1}^{n} s_m - \sum_{m=1}^{n} s_m\right)\right) \end{bmatrix}$$

and therefore,

$$\begin{bmatrix} -1+C\left(1+\sum_{m=1}^{n} s_m\right) & 0 & \cdots & 0 & -Cs_1 \\ 0 & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & & \vdots & -Cs_2-Cs_1 \\ 0 & 0 & \ddots & 0 & \\ \vdots & \ddots & \ddots & -1+C\left(1+\sum_{m=1}^{n} s_m\right) & -C\sum_{m=1}^{n-1} s_m \\ 0 & 0 & 0 & 0 & -1+C \end{bmatrix}$$

Call the resulting matrix E'. Now,

$$\det E = \det E' = \left(-1+C\left(1+\sum_{m=1}^{n} s_m\right)\right)^{n-1}(1-C). \qquad \text{(B.7)}$$

Note that since (B.6), C in (B.7) actually stands for $\frac{C}{P_0}$, and s_m stands for $(\Delta\lambda)s_m$.

Therefore,

$$\det E = \det E' = \left(-1 + \frac{C}{P_0}\left(1 + (\Delta\lambda)\sum_{m=1}^{n} s_m \right) \right)^{n-1} (1 - \frac{C}{P_0})$$

But from (B.5)

$$1 + (\Delta\lambda)(\sum_{m=1}^{n} s_m) = \frac{P_0}{C}$$

and therefore,

$$\det E = \det E' = \left(-1 + \frac{C}{P_0}\frac{P_0}{C} \right)^{n-1} (1 - \frac{C}{P_0}) = 0\,.$$

Therefore, coming back to (B.2)

$\det M = 0$.

This means that the stability cannot be determined for steady state where populations for all λ_i are non-zero.

Appendix C. Choosing a model for the parameter *essential uptake*, $U_e(s)$

C.1 Summary of the analysis

This appendix explores the sigmoidal functions that can be used to fit data on nitrogen used by plants at different times. Used N was chosen to estimate essential uptake $U_e(s)$. The analysis is presented as follows.

1. Data description.
2. Preliminary selection. Five types of functions were considered: Gompertz, logistic, Richards, Morgan-Mercer-Flodin (MMF), and Weibull. Qualitative evaluation of the fit showed that the Weibull and MMF were not appropriate models. Several variations of each of the remaining models were fit to the pooled plant as an initial evaluation of the models. The F-statistic, R^2, t-statistic for the parameters, and residuals plots were examined. This led to the selection of the logistic and Gompertz functions. The parameter values estimated from the pooled data were used as initial values when the models were fit to individual plants.
3. Model evaluation and selection for individual plants. Several versions of logistic and Gompertz functions were considered. For each plant, the parameters were estimated using least squares (Newton-Gauss also known as Marquardt method). To estimate the quality of the selected models the following were calculated for each individual plant and for all models: (a) curvature measures (intrinsic and parameter-effects); (b) Box's percentage bias in LS estimates; (c) parameter correlation matrices. The statistical analysis and biological considerations led to the conclusion that the model used in section 3.3.2 was appropriate.

C.2 Data description

To estimate the essential uptake $U_e(s)$, the amount of N used by plants between harvests (see Section 3.3.2) was used. The harvest was collected at 7 time points (see

Section 3.3.1). The data contained values of used N for 20 plants, at seven time points. Data for one of the plants was not complete, and therefore only 19 plants were used in the analysis. The difficulty with the data was the small number of points for each plant, a common difficulty with biological data.

C.3 Preliminary selection

Plant uptake as a function of plant development stage has a sigmoidal shape (Grime *et al.* 1988). Several functions are commonly used to model sigmoidal growth (Ratkowsky 1983): logistic, Gompertz, Richards, Morgan-Mercer-Flodin (MMF), and Weibull (Table C.1). In this work, several forms of each model were considered. For logistic, Gompertz, and Richards four forms were considered: two with three parameters (models numbered 1 and 3), and two with four parameters (models numbered 2 and 4). Models numbered 1 and 3 were re-parameterized versions of each other, as were models numbered 2 and 4. Similarly for MMF models 1 and 2.

All of the models were fit to the data. Since the data for each individual plant were sparse, the data for all plants were pooled (so that for each time point there were 19 observations for uptake). The pooled data were used to evaluate the qualitative adequacy of the models. For two models, MMF and Weibull, the fit was not satisfactory, as the models did not approach maximum at the last observation point (Figure 1). For the remaining models, logistic, Gompertz, and Richards, the statistics characterizing the fit are summarized in Table C.2. All models had very similar R^2. The value of y_o was estimated to be zero for the Richards models 2 and 4. Therefore, their fit did not differ from Richards 1 and 3.

Table C.1 Common models for sigmoidal growth (Ratkowsky 1983). Several forms of each model were considered.

Gompertz	Gompertz 1	$f(s)=ae^{-e^{s_0-bs}}$
	Gompertz 2	$f(s)=y_0+ae^{-e^{s_0-bs}}$
	Gompertz 3	$f(s)=ae^{-e^{-\frac{s-s_0}{b}}}$
	Gompertz 4	$f(s)=y_0+ae^{-e^{-\frac{s-s_0}{b}}}$
Logistic	Logistic 1	$f(s)=\frac{a}{1+e^{s_0-bs}}$
	Logistic 2	$f(s)=y_0+\frac{a}{1+e^{s_0-bs}}$
	Logistic 3	$f(s)=\frac{a}{1+e^{-\frac{s-s_0}{b}}}$
	Logistic 4	$f(s)=y_0+\frac{a}{1+e^{-\frac{s-s_0}{b}}}$
Richards	Richards 1	$f(s)=\frac{a}{\left(1+e^{s_0-bs}\right)^{1/c}}$
	Richards 2	$f(s)=y_0+\frac{a}{\left(1+e^{s_0-bs}\right)^{1/c}}$
	Richards 3	$f(s)=\frac{a}{\left(1+e^{-\frac{s-s_0}{b}}\right)^{c}}$
	Richards 4	$f(s)=y_0+\frac{a}{\left(1+e^{-\frac{s-s_0}{b}}\right)^{c}}$
Morgan-Mercer-Flodin (MMF)	MMF 1	$f(s)=\frac{dc+as^b}{c+s^b}$
	MMF 2	$f(s)=y_0+\frac{as^b}{c^b+s^b}$
Weibull	Weibull 1	$f(s)=a\left(1-e^{-cs^d}\right)$

To determine goodness-of-fit, the *t*-statistic of the parameters was considered for the logistic and Gompertz models with three and four parameters (models numbered 1 and 2 respectively), and for Richards 1 with three parameters (Table C.3). Since models 1 and 3 were equivalent, the quality of fit needed to be evaluated only for one of the models; similarly for models 2 and 4. Table C.3 shows that for both logistic 2 and Gompertz 2, the *t*-statistic was significant for all parameters. Note that Richards 1 was very similar in form to logistic 2 (Table C.1) with one difference: that the denominator of Richards 1 was raised to the power of $1/c$. The *t*-statistic for Richards 1 was significant for all parameters except c, for which the associated probability was 0.06. Considering that c was an extra parameter added to logistic 2, and that it was the only parameter that did not give a significant *t*-statistic, it did not add to the quality of fit. The number of observations available for each plant was small relative to the number of parameters. Therefore, unnecessary parameters were unjustifiable.

In logistic and Gompertz models with four parameters (Table C.3) the *t*-statistic for y_o was not as significant as it was for the other three parameters. However, biological considerations needed to be taken into account. The parameter y_o could be interpreted as the minimum uptake required for survival, whereas the other term of the equation could be seen to correspond to the uptake necessary for plant growth and development. The minimum uptake required for survival, y_o, was a convenient parameter that could be used to express variability between simulated plants. The other parameter that determined the intercept of the curve, a, changed not only the y-intercept but also the slope of the rise of the curve. Therefore, it did not have as clear a biological interpretation. This suggested that the models with four parameters should be used.

Residuals for all models were examined, and the associated probability that the distribution of residuals were normal was less than 0.08 for all models (according to Shapiro-Wilk and Anderson-Darling tests). This suggested that a further examination of the appropriateness of the model was required, as is described below.

Table C.2 R^2, F-statistic and associated probabilities for data fit to logistic, Gompertz, and Richards models.

	R^2	F	p
Logistic 1 and 3	0.94	685.1667	<0.0001
Logistic 2 and 4	0.94	1033.365	<0.0001
Gompertz 1 and 3	0.94	667.8965	<0.0001
Gompertz 2 and 4	0.94	974.3626	<0.0001
Richards 1 and 3	0.94	689.2573	<0.0001
Richards 2 and 4	Was not considered because value y_o was 0.		

Table C.3 Parameter values and their statistical characteristics for logistic, Gompertz, and Richards models.

Models	Parameters	Parameter Values	Std Errors	t	p
Logistic 1	a	219.455	6.002	36.567	<0.0001
	b	0.0263	0.0016	16.275	<0.0001
	S_o	3.244	0.1487	21.8212	<0.0001
Logistic 2	a	214.442	10.453	20.514	<0.0001
	b	0.0276	0.0028	9.715	<0.0001
	S_o	3.405	0.336	10.150	<0.0001
	y_o	3.011	5.391	0.558	0.578
Gompertz 1	a	260.306	14.726	17.677	<0.0001
	b	0.0131	0.0012	10.888	<0.0001
	S_o	1.4789	0.0796	18.578	<0.0001
Gompertz 2	a	233.282	14.307	16.306	<0.0001
	b	0.0156	0.0017	9.374	<0.0001
	S_o	1.762	0.158	11.188	<0.0001
	y_o	9.685	3.996	2.424	0.0167
Richards 1	a	209.470	7.352	28.491	<0.0001
	b	0.0392	0.0144	2.718	0.0075
	c	1.934	1.0193	1.897	0.06
	S_o	5.749	2.628	2.188	0.0305

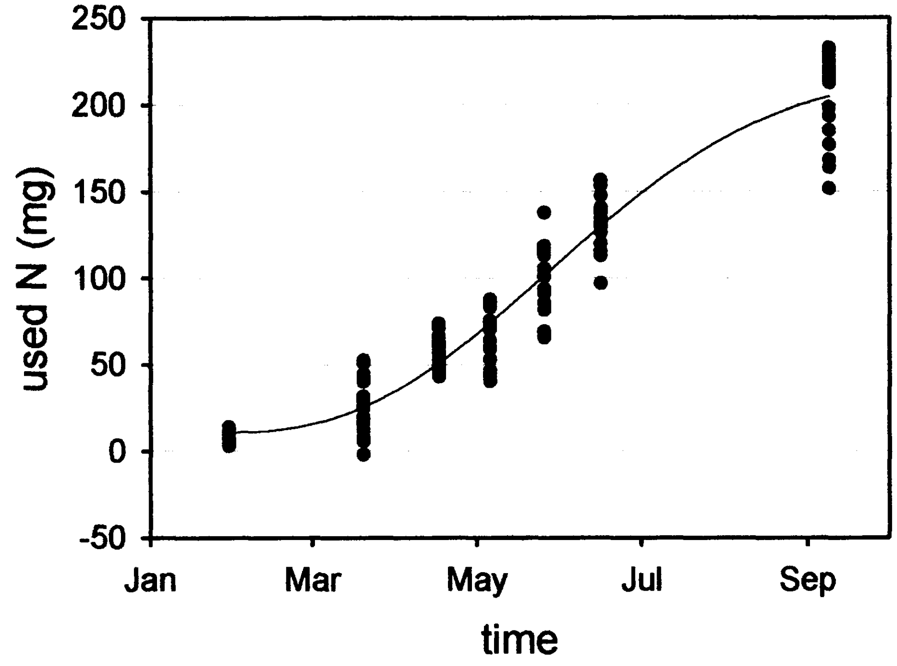


Figure C.1 Fit of Weibull model to pooled data for plants at different harvests. The model does not approach its maximum at the last harvest date.

C.4 Model evaluation and selection for individual plants

As the next step of analysis, logistic and Gompertz models were fit to data for individual plants. The fit was done using the Newton-Gauss (Marquardt) method in Mathematica. In addition, the curvature measures of nonlinearity of Bates and Watts were calculated, as well as the asymmetry measure of parameter bias (Ratkowsky 1983). When the models were fit to individual plant data, the initial parameter values were obtained from the pooled data. The *F*- and *t*-statistics and R^2 for the fits to individual plant data were similar to the fit to pooled plant data. The curvature measures of nonlinearity are presented in Table C.4. Overall logistic and Gompertz 1 had smaller values for intrinsic and parameter-effects curvatures than 2. Similarly, logistic and Gompertz 3 had smaller values than models 4. Curvatures of Gompertz models were, in general, larger than those of logistic ones.

Table C.4 shows that the intrinsic curvature for logistic and Gompertz models 1 and 3 was, in general, less than the critical value (i.e. the intrinsic curvature was not significant at the 0.05 level). Intrinsic curvature for logistic 2 and 4 in most cases exceeded the critical values. However, in most cases, the values did not exceed twice the critical value, except marked in grey in the Table where the values were very large.

This occurred in the logistic 4 model, and only when the value of y_o was estimated to be zero.

The parameter-effects curvatures were, in general, bigger than intrinsic curvatures. Moreover, they were, in most cases, larger than the critical values (i.e. the parameter-effects curvature was significant on the 0.05 level). This suggested at least one of the parameters was biased.

In order to find the parameters that caused nonlinearity in the models, Box's percentage bias was calculated for all models (Table C.5). Since the 4-parameter models were the most biologically appropriate, the biases were calculated using the 4-parameter models (numbered 2 and 4) except in those cases when the value of y_o was estimated to be zero. In these cases, the 3-parameter models were used to calculate bias. The values of parameter biases reflect the previous analysis of the parameter-effects curvatures. In particular, the bias values for Gompertz models were higher overall than those for logistic models.

In logistic and Gompertz models 1 and 2, y_o and a had high bias values, and therefore are responsible for the parameter-effects curvature of the models. The other two parameters, b and s_o, have low values of bias in these models, particularly parameter b. The biases of y_o were similar for the logistic and Gompertz models. The bias values for plants 12 and 13 were particularly high for parameter y_o in models 1 and 2, and for all the parameters in models 3 and 4. For most of the plants, the bias for a was higher in Gompertz. Comparison of models 1 and 2 versus 3 and 4 showed that bias values for b and s_o were much higher for the latter models.

Two conclusions can be drawn from the bias analysis. First, that the logistic models had lower curvature and parameter bias. Second, that parameters in models 1 and 2 are less biased than those in models 3 and 4. However, it was again necessary to consider the biological interpretation of the models. In models 3 and 4, the roles of parameters b and s_o could be clearly described. Parameter b was responsible for the steepness of the rise of the essential uptake curve. Parameter s_o was responsible for the time of the rise. In models 1 and 2, the roles of b and s_o could not be so clearly delineated. Therefore, for the purposes of using the selected model to represent the essential uptake curve, models 3 and 4 were preferable.

Finally, the correlation matrices of the parameters were considered (Table C.6). Presented are correlation matrices for pooled data of the logistic 4 and Gompertz 4 models. However, correlation matrices for all models and each plant were examined, and matrices presented in Table C.6 are characteristic of those not shown. For some parameters the correlation was quite high, e.g. between y_o and a, y_o and b, and a and b. However, these correlations were observed for all models, and were likely to be due to the small number of time points.

In summary, logistic model 4 appeared to be the most appropriate model from both statistical and biological points of view. This model performed statistically better than all other non-logistic models. From biological considerations, it was the best logistic model, because it had the necessary parameter structure to represent biological processes.

Table C.4 Intrinsic curvature measurements for all versions of logistic and Gompertz models. The upper and lower values show estimated maximum intrinsic (IN) and maximum parameter-effects (PE) curvatures, respectively, and CV is the corresponding confidence value. IN and PE should be less than or as close as possible to CV. The cells marked in grey are those where the parameter effects were very large.

Plant No.	**Logistic 4**				**Gompertz 4**			
	1	**2**	**3**	**4**	**1**	**2**	**3**	**4**
CV	***0.390***	***0.331***	***0.390***	***0.331***	***0.390***	***0.331***	***0.390***	***0.331***
1	0.452 1.408	0.808 4.323	0.452 1.081	0.807 63.09	0.588 3.950	1.111 5.858	0.587 1.870	1.111 15.27
2	0.315 1.533	0.564 4.261	0.315 1.039	0.564 21.53	0.592 5.917	0.669 7.870	0.592 2.096	0.669 7.137
3	0.160 0.563	0.262 1.974	0.160 0.402	**6.72** **$6.5x10^{16}$**	0.189 1.111	0.272 1.289	0.189 0.531	0.272 2.264
4	0.192 1.006	0.335 2.589	0.192 0.643	0.335 6.105	0.415 3.986	0.427 3.396	0.415 1.398	0.105 2.163
5	0.390 1.014	0.734 2.501	0.390 0.665	0.376 11.052	0.568 2.173	1.529 3.229	0.568 1.165	1.529 10.103
6	0.138 1.098	0.239 3.781	0.138 0.639	**1160.89** **$7.34x10^{18}$**	0.277 5.117	0.226 7.402	0.277 1.484	0.226 5.178
7	0.186 1.499	0.343 2.835	0.186 0.861	0.342 3.583	0.321 7.794	0.394 6.460	0.321 2.161	0.0955 2.582
8	0.667 2.190	1.152 5.919	0.667 1.285	1.152 19.02	0.934 3.948	1.496 5.274	0.934 1.962	1.497 8.678
9	0.229 1.006	0.404 2.217	0.229 99.845	0.404 3.536	0.517 3.913	0.498 3.918	0.517 1.480	0.498 2.97
10	0.322 0.912	0.547 3.040	0.322 0.701	**0.567** **$1.9x10^{14}$**	0.340 1.845	0.820 2.816	0.340 0.962	0.820 17.965
11	0.263 2.715	0.492 7.090	0.263 1.470	0.492 14.308	0.420 13.825	0.491 13.429	0.420 3.694	0.491 4.612
12	0.320 5.365	0.612 20.468	0.320 2.601	0.612 109.186	0.386 29.088	0.390 47.007	0.386 7.663	0.39 17.031
13	0.192 49.204	0.335 1.302	0.192 28.126	**870.145** **$6.31x10^{18}$**	**0.154** **488.61**	**0.244** **$5.1x10_{6}$**	**0.154** **264.304**	**0.393** **83445.2**
14	0.231 2.111	0.408 7.107	0.231 1.178	0.408 70.291	0.395 8.850	0.386 11.115	0.395 2.473	0.368 5.541
15	0.310 1.197	0.475 4.712	0.310 0.860	**0.147** **$5.19x10^{15}$**	0.386 2.602	0.524 4.045	0.386 1.180	0.524 17.307
16	0.257 2.569	0.361 21.063	0.257 1.398	**35.477** **$2.42x10^{17}$**	0.380 7.258	0.226 17.096	0.380 2.090	0.113 54.029
17	0.457 2.011	0.898 2.511	0.457 1.418	0.898 1.859	0.915 11.684	1.292 2.072	0.915 3.747	1.292 0.955
18	0.236 1.462	0.443 2.934	0.236 0.894	0.442 3.943	0.411 6.394	0.436 6.569	0.411 1.994	0.140 3.676
19	0.275 0.928	0.468 3.072	0.275 0.677	**0.47** **$1.62x10^{11}$**	0.337 2.101	0.688 2.735	0.337 1.013	0.688 4.191

Table C.5 Percentage bias in the least squares estimates of the parameters of logistic and Gompertz models. Lines marked in grey have very large values of the bias for at least one parameter.

	Logistic 1, 2				**Gompertz 1, 2**			
	y₀	**a**	**b**	**s₀**	**y₀**	**a**	**b**	**s₀**
1	-10.679	22.440	0.0043	0.510	-6.344	31.847	0.0031	0.357
2	-6.982	19.353	0.0015	0.211	-5.686	40.667	0.0009	0.139
3		0.769	0.0002	0.028	-0.373	1.671	0.0002	0.023
4	-3.079	6.799	0.0006	0.076	-1.914	9.461	0.0005	0.061
5	-3.798	6.049	0.0061	0.659	-3.371	10.502	0.0046	0.472
6		1.952	0.0001	0.021	-2.521	22.883	0.0000	0.021
7	-2.978	8.278	0.0005	0.076	-3.726	25.712	0.0003	0.054
8	-20.478	31.887	0.0146	1.425	-7.566	24.975	0.0105	1.004
9	-2.598	5.025	0.0012	0.133	-3.238	13.123	0.0009	0.096
10		2.082	0.0012	0.134	-1.734	7.817	0.0016	0.173
11	-8.937	34.740	0.0007	0.149	-7.029	75.483	0.0002	0.091
12	-31.507	152.888	-0.0005	0.261	-32.439	440.640	-0.0015	0.139
13		487.218	0.0001	0.629		18342.4	0.0001	0.333
14	-8.402	31.292	0.0003	0.097	-5.752	52.623	0.0001	0.053
15		3.842	0.0008	0.102	-3.500	16.450	0.0008	0.095
16		9.802	0.0004	0.080	-14.510	104.300	-0.0005	0.013
17	-3.883	7.651	0.0069	0.856	-2.599	7.134	0.0068	0.816
18	-3.379	7.659	0.0011	0.138	-5.223	25.476	0.0005	0.070
19		2.404	0.0007	0.085	-1.678	8.096	0.0011	0.124
	Logistic 3, 4				**Gompertz 3, 4**			
1	-10.678	22.437	5.665	0.674	-10.076	31.849	10.780	6.122
2	-6.981	19.350	4.611	2.516	-3.095	40.671	12.733	9.101
3		0.769	0.218	0.381	-0.311	1.671	0.568	0.290
4	-3.079	6.799	1.867	0.361	-0.497	9.462	3.528	1.865
5	-3.797	6.046	1.357	-0.628	-5.462	10.504	3.182	1.213
6		1.952	0.322	0.917	-1.167	22.883	6.817	5.516
7	-2.978	8.278	1.971	1.082	-0.735	25.706	8.132	5.584
8	-20.514	31.953	8.688	-4.824	-5.215	24.951	9.368	3.776
9	-2.598	5.025	1.467	-0.053	-0.887	13.124	5.540	2.237
10		2.082	0.667	1.016	-9.629	7.812	2.543	1.435
11	-8.938	34.742	7.329	7.373	-1.710	75.428	20.500	18.214
12	-31.514	152.932	32.290	42.345	-9.120	440.689	119.776	117.402
13		487.008	5.566	75.959		18342	218.605	588.433
14	-8.402	31.293	7.004	6.680	-1.839	52.622	15.667	12.752
15		3.843	0.919	1.762	-8.965	16.450	5.245	2.621
16		9.801	1.503	4.564	-26.391	104.290	32.380	22.226
17	-3.884	7.652	1.704	0.281	-0.366	7.136	1.814	0.504
18	-3.379	7.658	2.487	0.597	-1.230	25.470	11.636	5.756
19		2.404	0.616	1.057	-1.247	8.096	2.378	1.376

Table C.6 Parameter correlation matrices for logistic 4 and Gompertz 4 models.

Logistic 4					**Gompertz 4**			
y₀	***a***	***b***	***s₀***		***y₀***	***a***	***b***	***s₀***
1	-0.839	-0.799	0.172	***y₀***	1	-0.625	-0.563	0.145
	1	0.890	0.320	***a***		1	0.927	0.634
		1	0.297	***b***			1	0.612
			1	***s₀***				1

List of symbols

The list is divided into four sections, one for each model described in the thesis and one for the symbols describing experimental data.

Mean-field model

a – rate of death of fecund individuals;

b – rate of fecundity (number of offspring per unit of time);

$c\lambda$ – proportion of seeds that leave seed population due to germination or due to death;

$F(\lambda, t)$ – number of fecund individuals;

$Q[F(x,t),F(y,t)]$ – function describing frequency of crossing of individuals with germination rate x and y in populations of adult populations;

$I(\lambda)$ – the number of offspring produced in a population per unit time:

$$P\int_0^1\int_0^1 \rho(\lambda \mid x,y)H[F(x,\tau),F(y,\tau)]dxdy;$$

K – resource saturation constant;

λ – reproduction rate;

λ_c – the upper limit of λ;

P – the fraction $\left(\frac{\text{(lifetime)(unit time)}}{\text{number of offspring}}\right)$;

R – the fraction $\left(\frac{\text{lifetime}}{\text{minimum time to repoduction}}\right)$;

$\rho(\lambda \mid x,y)$ – probability that an individual of type λ will result from a cross of individuals of type x and y;

$S(\lambda, t)$ – number of seeds (non-reproducing individuals);

$\int_0^{\lambda_c} \kappa(l,\lambda)S(l,t)dl$ – competition term describing how seeds with different values of the germination rate λ affect each other;

$H(\lambda,t) = 1 + \int_0^{\lambda_c} \kappa(l,\lambda)S(l,t)dl$;

Simulation model of plant communities

B_i – band of lattice cells around location of the plant;

D_p – plant seed dispersal pattern;

D_u – spatial distribution of plant uptake;

N_{off} – number of offspring produced by a plant;

P_c – cumulative resource uptake defined by the following sum: $P_c = \sum_{i=5,000}^{50,000} P_{tot}(i)$ where $P_{tot}(i)$ is the plant uptake summed over all plants present on the lattice at time i;

P_d – probability of plant death, used in both the individual-based and the organisms interactions model;

P_s – plant resource storage partition trait;

R_b – plant reproductive biomass;

R_f – plant storage-fecundity relation;

r_g – plant general storage release proportion;

$R_{\min}$ – $U_e(s)$ is evaluated at the first development stage;

r_s – plants surplus storage release proportion;

R_t – time dependent reproduction relation for plant reproduction, described by a function $y = -a(s - s_0)^2 + y_0$;

r_u – requested/essential plant uptake ratio;

s – development stage of a plant;

S_r – the plant storage available for reproduction;

$U_e(s)$ – essential uptake described by a function $y = y_0 + \frac{\alpha}{1 + e^{-(s-s_0)/\beta}}$;

U_r – plant requested uptake;

V_t – plant minimum uptake required for survival;

V_p – plant survival period;

$y = mR_t + b$ - equation describing the trade off between R_t and R_b with slope m and y-intercept b;

Experimental data

N_l – N lost by a plant in new leaves and fine root during reproduction;

$N_{lf}(j)$ – the proportion of N lost from the new leaves and fine roots at harvest j;

N_{lt} – N lost from the tap root;

$N_s(i,j)$ – the stored N that a plant i used between harvests j and $(j+1)$;

$N_{tap}(j)$ – the proportion of N lost from the tap root at harvest j;

$N_u(i,j)$ – the used N, for plant i at harvest j;

$N_{up}(i,j)$ – the uptake of N for plant i at harvest j;

Organism interaction model

A_n – catchment area number;
A_r – the catchment area of an organism;
C_{ind} – cumulative number of individuals present on the lattice at each time point throughout the simulation;
C_{type} – cumulative number of types present on the lattice at each time point throughout the simulation;
D – dispersal distance;
M– metabolic rate;
N – number of offspring;
O_r – total resource request per organism;
P_{br} – basic resource probability;
P_d – random death probability, used in both the individual-based and the organisms interactions model;
P_m – mutation probability;
R_{cell} –maximum number of resources per cell;
R_{cell} – maximum number of resources per cell;
R_{init} – initial resource distribution proportion;
R_{re} – resource renewal proportion;
T_p – number of types of persisting organisms;
T_{rep} – number of utility points necessary for reproduction;
U_{init} – initial utility points;
X – environment size;

References

Adami, C., Taylor C., and Belew, R. (eds.) 1998. *Artificial Life VI : Proceedings of the Sixth International Conference on Artificial Life.* Complex Adaptive Systems, No. 6. Bradford Books.

Adler, F.R. and Mosquera, J. 2000. Is space necessary? Interference competition and limits to biodiversity. *Ecology* 81: 3226-3232.

Barbour, M.G., Burk, J.H., Pitts, W.D. and Shwartz, M.W. 1999. *Terrestrial Plant Ecology.* 3rd Edition. Benjamin Cummings.

Barricelli, N.A. 1962. Numerical testing of evolution theories. Part I. Theroetical introduction and basic tests. *Acta Biotheoretica* XVI: 69-98.

Barricelli, N.A. 1963. Numerical testing of evolution theories. Part II. Preliminary tests of performance. Symbiogenesis and terrestrial life. *Acta Biotheoretica* XVI: 99-126.

Bausenwein, U., Millard, P., Thornton, B. and Raven, J.A. 2001. Seasonal nitrogen storage in the forb *Rumex acetosa. Functional Ecology* 15: 370-377.

Bedau, M.A., Snyder, E. and Packard, N.H. 1998. A classification of long-term evolutionary dynamics. In: Adami, C., Belew, R., Kitano, H., and Taylor, C. (eds.), *Proceedings of Artificial Life VI*, pp. 228-237, MIT press.

Botsford, L.W. 1992. Individual state structure in population models. In: DeAngelis, D.L. and Gross, L. J. (eds.), *Individual-Based Models and Approaches in Ecology*, pp. 213-236, Chapman and Hall.

Bown, J.L. 2000. *Issues of scale in individual-based models: applications in fungal and plant communities.* PhD thesis, University of Abertay Dundee.

Braun, M. 1993. *Differential Equations and Their Applications: An Introduction to Applied Mathematics*, 4th ed. Flushing.

Briggs, D. and Walters, S.M. 1997. *Plant Variation and Evolution.* Cambridge University Press.

Bronstein, J.L. 1994. Our current understanding of mutualism. *Quarterly Reviews of Biology* 69: 31-51.

Cardinale, B.J., Nelson, K. and Palmer, M.A. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* 91: 175-183.

Caswell, H. 1989. *Matrix Population Models: Construction, Analysis, and Interpretation.* Sinauer Associates.

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M. *et al.* 2000. Consequences of changing biodiversity. *Nature* 405: 234-242.

Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45: 227-276.

Conrad, M. and Pattee, H. 1970. Evolution experiments with an artificial ecosystem. *Journal of Theoretical Biology* 28:393-409.

Crawley, M.J. 1990. The population dynamics of plants. *Philosophical Transaction of the Royal Society of London B* 330: 125-140.

Crawley, M.J. 1997. *Plant Ecology.* Blackwell.

Crawley, M.J. and May, R.M. 1987. Population dynamics and plant community structure: competition between annuals and perrenials. *Journal of Theoretical Biology* 125: 475-489.

Crawley, M.J. and Harral, J.E. 2001. Scale dependence in plant biodiversity. *Science* 291: 864-868.

D'Agostino, R.B. and Stephens, M.A. 1986. *Goodness-of-fit Techniques.* Marcel Dekker.

Draper, N.R. and Smith, H. 1981. *Applied Regression Analysis.* John Wiley & Sons.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L. *et al.* 1995. Spatially explicit population models: Current forms and future cases. *Ecological Modelling* 5: 3-11.

Fahse, L., Wissel, C. and Grimm, V. 1998. Reconciling classical and individual-based approaches in theoretical population ecology: a protocol for extracting population parameters from individual-based models. *The American Naturalist* 152: 838-852.

Geritz, S.A.H., van der Meijden, E. and Metz, J.A.J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology* 55: 324-343.

Gleeson, S.K, and Tilman, D. 1990. Allocation and the transient dynamics of succession on poor soils. *Ecology* 71: 1144-1155.

Gordon, C.E. 2000. The coexistence of species. *Revista Chilena de Historia Natural* 73: 175-198.

Green, D. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* 82: 139-153.

Grime, J.P., Hodgson, J.G. and Hunt, R. 1988. *Comparative Plant Ecology: A Functional Approach to Common British Species.* Unwin Hyman.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115: 129-148.

Gross, L.J., Rose, K.A., Rykiel, E., Van Winkle, W. and Werner, E.E. 1992. Individual-based modelling: summary of a workshop. In: DeAngelis, D.L. and Gross, L.J. (eds.), *Individual-Based Models and Approaches in Ecology*, pp. 511-522, Chapman and Hall.

Guo, Q., Brown, J.H., Valone, T.J. and Kachman, S.D. 2000. Constraints of seed size on plant distribution and abundance. *Ecology* 81: 2149-2155.

Hairer, E., Norsett, S.P. and Wanner, G. 1993. *Solving Ordinary Differential Equations. Nonstiff Problems*. 2nd edition. Springer Series in Computational Mathematics, vol. 8, Springer.

Harper, John L. 1977. *Population Biology of Plants*. Academic Press.

Hassel, M.P., Comins, H.N. and May, R.M. 1994. Species coexistence and self-organizing spatial dynamics. *Nature* 370: 290-292.

Hastings, A. 1990. Spatial heterogeneity and ecological models. *Ecology* 71: 426-428.

Hastings, A. 1997. *Population Biology: Concepts and Models*. Springer.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M. *et al.* 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123-1127.

Helfield, J.M. and Naiman, R.J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82: 2403 – 2409.

Hogeweg, P. and Hesper, B. 1990. Individual-oriented modelling in ecology. *Mathematical and Computer Modelling* 13: 83-90.

Holland, J.H. 1995. *Hidden Order: How Adaptation Builds Complexity*. Addison Wesley/Helix Books.

Hooper, D.U. and Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305.

Hraber, P.T., Jones, T. and Forrest, S. 1997. The ecology of Echo. *Artificial Life* 3(3), 165-190.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Monographs in Population Biology 32. Princeton University Press.

Huisman, J. and Weissing, F.J. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407-410.

Humphries, H.C., Coffin, D.P. and Lauenroth, W.K. 1996. An individual-based model of alpine plant distributions. *Ecological Modelling* 84: 99-126.

Huston, M. 1994. *Biological Diversity: The coexistence of species in changing landscapes*. Cambridge University Press.

Huston, M., DeAngelis, D.L. and Post, W.M. 1988. New computer models unify ecological theory. *Bioscience* 38: 682-691.

Hutchinson, G.E. 1951. Copepodology for the ornithologist. *Ecology* 32: 571-577.

Kaitala, V., Alaja, S. and Ranta, E. 2001. Temporal self-similarity created by spatial individual-based population dynamics. *Oikos* 94: 273-278.

Kiers, E.T., Lovelock, C.E., Krueger, E.L. and Herre, E.A. 2000. Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. *Ecology Letters* 3:106-113.

Kleidon, A. and Mooney, H. 2000. A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology* 6: 507-523.

Köhler, P. and Huth, A. 1998. The effects of tree species grouping in tropical rainforest modelling: Simulations with the individual-based model Formind. *Ecological Modelling* 109: 301-321.

Kubo, T. and Ida, H. 1998. Sustainability of an isolated beech-dwarf bamboo stand: analysis of forest dynamics with individual based model. *Ecological Modelling* 111: 223-235.

Lavorel, S. and Chesson, P. 1995. How species with different regeneration niches coexist in patchy habitats with local disturbances. *Oikos* 74: 103-114.

Lawton, J.H. 1999. Are there general laws in ecology? *Oikos* 83: 177-192.

Leishman, M.R. and Murray, B.R. 2001. The relationship between seed size and abundance in plant communities: model predictions and observed patterns. *Oikos* 94: 151-161.

Levin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist* 104: 413-423.

Levin, S.A. 1974. Dispersion and population interactions. *The American Naturalist* 108: 207-228.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulleting of the Entomological Society of America* 15: 237-240.

Levins, R. and Culver, D. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences USA* 68: 1246-1248.

Mladenoff, D. and Baker, W. (eds.) 1999. *Spatial Modeling of Forest Landscape Change*. Cambridge University Press.

Lomnicki, A. 1988. *Population ecology of individuals*. Princeton University Press.

Lomnicki, A. 1999. Individual-based models and the individual-based approach to population ecology. *Ecological Modelling* 115: 191-198.

Loreau, M. 1992. Species abundance patterns and the structure of ground-beetle communities. *Annales Zoologici Fennici* 28: 49-56.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3-17.

MacArthur, R.H. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences USA* 43: 293-295.

MacArthur, R.H. and Wilson, E.O. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-87.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*, Princeton University Press.

May, R.M. 1976. *Theoretical Ecology*. Blackwell Scientific Publications.

Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press.

Metz, J.A.J and Diekmann, O. (eds.) 1986. *The Dynamics of Physiological Structured Population*. Lecture Notes in Biomathematics 68. Springer-Verlag.

Metz, J.A.J., de Roos, A.M. and van den Bosch, F. 1988. Population models incorporating physiological structure: a quick survey of the basic concepts and an application to size-structured population dynamics in waterfleas. In: Ebenman, B. and Persson, L. (eds.) *Size-structured populations*, pp. 106-126, Springer-Verlag.

Metz, J.A.J. and de Roos, A.M. 1992. The role of physiologically structured population models within a general individual-based modeling perspective. In: DeAngelis, D.L. and Gross, L.J. (eds.) *Individual-based models and approaches in ecology*, pp. 88-111 , Chapman and Hall.

Murray, J. D. 1989. *Mathematical Biology*. Springer-Verlag.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.

Naeem, S., Knops, J., Tilman, D., Howe, K.H., Kennedy, T. and Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97-108.

Nijs, I. and Roy, J. 2000. How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. *Oikos* 88: 57-66.

Pacala, S.W. 1986. Neighborhood models of plant population dynamics. 2. Multi-species models of annuals. *Theoretical Population Biology* 29, 262-292.

Pacala, S.W. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. *Theoretical Population Biology* 31, 359-392.

Pacala, S.W. and Silander, J.A. Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. *The American Naturalist* 125: 385-411.

Pachepsky, E., Crawford, J.W., Bown, J.L., Squire, G. 2001. Towards a general theory of biodiversity. *Nature* 410: 923-926.

Pachepsky, E., Taylor, T., Jones, S. 2002. Mutualism promotes diversity and stability in a simple artificial ecosystem. *Journal of Artificial Life* 8: 5-24.

Pearson, T.H., Gray, J.S. and Johannessen, P.J. 1982. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. 2. Data analyses. *Marine Ecology-Progress Series* 12: 237-255.

Pepper, J.W. and Smuts, B.B. 2000. The evolution of cooperation in an ecological context: An agent-based model. In: Kohler, T.A. and Gumerman, G.J. (eds.) *Dynamics in Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes.* Oxford University Press.

Pielou, E.C. 1977. *Mathematical Ecology.* Wiley.

Preston, F.W. 1948. The commonness, and rarity, of species. *Ecology* 29: 254-283.

Pugnaire, F.I. and Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42-49.

Putman, R.J. 1994. *Community Ecology.* Chapman and Hall.

Ray, T.S. 1991. An approach to the synthesis of life. In: Langton, C.G., Taylor, C., Farmer, J.D. and Rasmussen, S. (eds.), *Artificial Life II*, pp. 371-408, Addison-Wesley.

Ratkowsky, D.A. 1983. *Nonlinear Regression Modelling. A Unified Practical Approach.* Marcel Dekker.

Read, D.J. 1996. *Mycorrhizal Symbiosis.* Harcourt Brace & Co.

Rees, M. and Westoby, M. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78: 116-126.

Ricklefs, R.E. and Schluter, D. 1993. *Species diversity in ecological communities.* The University of Chicago Press.

Ricklefs, R.E. and Miller, G.L. 1999. *Ecology*. W. H. Freeman.

Rodwell, J.S. (ed.) 1992. *British Plant Communities, Volume 3. Grassland and montane communities*. Cambridge University Press.

Rosenzweig, M. 1995. *Species Diversity in Space and Time*. Cambridge University Press.

Schmitz, O.J. 2000. Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system. *Oikos* 89: 471-484.

Schulze, E.-D. and Mooney, H.A. 1994. *Biodiversity and Ecosystem Function*. Springer.

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. *et al.* 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oekologia* 122: 297-305.

Shimatani, K. 2001. On the measurement of species diversity incorporating species differences. *Oikos* 93: 135-147.

Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55.

Shugart, H.H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag.

Silvertown, J., Holtier, S., Johnson, J. and Dale, P. 1992. Cellular automaton models of interspecific competition for space - the effect of pattern on process. *Journal of Ecology* 80: 527-534.

Skellam, J.G. 1951. Random dispersal in theoretical populations. *Biometrica* 38: 196-218.

Slatkin, M. 1974. Competition and regional coexistence. *Ecology* 55: 128-134.

Stachnowicz, J.J. 2001. Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51: 235-246.

Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. *The American Naturalist* 116: 770-787.

Sumpter, D.J.T. and Broomhead, D.S. 2001. Relating individual behaviour to population dynamics. *Proceedings of the Royal Society B* 286: 925-932.

Symstad, A.J. and Tilman, D. 2001. Diversity loss, recruitment limitation, and ecosystem functioning lessons learned from a removal experiment. *Oikos* 92: 424-435.

Tanton, J.H. 1995. End of the migration epoch. *The Social Contract* IV: 162 – 173.

Taylor, T. 1999. *From Artificial Evolution to Artificial Life*. PhD thesis, University of Edinburgh.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455-1474.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363-365.

Tilman, D. and Kareiva, P. 1997. *Spatial Ecology*. Princeton University Press.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M.E. *et al.* 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.

Turing, A.M. with 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London B* 237: 37-72.

Uchmanski, J. and Grimm, V. 1996. Individual-based modelling in ecology: what makes the difference? *Trends in Ecology and Evolution* 11: 437-441.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science* 277: 494- 499.

Walker, B., Kinzig, A.P. and Langridge, J. 1999. Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95-113.

Warren, J.M. and Topping, C.J. 1999. A space occupancy model for the vegetation succession that occurs on set-aside. *Agriculture, Ecosystems and Environment* 72:119-129.

Weber, G.E., Jeltsch, F., vanRooyen, N. and Milton, S. 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. *Journal of Applied Ecology* 35: 687-699.

Weiner, J. and Conte, P.T. 1981. Dispersal and neighborhood effects in a annual plant competition model. *Ecological Modelling* 13: 131-147.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-260.

Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biological Review of Cambridge Philosophical Society* 42: 207-264.

Whittaker, R.H. 1970. Evolution and measurement of species diversity. *Taxon* 21: 213-251.

Whittaker, R.H. 1999. Ecology: Scaling, energetics and diversity. *Nature* 401: 865-866.

Wilkinson, H.H. and Parker, M.A. 1996. Symbiotic specialization and the potential for genotypic coexistence in a plant-bacterial mutualism. *Oecologia* 108: 361-367.

Winkler, E., Fischer, M. and Schmid, B. 1999. Modelling the competitiveness of clonal plants by complementary analytical and simulation approaches. *Oikos* 85: 217-233.

Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the USA* 96: 1463-1468.

Young, I.M. and Crawford, J.W. 1991. The fractal structure of soil aggregates: its measurement and interpretation. *The Journal of Soil Science*, 42: 187 – 192.