

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.

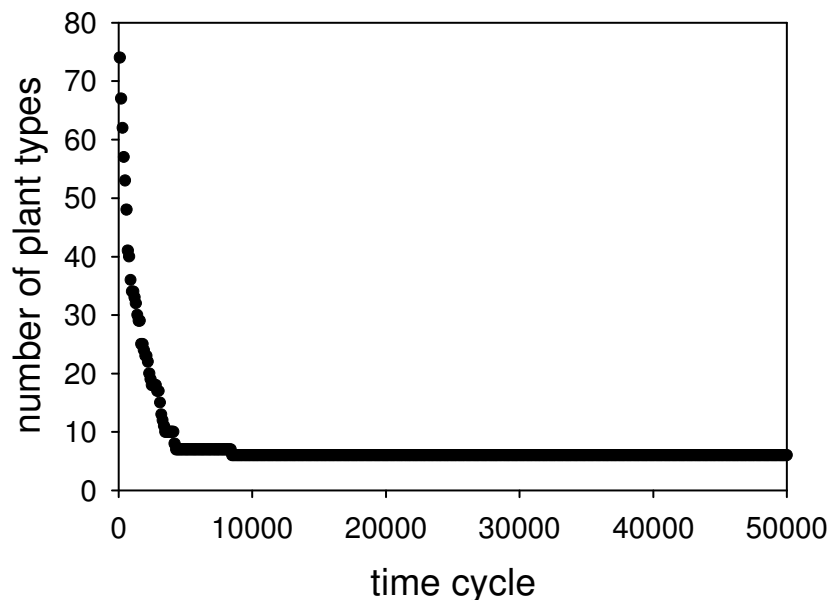


Figure 4.1 The number of plant types as a function of time for a typical simulation. Diversity drops and quickly settles to a steady number of coexisting plant types.

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 m². 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 in Table 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.

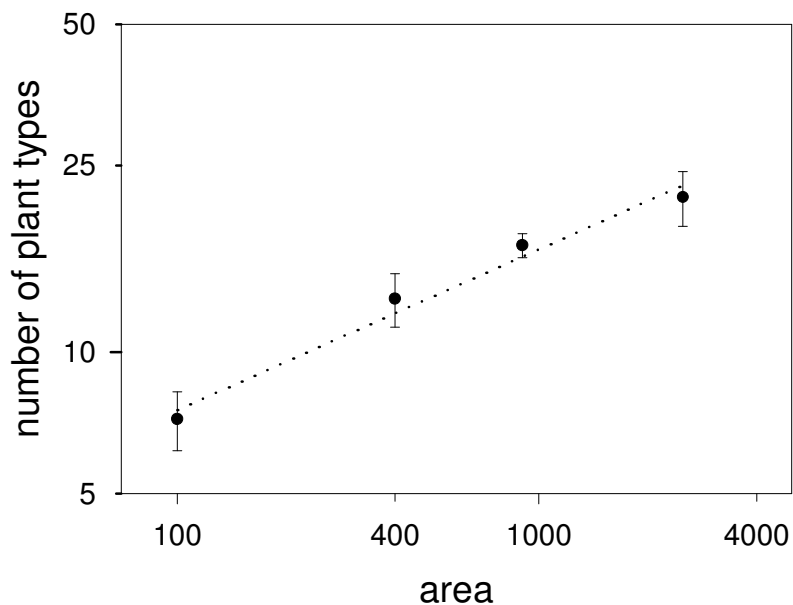


Figure 4.2 Relationship between the number of coexisting plant types and the lattice area. This is an analogue of the species-area curve in the model, with plant types replacing species. The area is the number of cells on the simulated lattice; the number of plant types is given at the end of the simulation. 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.

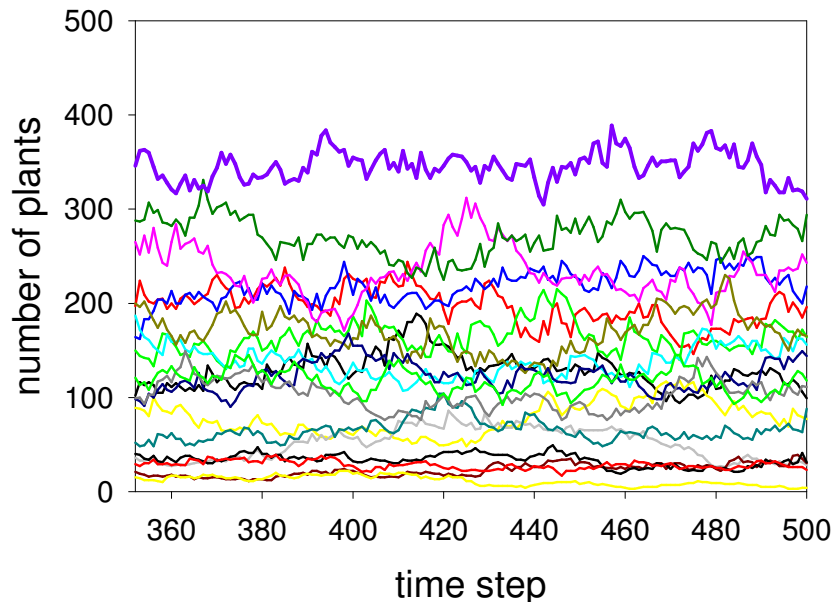


Fig. 4.3 a) Stratification of different plant types into rank groups in the final stage of a simulation on a 50 x 50 lattice, with 19 coexisting plant types. The most abundant type dominates, several types are consistently rare, and other types range across the intermediate abundances.

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.

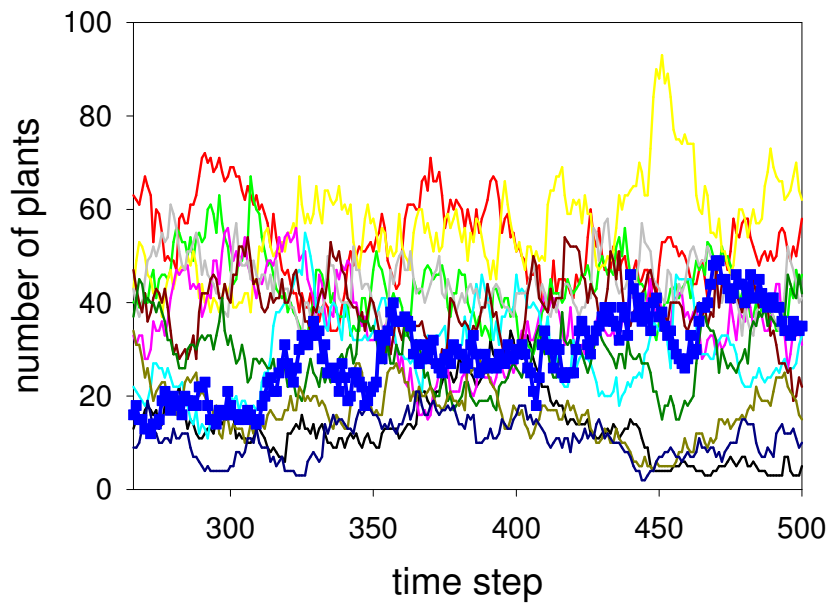


Fig. 4.3 b) The final stage of a simulation on a 20 x 20 lattice, with 12 coexisting plant types. There is not one most abundant type, and low-ranking types time can become high ranking, *e.g.* the one in blue.

Figure 4.3 Abundances of coexisting plant types.

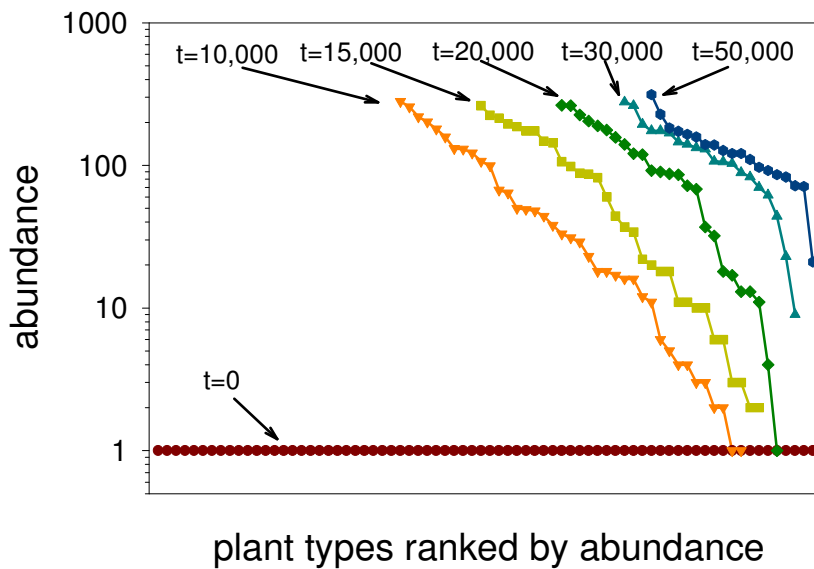


Figure 4.4 Change in the ranked plant type abundances over time for a simulation on a 50 x 50 lattice.

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 than 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).

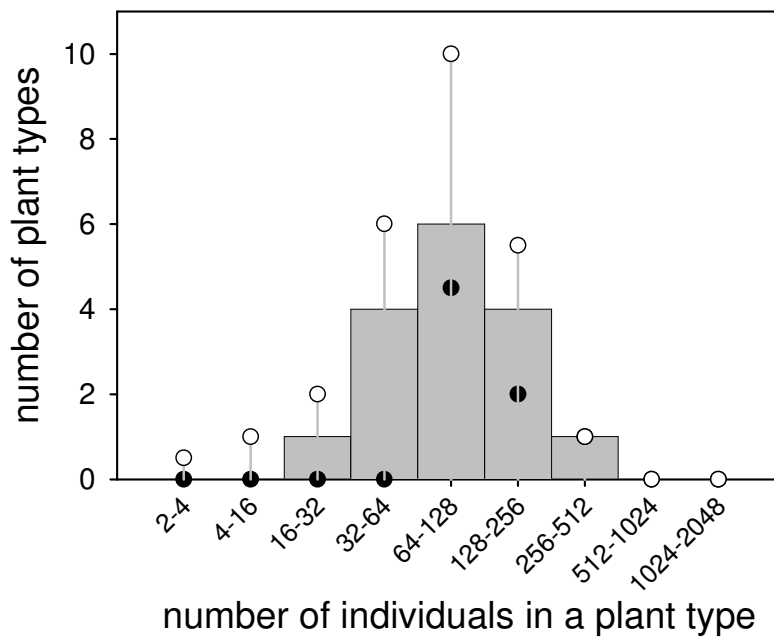


Figure 4.5 Plant type abundance distribution for a simulation on a 30 x 30 lattice. The distribution is plotted on a \log_2 scale, after Preston (1948). Circles indicate the maximum (white circles) and minimum values over the length of the simulation.

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_0 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	
y_0	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	

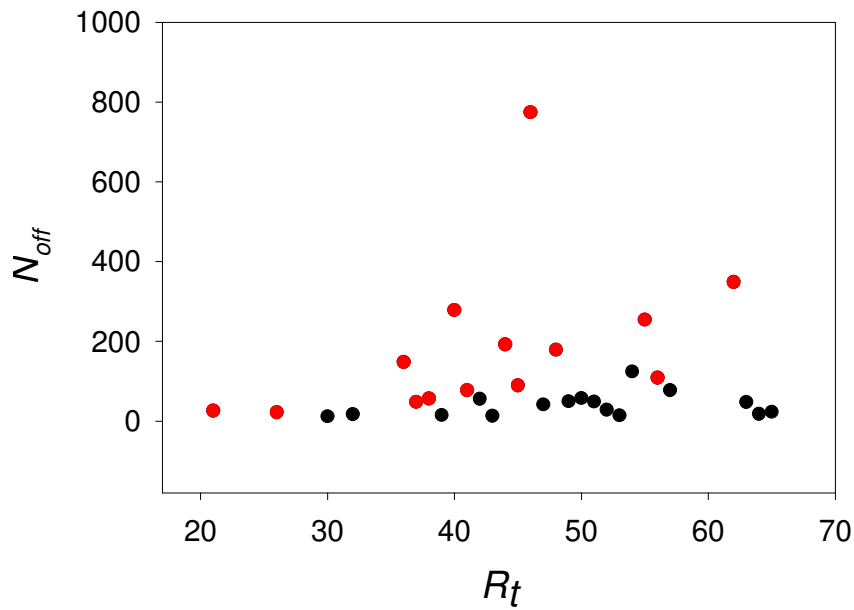


Figure 4.6 Plot of average number of offspring produced N_{off} vs. time to reproduction R_t . Red dots correspond to plant types that survived until the end of the simulation, and black dots to those that did not.

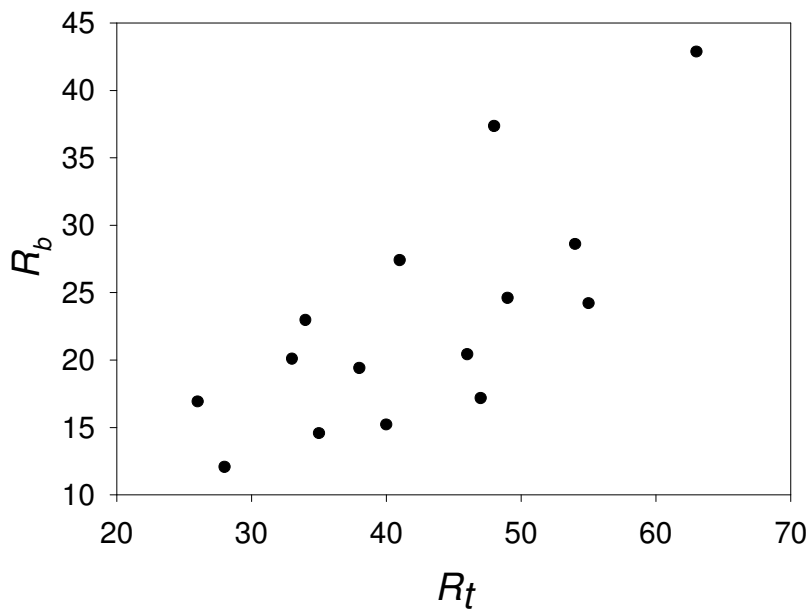


Figure 4.7 The positive correlation between the time to reproduction R_t and the reproductive biomass R_b of coexisting plant types for a simulation in a 20 x 20 lattice.

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).

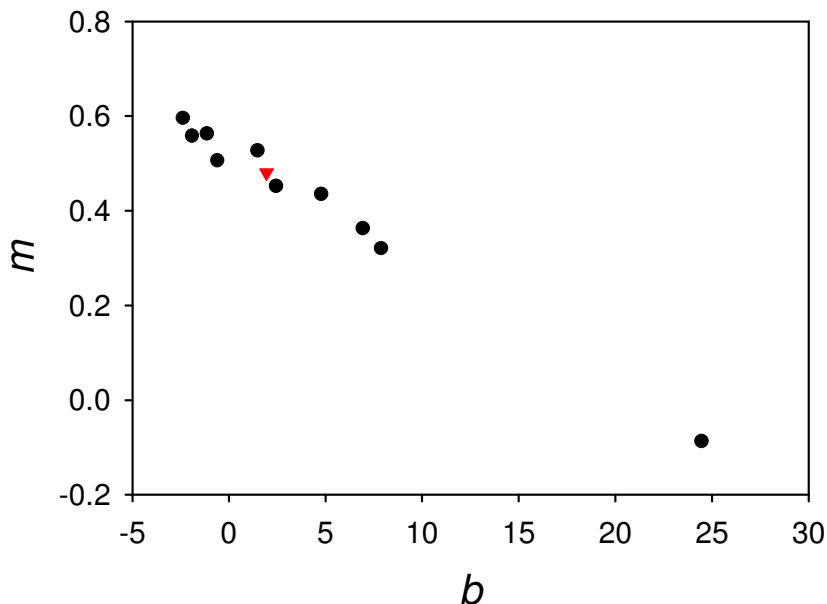


Figure 4.8 The relationship between the slope m and the constant b of the lines fitted to the reproductive biomass *vs.* R_t . Dots correspond to the values obtained from fitting the lines for 10 simulations on a 20 x 20 lattice, and the triangle is the average.

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).

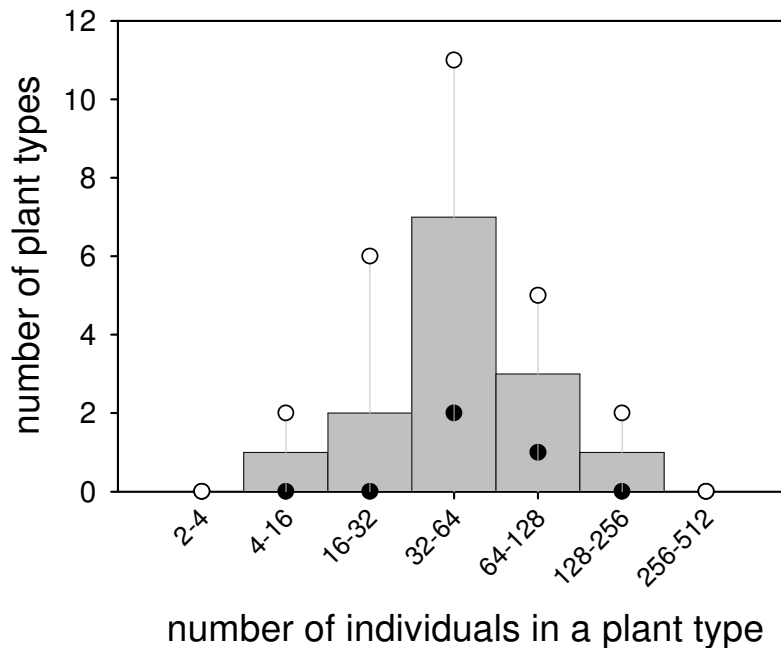


Figure 4.9 The plant type abundance distribution on a 20 x 20 lattice in a simulation with the simplified model. Circles indicate the maximum (white circles) and minimum values over the length of the simulation.

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.

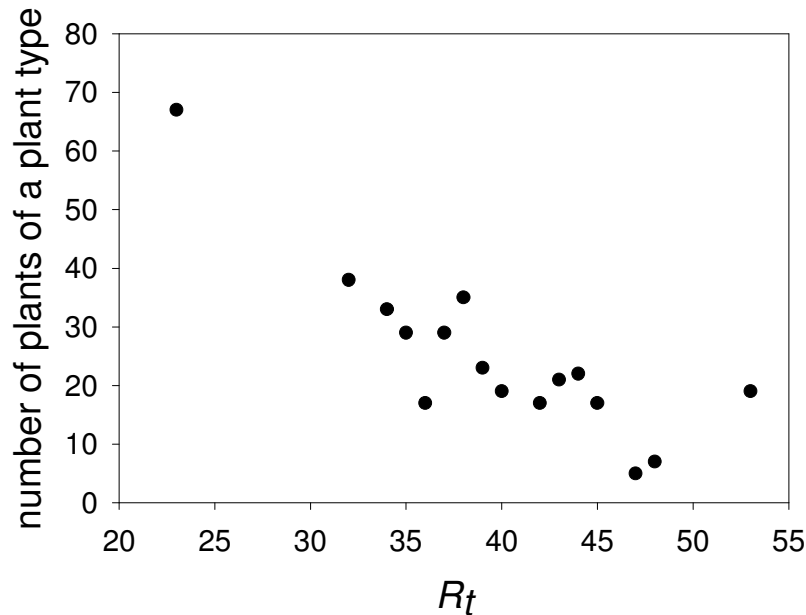


Figure 4.10 The relationship between R_t and abundance for each plant type at the last time cycle in a simulation on a 20 x 20 lattice.

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.

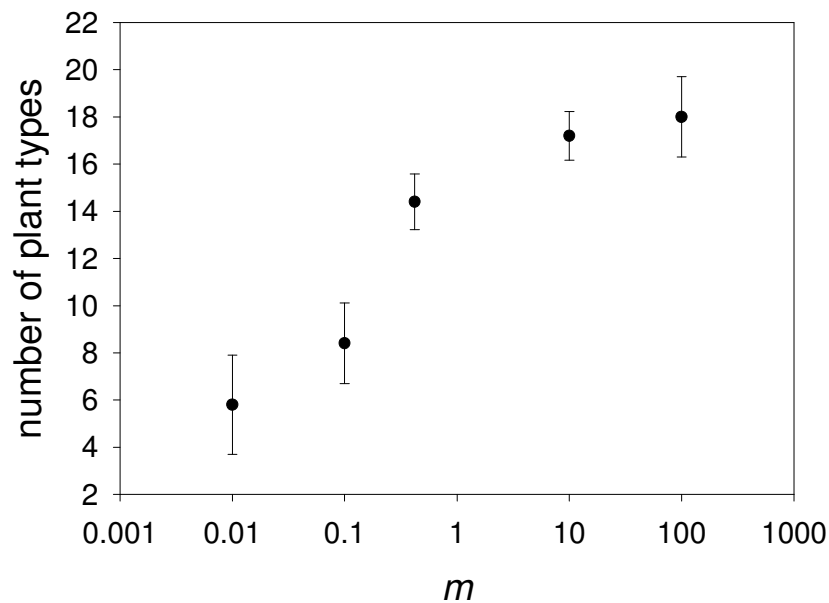


Figure 4.11 The effect of varying the slope m of the linear trade-off in the simplified model. The dots are the number of coexisting plant types averaged over ten simulations, with standard deviations denoted by bars.

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

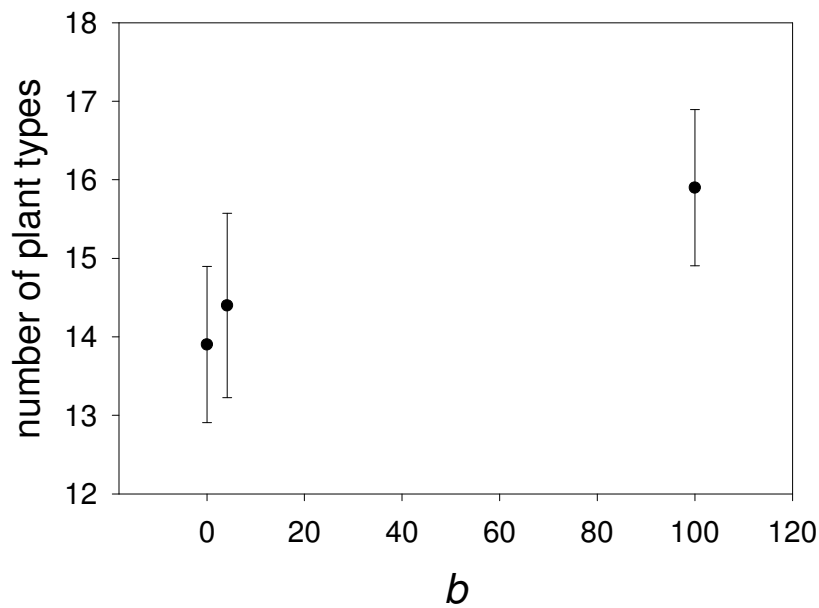


Figure 4.12 The effect of varying the constant value b of the linear trade-off in the simplified model. The dots are the number of coexisting plant types averaged over ten simulations, with standard deviations denoted by bars.

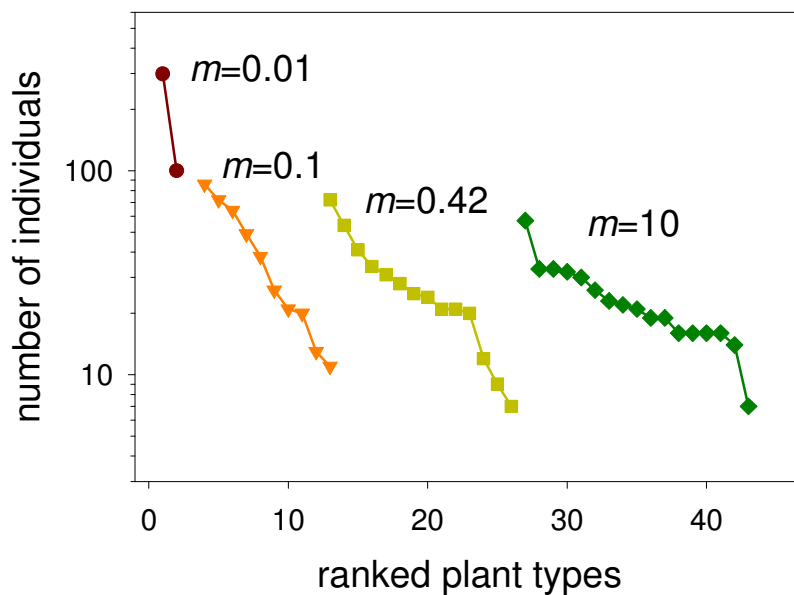


Figure 4.13 The change in the species abundance distribution as a function of the trade-off slope m .

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.