

## **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<sup>2</sup> 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	<b>p=0.001</b> , t(8.009)=-5.017	<b>p=0.001</b> , t(8.071)=4.926	<b>p=0.001</b> , t(8.036)=-5.480	<b>p&lt;0.001</b> , t(8.009)=-6.882
	Variance	<b>p &lt; 0.001</b> , F=22.361	<b>p=0.001</b> , F=16.905	<b>p&lt;0.001</b> , F=36.202	<b>p=0.003</b> , 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 ( $\times 10^4$ ), <b>H<sub>0</sub></b>	18.51 (0.02)	128.1 (0.3)	1.9 (0.10)	190.03 (0.07)
Productivity in heterogeneous communities ( $\times 10^4$ ), <b>H<sub>1</sub></b>	20.21 (0.9)	122.5 (4.9)	188.4 (2.2)	196.2 (2.6)
	<b>H<sub>0</sub> &lt; H<sub>1</sub></b>	<b>H<sub>0</sub> &gt; H<sub>1</sub></b>	<b>H<sub>0</sub> &lt; H<sub>1</sub></b>	<b>H<sub>0</sub> &lt; H<sub>1</sub></b>

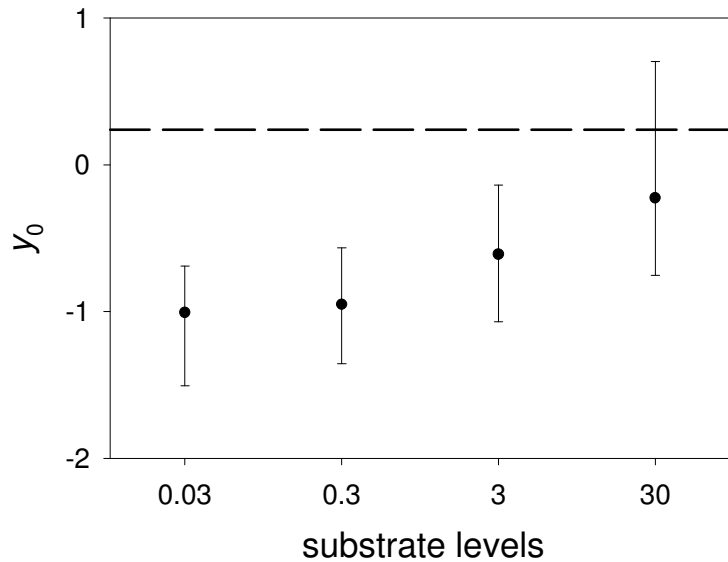
#### 5.4.4 Differences in parameter values of homogeneous vs. diverse communities

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  $\beta$ , 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  $\beta$  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.

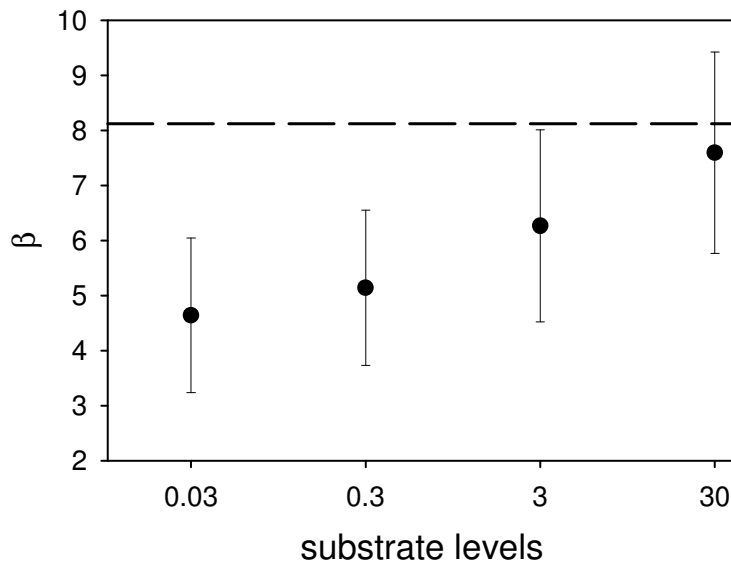
Increase in the median  $y_0$  value of coexisting plant types was observed with increase in substrate level. Figure 5.1 shows the median value of  $y_0$  in surviving plant types for different substrate levels. In the poorer substrates of 0.03, 0.3 and 3, the surviving plants had a lower median  $y_0$  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  $\beta$  in surviving plant types for different substrate levels. Similar to  $y_0$ , the mean value of parameter  $\beta$  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  $\beta$  determined the steepness of the uptake curve, and therefore the time that the uptake curve began to increase. The lower the value of  $\beta$ , the later the curve rose. Therefore, similarly to the effect of decreasing  $y_0$ , lower values of  $\beta$  facilitated survival on lower substrates.

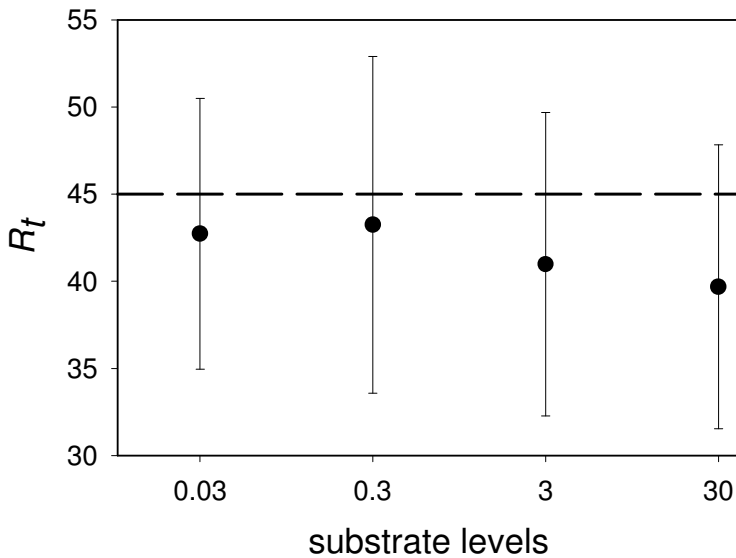


**Figure 5.1** The median  $\pm$  a quartile of the values of parameter  $y_0$  in different substrate levels. The dashed line represents the value of the parameter for the plants in a homogeneous population.

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  $\beta$  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 ( $\mu_1$ ) and heterogeneous ( $\mu_2$ ) 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	<b>p&lt;0.001,</b> t(18)=-7.357	<b>p=0.285,</b> t(9.976)=-1.130
	Variance	<b>p=0.443,</b> F=0.642	<b>p=0.002,</b> 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 became 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.