Chapter 12
The effects of heterogeneity on dispersal and colonization in plants

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Introduction

Heterogeneity, in its various guises, is a ubiquitous feature of ecological systems. To see this, one need only look at any published experimental study, where complex statistical analyses are used to disentangle the signal, generated by the experimental treatments, from the universally present heterogeneity or 'noise'. This noise is often seen as problematic, complicating analyses and making inference difficult. However, ecologists have recently started viewing the noise as an intrinsic property of the system rather than a complication to be ignored or averaged over. For example, Rees *et al.* (1996) found that changes in population size in a guild of winter annuals were influenced by previous population sizes, and the spatial distribution of the populations. Thus, heterogeneity in the spatial distribution of competitors influenced the observed population sizes in this guild.

Studies of heterogeneity fall into two broad categories: the first asks what are the potential effects of heterogeneity, while the second attempts to evaluate the actual impact of heterogeneity. In this chapter, we illustrate both these approaches. We start with general definitions of dispersal and heterogeneity, and then look at how dispersal can generate a heterogeneous distribution of competitors. The consequences of this heterogeneity for community structure are then explored. We then turn our attention to how heterogeneity can influence dispersal. We illustrate this by analysing how heterogeneity influences the reproductive decisions in monocarpic plants and how this in turn results in temporal dispersal. In each case we show how the interplay between the development of simple general models and data leads to the development of new, more complex models, and greater understanding of natural systems.

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What is dispersal?

We define dispersal to be any demographic process that results in members of a cohort experiencing different environments. Dispersal is one process that exposes organisms to heterogeneity, see below, and can occur in both time and space (Harper 1977). In addition to the usual processes that result in dispersal, namely seed movement, dormancy and clonal growth, this definition includes repeated reproduction and delayed reproduction in monocarpic plants. Both the latter processes result in members of a cohort experiencing different environments, and so can be considered as types of temporal dispersal. For example, reproduction in a single cohort of *Carlina vulgaris*, a monocarpic perennial, at an unproductive site in the Netherlands was spread over at least a 7-year period (Klinkhamer *et al.* 1996). Because each of these processes performs a similar population dynamic function we would expect trade-offs to exist between the different types of dispersal (Venable and Brown 1988; Rees 1994) and this is indeed the case (Rees 1993; Rees 1996).

What is heterogeneity?

Heterogeneity is defined as any factor that can cause variation in individual demographic rates, and may have a biotic or an abiotic origin. Clearly, this is a very broad definition including such factors as genetic differences, variation caused by the predators or pathogens, and spatial and temporal variation in the abiotic and biotic environment. This definition is similar to that of Milne (1991), see Wiens, this volume. However, Milne (1991) suggests that heterogeneity is the complexity caused by the spatial distribution of constraints and organisms' responses to them, whereas we prefer to focus on the demography. In this way, the magnitude of different forms of heterogeneity, and their potential effects, can be quantified. Different types of heterogeneity can often be arranged in a hierarchical way, see also chapters by Wiens and Pickett. For example, within an area, all habitats might experience common yearly influences caused by the weather. Then there might be habitat-specific heterogeneity caused by local conditions unique to a given habitat. In addition to this, individuals within a habitat might experience individual-specific heterogeneity related to their position or genetic makeup, and there might be non-specific heterogeneity, associated with chance events that affect individuals in a way unrelated to their identity. This simple hierarchical organization of heterogeneity will be discussed further, and methods for quantifying the different components presented in later sections.

Evolution and ecological consequences of seed dispersal

There is a large and growing literature on the evolution and ecological implications of spatial seed dispersal (Hamilton and May 1977; Comins *et al.* 1980; Bulmer 1984; Levin *et al.* 1984; Comins and Noble 1985; Pacala and Silander 1985; Pacala 1986a,b; Klinkhamer *et al.* 1987b; Pacala 1987; Venable and Brown 1988; Venable

and Brown 1993; Tilman 1994; Dytham 1995; Watkinson and Sutherland 1995; Tilman *et al.* 1997; Pacala and Rees 1998). In order to understand the role of spatial dispersal several studies have used a phenomenological approach, replacing explicit models of dispersal with aggregated probability distributions, such as the negative binomial distribution (Atkinson and Shorrocks 1981; Ives and May 1985). A partial justification for this approach is given by simulation studies which show aggregated distributions can be generated by local dispersal (Pacala and Silander 1985). However, local dispersal will generally result in positive covariance between parents and offspring, a complication we ignore in the model discussed below. The use of aggregated distributions has the advantage of analytical tractability but, as in any abstraction of this type, there is a potential difficulty with linking the aggregated distribution with a biological generative mechanism (May 1978).

Here we illustrate some of the potential difficulties of using this approach. Consider two species of annual plant competing for microsites, the first is the competitive dominant and excludes the second from any microsites where they both occur. Both species have identical dispersal mechanisms and the resulting distribution of seeds can be described by independent negative binomial distributions with a common aggregation parameter, κ. As κ becomes smaller so the distribution becomes more aggregated. The dynamics of the first species can be described using a simple equation of the form

$$p_1(t+1) = 1 - \left(1 + \frac{F_1 p_1(t)}{\kappa}\right)^{-\kappa}, \tag{12.1}$$

where $p_1(t)$ is the proportion of sites occupied by species 1 in year t and F_1 is the per microsite fecundity of species 1. Providing $F_1 > 1$ this model has a single, globally stable equilibrium, p_1^*; this follows from the fact that $dp_1(t+1)/dp_1(t)$ is strictly positive.

The dynamics of the second species can be described by

$$p_2(t+1) = (1 - p_1(t))\left(1 - \left(1 + \frac{F_2 p_2(t)}{\kappa}\right)^{-\kappa}\right) \tag{12.2}$$

where the subscript 2 refers to the second species. The equation has two parts: the first is the free space left by the first species; the second the fraction of sites colonized by species 2. For coexistence, species 2 must be able to invade once species 1 has reached equilibrium, p_1^*. This leads to the condition:

$$F_2\left(1 - p_1^*\right) > 1. \tag{12.3}$$

We note two things from this:

1 Invasion of species 2 is independent of its spatial distribution, and hence dispersal characteristics.

2 Invasion, and hence coexistence, becomes easier as F_1 and κ become smaller, as decreases in these parameters lead to lower p_1^*.

The first of these results has been noted by several authors (Atkinson and

Shorrocks 1981; Ives and May 1985; Silvertown and Smith 1989; Rees and Long 1992) and is intuitively surprising, as one would expect dispersal to influence the success of an invading species. Further insight into this model can be obtained by considering the special case $\kappa=1$, which gives $p_1^*=1-1/F_1$ and leads to the simple invasion condition,

$$F_2 > F_1. \tag{12.4}$$

From which we conclude that for values of $\kappa<1$ the critical value of F_2 is less than F_1, (Fig. 12.1). How can an inferior competitor, which loses in competition whenever it co-occurs with species 1, and has identical patterns of dispersal invade species 1 when it has a lower fecundity? To understand this apparent paradox, consider the invasion condition, equation (12.3). This states that the probability species 2 finds an empty site, $1-p_1^*$, multiplied by species 2's fecundity, F_2, must be greater than unity. This implicitly assumes that species 2 samples the habitat at random, which in turn implies that species 2 has global dispersal. The apparent paradox is therefore generated by unwittingly making species 2 a better disperser than species 1. In fact, the model has become an example of a competition–colonization trade-off (Skellam 1951; Levins and Culver 1971; Tilman 1994). Note this is not an explicit assumption of the model but an implicit assumption of the invasion analysis. The difficulties in interpreting these models have been discussed by several authors (Green 1986; Chesson 1991; Remer and Heard 1998).

There are several examples where the outcome of competition, between species with finite dispersal, is not correctly predicted by a simple invasion analysis, which

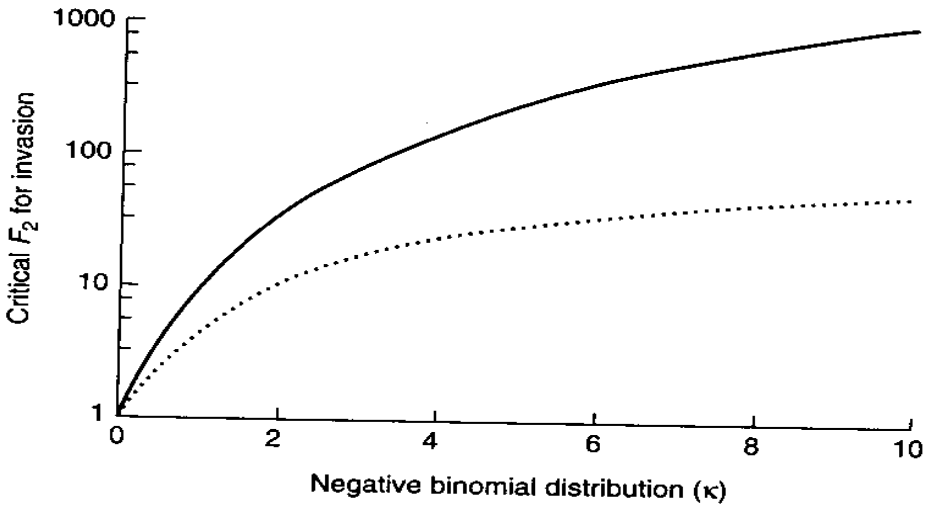

Figure 12.1 The critical value of F_2 required for invasion as a function of the negative binomial parameter, κ, of species 1, the competetive dominant. At values of $\kappa<1$ invasion by an inferior competitor with fecundity less than the superior competitor is possible. Solid curve, $F_1=10$, dotted curve, $F_1=5$.

assumes that species sample the habitat at random, see Pacala (1986b). To predict the outcome of competition correctly we need to understand the dynamics of spatial pattern formation. The use of moment-closure methods permits this to be done (Pacala and Levin 1997). Moment closure is a mathematical technique used to derive equations for the spatial moments of a system. In biological terms, these are equations for the average density of competitors, their variances and covariances (Pacala and Levin 1997; Bolker and Pacala 1999). The invasion criterion for interspecific competition models takes the following form (Bolker and Pacala 1999),

$$\text{Spatial invasion rate} = \text{growth rate at low densities} - \text{intraspecific clustering} + \text{interspecific clustering} + \text{spatial segregation}. \quad (12.5)$$

The first term gives the non-spatial invasion rate (i.e. equation [12.3] in the previous model), the second term is negative, because when a species forms clusters intraspecific competition will operate, even at low densities, so slowing the rate of invasion. The last two terms represent the effects of interspecific clustering and segregation; both of these reduce interspecific competition so increasing the invasion rate (Bolker and Pacala 1999).

In these models, long-range dispersal of the inferior competitor does not always promote coexistence. If growth is sufficient to allow gaps to be fully exploited then long-range dispersal aids coexistence, whereas short-range dispersal makes coexistence more difficult. However, if local population growth is necessary for exploiting gaps then short-range dispersal of the inferior competitor may favour coexistence. In this case, short-range dispersal allows rapid population growth in gaps, resulting in a greater number of seeds dispersing although the proportion dispersing is smaller (Pacala and Levin 1997; Bolker and Pacala 1999).

Clearly, when using simple phenomenological models, great care is required in linking biological mechanisms with the simple descriptive functions used in model formulation. Invasion analyses of such models also need to be interpreted with caution.

Much of the recent work on dispersal has focused on the competition–colonization trade-off, and how systems where diversity is maintained by this mechanism respond to habitat destruction (Dytham 1994; Tilman *et al.* 1994; Moilanen and Hanski 1995). This simple model is particularly attractive because the coexistence mechanism operates in a homogeneous world, so there is no need to invoke environmental heterogeneity, and each species is characterized by just three parameters; one for dispersal, one for mortality and a position in the competitive hierarchy. Coexistence occurs because the good competitors are also the worst colonizers and so, although superior competitors always exclude inferior competitors when they co-occur, the superior competitors fail to colonize all sites and so leave space to be exploited by the inferior competitors. If this mechanism allowed coexistence in natural systems then community ecology would be much simpler as one would no longer need to worry about complex, high dimensional

niche axes. Several field systems appear to conform to this simple model (Tilman 1994; Rees 1995; Rees *et al.* 1996; Turnbull *et al.*, in press, b).

Tests of the competition–colonization mechanism of coexistence are possible using seed sowing experiments (Tilman 1994; Pacala and Rees 1998; Turnbull *et al.*, in press, a). By sowing saturating densities of all species, one removes all colonization limitation from the system and diversity should collapse leaving the best competitor growing in isolation. Turnbull *et al.* (in press, b) tested this idea using a guild of co-occurring annual species growing in limestone grassland in south Wales. Previous studies of similar annual plant guilds suggested that small-seeded species produced more seeds per plant but were inferior competitors (Rees 1995; Rees *et al.* 1996); this generates a competition–colonization trade-off, which could be important in maintaining diversity. Turnbull *et al.* (in press, b) showed that large-seeded species do indeed produce fewer seeds per plant and so have lower colonization potential than small-seeded species (Fig. 12.2). In an experiment where seeds of all species were added to quadrats in equal numbers, the large-seeded species were found to dominate the community when sowing density was high (Fig. 12.3). This is consistent with the idea that large-seed size confers a competitive advantage, as assumed by the competition–colonization model. However, even at the highest sowing density the inferior competitors were not excluded from the system suggesting the presence of species-specific niches.

How does the presence of species-specific niches affect the predictions of the simple competition–colonization model? This question was addressed by Pacala and Rees (1998) who modified the standard model (Levins and Culver 1971) to allow finite rates of competitive exclusions: the standard model assumes instanta-

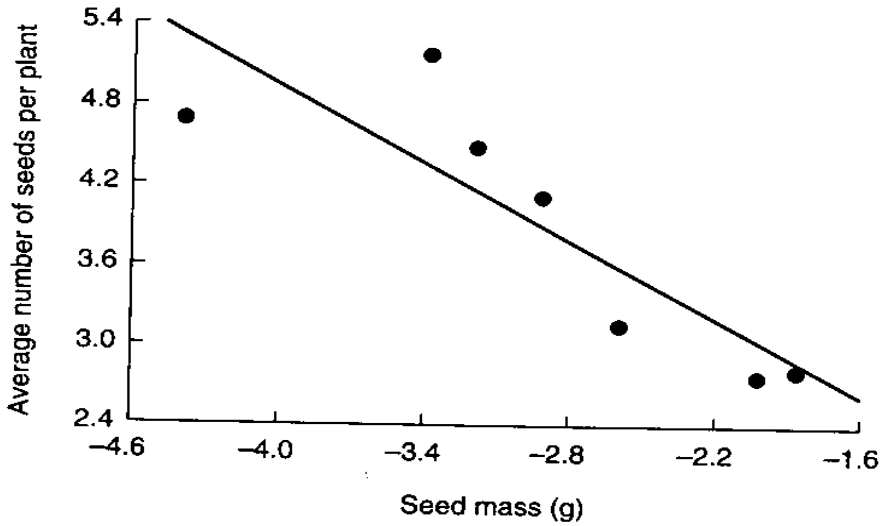

Figure 12.2 Relationship between average seed output per plant for seven co-occurring annual plants species and average seed mass; both axes are log scales. The fitted line is $y = 1.10 - 0.96x$, $r^2 = 0.74$. The species are, in order of decreasing seed mass, *Aphanes microcarpa*, *Myosotis ramosissima*, *Veronica arvensis*, *Arenaria serpyllifolia*, *Cerastium diffusum*, *Cerastium globmeratum* and *Saxifraga tridactylites*. Redrawn from Turnbull *et al.* (1999b).

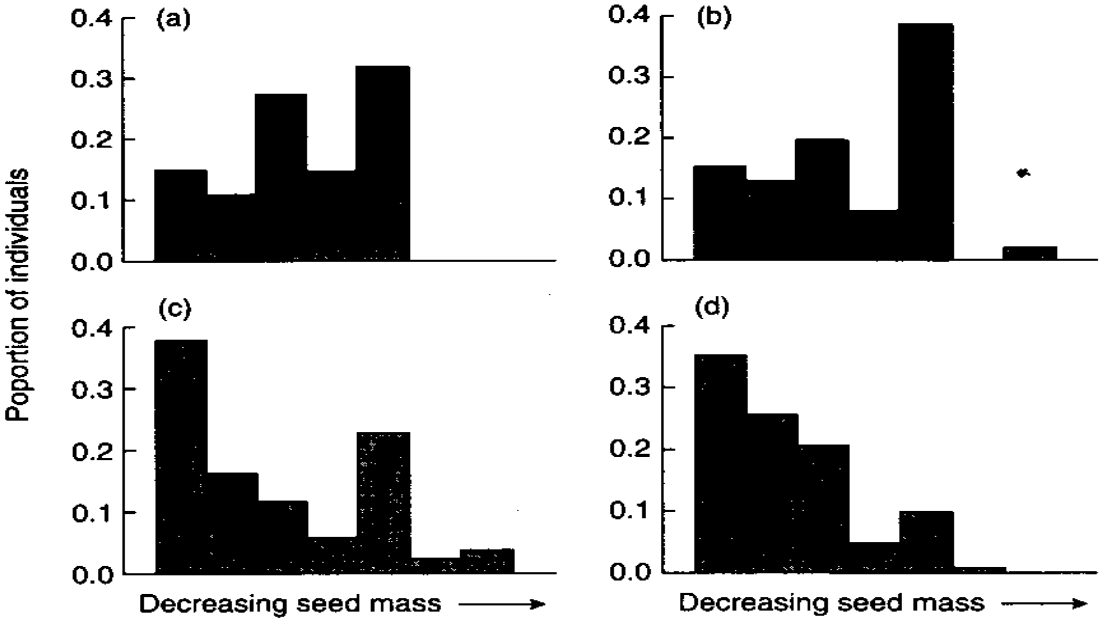

Figure 12.3 Impact of increased sowing density (equal numbers of all species) on community composition in a guild of co-occurring annual species. (a) No seeds sown, (b) 10 seeds sown, (c) 50 seeds sown and (d) 200 seeds sown. At low sowing densities there is no relationship between seed weight, a surrogate for competitive ability and composition, whereas at high sowing density the large-seeded species dominate the community. Redrawn for Turnbull *et al.* (1999b).

neous exclusion of competitively inferior species. By allowing finite rates of competitive exclusion, Pacala and Rees (1998) incorporate a successional niche whereby early successional species, which are poor competitors, can dominate recently disturbed sites although they are ultimately excluded by the late successional species. In this model, adding saturating densities of seeds to all sites does not cause a collapse of diversity because the early successional species is able to reproduce in recently disturbed sites, regardless of the abundance of the late successional, superior competitor.

Pacala and Rees (1998) suggest that by combining seed sowing and competitor removal experiments, the relative importance of the competition–colonization and niche mechanisms can be assessed. In addition, they argue that in many systems where disturbances are of small spatial extent, the niche mechanism will be more important than competition–colonization. This is because late successional, superior competitors eventually occupy almost all sites. Disturbed areas therefore always contain propagules of the superior competitor, making it impossible for the early successional, poor competitor to persist. The seed sowing experiments of Crawley *et al.* (unpublished) have shown that when saturating densities of all species are sown in a mesic grassland it is the early successional forbs that increase in abundance, not the late successional species, as predicted by the competition–colonization model. This suggests that early successional species are more

recruitment limited than late successional species, making coexistence via the competition–colonization trade-off impossible.

The distinction between the niche and competition–colonization hypotheses is important, in part because the two hypotheses have strikingly different management implications. In systems where diversity is maintained by the competition–colonization mechanism even small amounts of habitat destruction lead to extinction of late-successional species (Nee and May 1992). The reason is that rare, late-successional species are near the brink of extinction because of their poor colonizing ability. Any habitat destruction causes them to waste seeds that disperse into unsuitable areas. This small loss of colonizing ability pushes rare late-successional species to extinction. In contrast, because species can coexist even when all sites are colonized when there is a successional niche, small amounts of habitat loss may not result in any extinctions. However, when there is recruitment limitation, resulting in failure to colonize some sites, habitat destruction can result in extinction of either early or late successional species depending on which is more recruitment limited (Pacala and Rees 1998).

Spatial seed dispersal can evolve in response to a range of different types of environmental heterogeneity (Venable and Brown 1993). Not all types of heterogeneity favour the evolution of dispersal, for example, if the habitat consists of a fixed mosaic of habitat patches then no dispersal from the parental site is the evolutionarily stable strategy (ESS) (Hastings 1983). This occurs because dispersal results in net movement of seeds from good patches to bad ones so lowering fitness and selecting against dispersal. Dispersal can evolve as a bet hedging strategy only when there is global temporal variation in reproductive success. Here dispersal reduces the variance in reproductive success, which increases the geometric mean fitness (Levin *et al.* 1984). In a temporally stable environment, dispersal can evolve to reduce the effects of local crowding, and this requires spatial variation in the quality of the environment but no global temporal variation (Venable and Brown 1993). Finally, if there is genetic structure, dispersal can evolve as a way of reducing competition between relatives (Hamilton and May 1977; Comins *et al.* 1980). When there is temporal variation in the environment, either local or global, the pattern of variation, whether it shows positive or negative covariation, also becomes important and can lead to the evolution of multiple dispersal types (Ludwig and Levin 1991). Olivieri *et al.* (1995) put these ideas in a successional framework and show that there are conflicting selection pressures within and between populations (demes). Within population selection favours low dispersal, while between population selection favours migrants, and this can lead to the coexistence of genotypes with different dispersal rates.

How will habitat destruction influence the evolution of dispersal and population persistence? Increasing urbanization and conversion of natural habitats to agriculture creates areas which are permanently unsuitable for population growth. This situation is analogous to the colonization of oceanic islands, where each population is surrounded by large areas of unsuitable habitat. This can lead to rapid evolution resulting in reduced dispersal ability (Cody and Overton 1996). This in turn makes the populations more isolated, resulting in habitat specializa-

tion, and reducing the likelihood of metapopulation persistence. This topic is explored further by Dytham (this volume).

Evolution and ecological consequences of delayed and repeated reproduction

Both delayed reproduction in monocarpic plants and repeated reproduction in iteroparous species result in offspring experiencing different environments and so both processes can be considered forms of dispersal. The ages at flowering of individuals of *Onopordum illyricum* and *Carlina vulgaris* are shown in Fig. 12.4; clearly there is considerable variation in the age at which individuals flower resulting in individuals within a cohort, experiencing very different environments. These data pose two evolutionary questions: (i) Why do plants wait to flower, and a corollary of this, can we predict the optimal age at flowering; and (ii) Why is there such a large spread in the timing of reproduction? This section will be devoted to monocarpic plants simply because the fitness consequences of delayed reproduction are simpler to quantify in species that reproduce only once. In species with multiple reproductive episodes there are additional problems associated with quantifying the costs of reproduction and possible effects of mast seeding. Having said this,

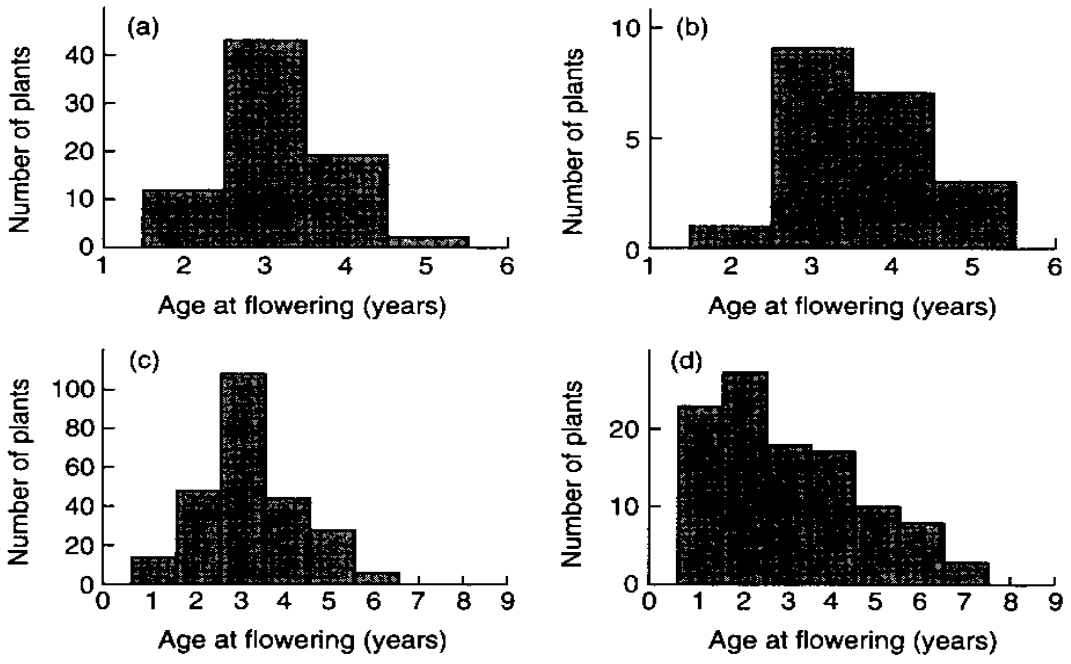

Figure 12.4 Age at flowering in monocarpic perennials. In all cases there is considerable spread in the timing of the reproduction. (a) and (b) *Onopordum illyricum* at two sites in the south of France ((a) Viols and (b) La Crau; see Rees *et al.* (1999)). (c) and (d) *Carlina vulgaris* at two sites. (c) *Salix* vegetation in the Meijendal dune system, the Netherlands (Klinkhamer *et al.* 1996) and (d) chalk grassland at Castle Hill National Nature Reserve, near Brighton. Data kindly supplied by Peter Grubb.

many of the ideas developed for monocarpic plants are directly applicable to iteroparous species, see Charnov (1993).

The main deterministic selective forces influencing delayed reproduction in monocarpic plants are:

1 Increased mortality as a result of delaying reproduction;
2 Increased reproduction, as a result of growth.

These selective forces underpin the simple growth models used to predict the evolutionarily stable size and age at reproduction; this approach has an extensive pedigree in the animal literature (Roff 1984; Roff 1986; Roff 1992; Stearns 1992; Charnov 1993; Mangel 1996). We now outline these simple models, and assess their ability to predict patterns of flowering observed in the field.

Simple models ignoring heterogeneity

We assume that size on a log scale, $L(t)$, at time t can be described by a 3-parameter von Bertalanffy equation:

$$L(t) = L_\infty(1-\exp(-k(t-t_0))), \tag{12.6}$$

where L_∞ is the maximum possible size, k is a rate parameter and t_0 is the hypothetical (negative) age at which size would be zero. An important assumption implicit in this equation is that all individuals grow along a deterministic trajectory so that age and size are interchangeable. This could only be true if there is no heterogeneity in the environment. We assume a constant rate of mortality m, so the probability an individual survives to age t is $\exp(-mt)$. The probability a seed becomes an established plant is p. Finally, we assume that the seed production of an individual of size $L(t)$, is an exponential function of plant size, namely:

$$\text{seeds} = \exp(A + BL(t)), \tag{12.7}$$

where A and B are allometric parameters relating log-seed set to log-size (van der Meijden and van de Waals-Kooi 1979; Samson and Werk 1986; Rees and Crawley 1989). Combining these formulae, we obtain an expression for the expected number of offspring produced by an individual that reproduces at age t,

$$R_0 = p\exp(-mt)\exp[A + BL_\infty(1-\exp(-k(t-t_0)))]. \tag{12.8}$$

R_0 consists of two components: the first is the probability an individual survives to age t, and the second is the seed production of a plant of size $L(t)$ We can calculate the ESS flowering time, $\tilde{t}$, by solving $\partial R_0/\partial t = 0$ which gives:

$$\tilde{t} = \frac{\ln\left(\frac{BkL_\infty}{m}\right)}{k} + t_0, \tag{12.9}$$

and substituting this into equation (12.6) we find the ESS flowering size,

$$\tilde{L} = \text{Asymptotic size} - \text{mortality term}$$

$$= L_\infty - \frac{m}{Bk}. \tag{12.10}$$

Evolutionary stability occurs if $\partial R_0/\partial^2$ evaluated at $\tilde{t}$ is negative; which is always true in this case. In calculating the ESS in this way we are assuming that density dependence acts at the seedling stage (Charnov 1993; Kawecki 1993), which is a reasonable assumption for many plant species. As expected the ESS flowering size increases with the asymptotic length, and decreases with increasing mortality. The mortality term is, however, offset by the growth rate, k, and the slope of the fecundity relationship, B. In these simple models all forms of heterogeneity are assumed to be unimportant. We now ask, how well do these models describe actual flowering strategies?

Case studies ignoring heterogeneity

Rees *et al.* (1999) used the simple growth models, described above, to explore size-dependent flowering in *Onopordum illyricum* growing in the south of France. Using long-term demographic data, from two field sites, we parameterized the simple growth models and predicted the average size at flowering should be $\approx 1000\,\text{cm}^2$. At both sites, the prediction error was greater than 50%; the plants actually flowered at sizes approximately double the model predictions. Clearly, this approach, which ignores all forms of heterogeneity, does not accurately describe the flowering strategies of plants in the field.

Oenothera glazioviana is a monocarpic plant that often occurs in sand dune areas, and its demography has been extensively studied by Kachi and Hirose (Kachi and Hirose 1983; Kachi 1983; Kachi and Hirose 1985). For an *Oenothera* rosette relative growth rate (RGR), is given by:

$$\text{RGR} = \frac{L(t+1) - L(t)}{\Delta t} = -0.65L(t) + 0.96 + \varepsilon_{i,t}, \tag{12.11}$$

where $L(t)$ is log rosette diameter in May, $\Delta t = 1$ year, and $\varepsilon_{i,t}$ is a standard normal deviate with mean zero and standard deviation, $\sigma_{i,t} = 0.45$; this represents the residual scatter about the regression line. The probability of flowering is given by:

$$\text{p(flowering)} = 1.1L(t) - 2.29, \tag{12.12}$$

and the survivorship of vegetative rosettes by:

$$\text{p(rosette survival)} = 0.17L(t) + 0.36, \tag{12.13}$$

where the probability of rosette survival has an upper asymptote of 0.7. The number of seeds produced as a function of rosette diameter is given by:

$$\text{seeds} = \exp(2.22L(t) + 1.035). \tag{12.14}$$

Note, the parameters in Kachi and Hirose (1985) are given for log to the base 10 and we have converted to natural logarithms by dividing by ln(10). The number of recruits was independent of seed production suggesting density dependence acts on seedlings (Fig. 12.5). With these assumptions, we can implement the flow chart given in Kachi and Hirose (1985), their Fig. 1, using an individual-based approach. We used output from the simulation model to parameterize a von

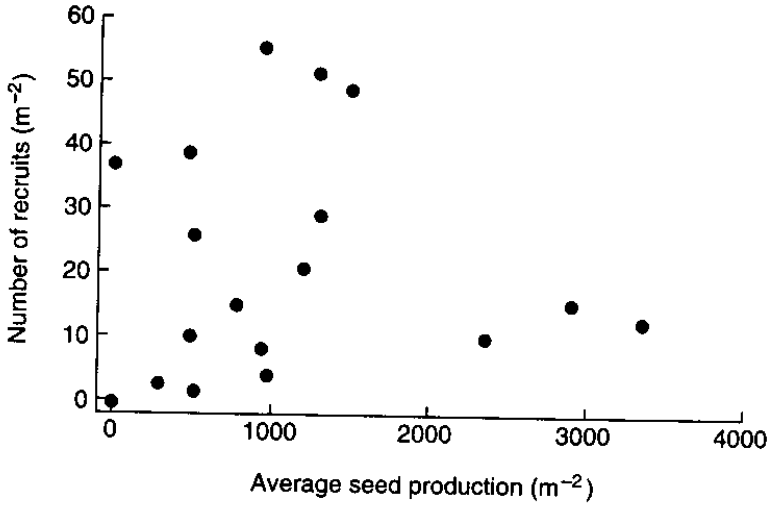

Figure 12.5 Relationship between the number of new *Oenothera* recruits and the previous years' seed production (data from Kachi (1983)). There is no significant relationship between seed production and subsequent recruitment (linear regression $F_{1,16}=0.001$, $p>0.1$).

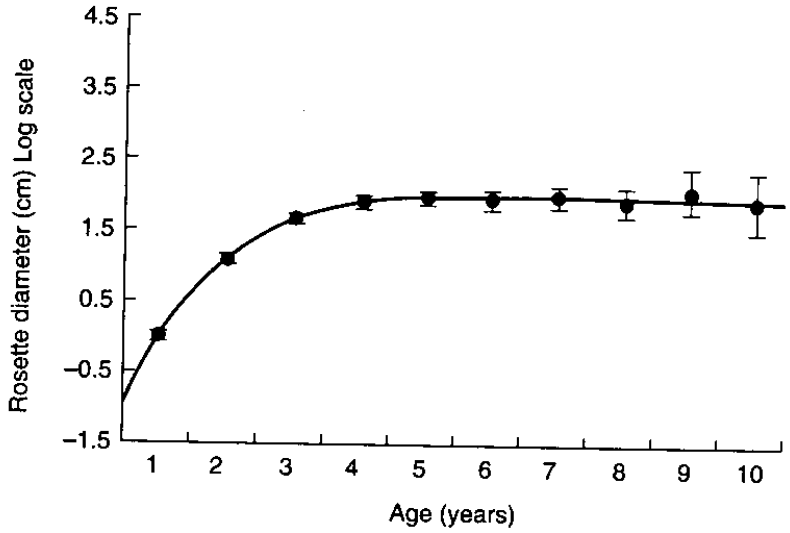

Figure 12.6 Relationship between predicted rosette diameter and plant age. The solid circles are means of data generated from an individual-based simulation, using the parameterized growth equation of Kachi and Hirose (1985), see text for details. The fitted line is a 3-parameter von Bertalanffy equation. Estimated parameters $L_\infty=2.17$, $k=0.72$ and $t_0=1.05$. $r^2=0.53$. The vertical bars are 2 standard errors.

Bertalanffy growth model (equation 12.6), see Fig. 12.6. As in the Kachi and Hirose (1985) simulation, plant size reached an asymptote of ≈ 9 cm rosette diameter. We also used the simulation model to estimate the probability of a plant surviving to age t, this probability is accurately described ($r^2=0.99$, $n=9$) by:

$$p(\text{survival to age } t) = 0.57\exp(-0.54t). \qquad (12.15)$$

Substituting the parameter estimates into equations 12.9 and 12.10 we obtain, $\tilde{t}=$ 3.6 years and $\tilde{L}=1.84$ (log scale) which corresponds to a diameter of 6.3 cm. Average size at flowering is ≈18 cm (Kachi and Hirose 1983), with a median flowering size of 14 cm. The ESS prediction is considerably lower than the observed values, and indeed is smaller than the smallest flowering size ever observed. *O. glazioviana* takes between 3 and 6 years to flower in rough agreement with the theoretical prediction (Hirose and Kachi 1982). Clearly, as in *Onopordum*, the simple growth model approach has failed to capture the important evolutionary trade-offs that determine flowering size in *Oenothera*.

We also applied this approach to the long-term data set on *Carlina vulgaris* collected by Peter Grubb (Rees *et al.* in preparation). In this study, the fate of over 1000 individuals was followed over an 18-year period. All individuals were sized and whether they flowered or died recorded. Using these data, we parameterized the simple growth and survival models described above. The fitted relationships and parameter estimates are given in Fig. 12.7. We do not have good data on reproductive allocation and so have assumed constant proportional reproductive allocation; this corresponds to $B=1$ in equation (12.7). This provides a good description of reproductive allocation in several monocarpic species (Reinartz 1984a; de Jong *et al.* 1989; Klinkhamer and de Jong 1993). Using these parameter estimates, we predicted that plants should flower at 7 mm, whereas the average size of flowering plants was 49.5 mm (Fig. 12.8). The model predictions are smaller than the smallest size ever observed flowering in an 18-year study (Rees *et al.* in preparation). As in the other species this simple approach, which ignores all forms of heterogeneity, considerably underestimates the size at flowering. The main

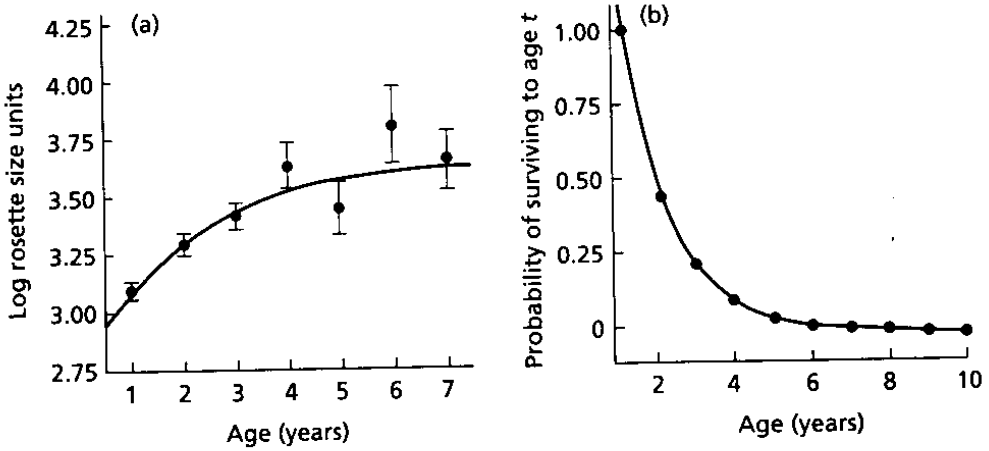

Figure 12.7 Age-specific demography of *Carlina vulgaris*. (a) Rosette diameter as a function of plant age. The line is the fitted von Bertalanffy growth curve; the vertical bars are standard error. Parameter estimates $L_\infty=3.68$, $k=0.45$ and $t_0=-3$. (b) The probability a rosette survives to age t; the line is the fitted function $p\exp(-mt)$ where t is plant age. Parameter estimates $p=2.18$ and $m=0.74$. Data kindly supplied by Peter Grubb.

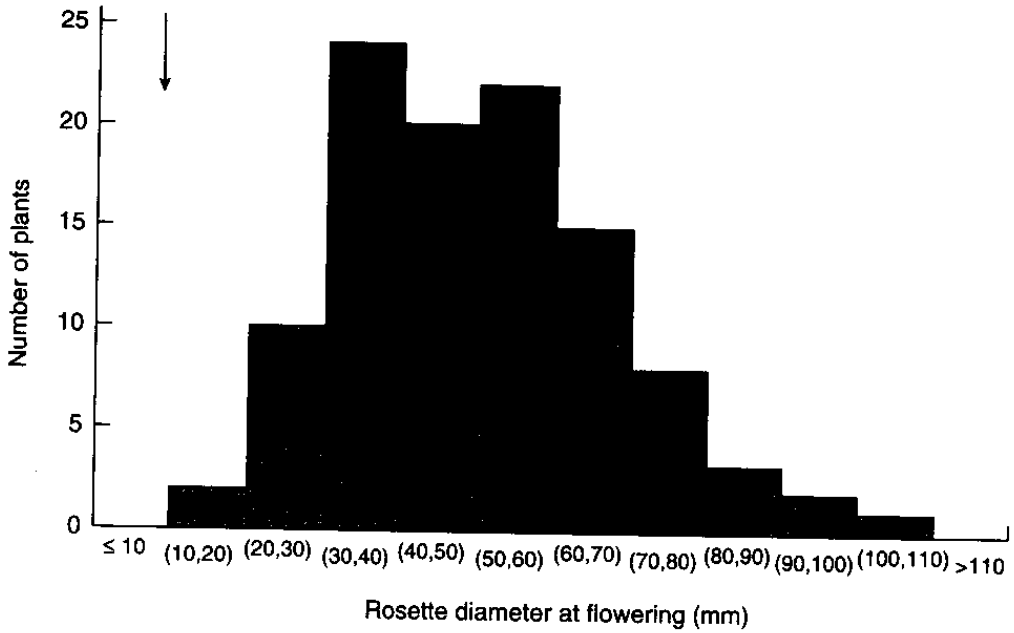

Figure 12.8 Size distribution of flowering plants in *Carlina vulgaris*. The arrow indicates the predicted size at flowering assuming there is no heterogeneity in the system. Data kindly supplied by Peter Grubb.

reason these models make predictions far too small is that the asymptotic size predicted by the growth models is too small. In order to predict the flowering strategies observed in field populations, we need to understand how various forms of heterogeneity influence flowering decisions, and then quantify these sources of heterogeneity. Once quantified, we can use modelling approaches to determine whether the measured levels of heterogeneity are sufficient to explain the observed pattern of flowering.

Analytical models exploring the effects of heterogeneity

In order to begin to understand the effects of heterogeneity it is useful to classify different types of heterogeneity; the different forms of heterogeneity should ideally be easily estimated from field data. In this way, the impact of various forms of heterogeneity on population dynamics and evolution can be explored. Three types of heterogeneity are considered:

1 *non-specific heterogeneity* where individuals experience different environments in different years;

2 *individual-specific heterogeneity* where individuals experience different environments but the effects are constant throughout their lifetime; and

3 *temporal heterogeneity* where all individuals experience the same environment in a given year but the effects vary between years.

This simple classification requires some explanation, consider the following simple model for plant growth:

$$L_i(t+1) = a_g + b_g L_i(t) + \varepsilon_{i,t} \tag{12.16}$$

where a_g and b_g are parameters, $L_i(t)$ is the log size of plant i at time t and $\varepsilon_{i,t}$ follows a Normal distribution with mean zero and variance $\sigma^2_{i,t}$. Therefore, in each year, each plant grows according to a linear model and each receives a different value of $\varepsilon_{i,t}$. This is an example of non-specific heterogeneity. Note, because the expected values (averages) of a_g, b_g and and $\varepsilon_{i,t}$ do not vary with time there is no temporal heterogeneity in this model. Also as each individual gets a new value of $\varepsilon_{i,t}$ in each time interval there is no individual-specific heterogeneity. We can include individual-specific heterogeneity by adding a new error term to the model, so we have:

$$L_i(t+1) = a_g + b_g L_i(t) + \varepsilon_{i,t} + \varepsilon_i. \tag{12.17}$$

In this model, each individual has its own growth intercept given by $a_g+\varepsilon_i$, and this does not vary from year to year. Again, because the expected values of the model parameters do not vary between years there is no temporal heterogeneity. The final model includes temporal heterogeneity, and so we have

$$L_i(t+1) = a_g + b_g L_i(t) + \varepsilon_{i,t} + \varepsilon_i + \varepsilon_t, \tag{12.18}$$

where the term ε_t represents temporal variation in the intercept of the growth equation; that is the intercept of individual i in any particular year is $a_g+\varepsilon_i+\varepsilon_t$. These different forms of heterogeneity can be quantified using linear mixed models (Venables and Ripley 1997); see Rees *et al.* (1999) for a biological example of this approach.

For a plant to grow, we require that $a_g>0$ and for it to achieve an asymptotic size, $b_g<1$. In that case the asymptotic size, on a log scale, is found by setting $\tilde{L}_i = a_g + b_g \tilde{L}_i + \varepsilon_i$, so that:

$$\tilde{L}_i = \frac{a_g + \varepsilon_i}{(1-b_g)}. \tag{12.19}$$

Averaging over individuals, we find the average asymptotic size in the population, $\bar{L} = a_g/(1-b_g)$. This assumes the average value of ε_i is zero.

How do these different forms of heterogeneity influence the evolution of size-dependent flowering? The effects of individual-specific and non-specific heterogeneity can be explored analytically using the one-year look-ahead approach developed in Rees *et al.* (1999). This approach leads to a switching value L_s. Plants with $L(t)>L_s$ are predicted to reproduce in year t, whereas those with $L(t)<L_s$ are predicted to continue to grow. We compare reproduction given the current size, $L(t)$, with the expected reproduction in the next year, taking growth and survival into account. The switch value will be the size that makes these equal. It should be realized that this approach is only approximate because growth opportunities more than one-year ahead will influence the optimal switch value. However, comparing this approach with a dynamic state variable model indicates that the error involved is generally less than 10% (Rees *et al.* 1999). We assume that mortality is

independent of plant size, which is a reasonable assumption for large-sized individuals, and that seed production is described by equation (12.7). Non-specific heterogeneity in growth is described by equation (12.16), and this leads to the following equation, which the switching value satisfies

$$\exp(A+BL_s)=\int f(\varepsilon_{i,t})\exp(-d_0+A+B(a_g+b_gL_s+\varepsilon_{i,t}))d\varepsilon_{i,t} \tag{12.20}$$

where $f(\varepsilon_{i,t})$ denotes the probability density function for $\varepsilon_{i,t}$ and $\exp(-d_0)$ is the probability of survival. The term on the left-hand side of equation represents current reproduction and the term on the right-hand side expected future reproduction, taking growth and survival into account. The integral on the right-hand side can be evaluated by completing the square in the Gaussian integral, remembering that $\varepsilon_{i,t}$ follows a Normal distribution (see Hilborn and Mangel (1997) page 75) and is:

$$\int f(\varepsilon_{i,t})\exp(B\varepsilon_{i,t})d\varepsilon_{i,t}=\exp(B^2\sigma_{i,t}^2/2). \tag{12.21}$$

Making this substitution and solving for L_s gives:

$$\begin{aligned}L_s &= \text{Asymptotic size} + \text{variance term} - \text{mortality term}\\ &=\frac{a_g}{1-b_g}+\frac{B\sigma_{i,t}^2}{2(1-b_g)}-\frac{d_0}{B(1-b_g)}\end{aligned} \tag{12.22}$$

The dependence of the switching value on d_0 is intuitive and sensible: as the chance of mortality increases, the payoff from immediate reproduction is greater than the payoff from waiting, and thus we predict a decrease in the switching value. That it scales by $B(1-b_g)$ could not be anticipated without analysis. Furthermore, and perhaps more importantly, equation (12.22) demonstrates that non-specific heterogeneity in growth is important for the switching value. In particular, because the variance term is always positive, as variability increases, the predicted size at switching increases.

Assuming there is no variance in growth ($\sigma_{i,t}^2=0$) gives:

$$L_s=\frac{a_g}{1-b_g}-\frac{d_0}{B(1-b_g)}, \tag{12.23}$$

which is the same form as the ESS prediction derived from the von Bertalanffy growth model with $L_\infty=a_g/(1-b_g)$, $m=d_0$ and $k=(1-b_g)$, see equation (12.10) (Charnov 1993; Mangel 1996).

We can also incorporate individual-specific heterogeneity into this framework, which leads to the following equation for the switching value:

$$\begin{aligned}\exp(A+BL_s)&=\iint f(\varepsilon_{i,t})f(\varepsilon_i)\exp(-d_0+A+B(a_g+b_gL_s+\varepsilon_{i,t}+\varepsilon_i))d\varepsilon_{i,t}d\varepsilon_i\\ &=\frac{a_g}{1-b_g}+\frac{B(\sigma_{i,t}^2+\sigma_i^2)}{2(1-b_g)}-\frac{d_0}{B(1-b_g)}\end{aligned} \tag{12.24}$$

where σ_i^2 is the variance of the individual-specific heterogeneity distribution, which is also assumed to follow a Normal distribution. As with non-specific

heterogeneity, this form of heterogeneity increases the predicted switching value. Both these models assume that plants have no information on the heterogeneity in the system. If plants had complete information on their individual-specific heterogeneity then we would expect individuals to flower at different sizes, and the switching value for an individual would be:

$$L_{s,i} = \frac{a_g + \varepsilon_i}{1-b_g} + \frac{B\sigma^2_{i,t}}{2(1-b_g)} - \frac{d_0}{B(1-b_g)}. \tag{12.25}$$

Note, however, that when plants have complete information on individual-specific heterogeneity then the average switch value, $\tilde{L}_s$, does not change:

$$\begin{aligned}\tilde{L}_s &= \int f(\varepsilon_i)\left(\frac{a_g + \varepsilon_i}{1-b_g} + \frac{B\sigma^2_{i,t}}{2(1-b_g)} - \frac{d_0}{B(1-b_g)}\right)d\varepsilon_i \\ &= \frac{a_g}{1-b_g} + \frac{B\sigma^2_{i,t}}{2(1-b_g)} - \frac{d_0}{B(1-b_g)}\end{aligned} \tag{12.26}$$

These models illustrate how individual-specific and non-specific heterogeneity influence the reproductive decisions of monocarpic plants. If plants have no information on the heterogeneity in growth, then the optimal switch value, L_S, generally increases with increasing heterogeneity, equation (12.24). In this model, there is an optimal switch value and any variation about this is maladaptive. When plants have information on the heterogeneity acting on them and can adjust their switch value appropriately, either through a phenotypic or genetic response, then the optimal switch value varies from individual to individual, but the population average value does not change, equation (12.26).

In natural populations the relationship between the probability of flowering and plant size is often relatively shallow, with substantial overlap between the size distributions of flowering and non-flowering plants (Werner 1975; Baskin and Baskin 1979; van der Meijden and van de Waals-Kooi 1979; Gross 1981; Hirose and Kachi 1982; van Baalen and Prins 1983; Reinartz 1984b; Wesselingh *et al.* 1993; Bullock *et al.* 1994; Klinkhamer *et al.* 1996). It has been suggested that this overlap results from the additional factors, weakly correlated with size, influencing the control of flowering (de Jong *et al.* 1986). However, this would lead to equal within-population variance in flowering size and the data in Wesselingh *et al.* (1993) contradicts this idea. For example, in populations of *Cynoglossum officinale* from botanical gardens, there was virtually no overlap in the distributions of flowering and non-flowering plants, whilst in natural populations there was considerable overlap (Wesselingh *et al.* 1993). Weak selection against large threshold sizes for flowering is another possible explanation. A third possible explanation is that the graded response of flowering to plant size is a consequence of an adaptive response to spatially or temporally varying selection pressures. This adaptive response could either have a phenotypic or genetic basis; however, it should be noted that selection experiments have shown there is substantial genetic variance in the threshold size for flowering (Wesselingh and de Jong 1995; Wesselingh and Klinkhamer 1996).

We cannot explore the effects of temporal heterogeneity using the one-year look-ahead approach, as the geometric mean fitness is the appropriate fitness measure and individual optimization fails (Metz *et al.* 1992; McNamara *et al.* 1995). However, simulation studies, using an individual-based model incorporating a simple genetic algorithm, have shown that temporal heterogeneity in the growth equation makes delaying reproduction more risky, and this selects for smaller sizes at flowering (Rees *et al.* 1999).

Case studies including heterogeneity

In order to explore the discrepancy between the analytical predictions of the growth models and the field data, we developed a range of models that allow heterogeneity to be incorporated. Specifically, we used the one-year look-ahead approach, a dynamic state variable model (Mangel and Clark 1988; Mangel and Ludwig 1992), and an individual-based simulation, which incorporated a simple genetic algorithm and so allows the flowering strategy to evolve.

For *Oenothera glazioviana*, we modified the one-year look-ahead approach to use the parameterized functions for growth, survival and flowering, see equations (12.11), (12.12), (12.13) and (12.14) (Kachi and Hirose 1985). For this species, we only have information on non-specific heterogeneity, $\varepsilon_{i,t}$, in the growth equation. Using the published parameter values gives a predicted switch value, L_s, of 2.78, which using forward iteration (Mangel and Clark 1988), corresponds to an average size at flowering of 24 cm. The one-year look-ahead is 'myopic' in the sense that it ignores all growth opportunities except for those in the following year. For example, in small plants, the expected seed production from waiting 2 years may be greater than from waiting one year because of the stochastic variation in growth. So for a given plant size, the optimal decision based on the one year look-ahead might be to flower, whereas using a 2-year look-ahead the optimal decision might be to wait. We therefore require a technique that allows growth opportunities several years ahead to influence the optimal flowering strategy. Dynamic state variable (DSV) models allow this type of calculation to be easily performed (Mangel and Clark 1988; Mangel and Ludwig 1992). In this model, we assume that there is a terminal time, T, at which the plant must reproduce; the time T can be interpreted alternatively as the time of reproductive senescence or the time at which successional changes make reproduction mandatory, see Rees *et al.* (1999) for details of model construction. The DSV model allows the calculation of switch values, L_s, allowing for growth opportunities several years ahead. The approach calculates the optimal decision at time $T-1$, and then works backward in time and in this way allows for growth opportunities several years ahead. The DSV and one-year look-ahead approaches agree at time $T-1$ because there is only a single growth opportunity at this time. The DSV solutions are age-dependent although mortality up to time T is age-independent (Fig. 12.9). However, when there is little variance about the growth curve, the flowering strategy is age-independent. The DSV model predicts, using forward iteration, an average size at flowering of 26 cm; clearly, the one-year look-ahead approach is a good approximation to the DSV model. If we ignore

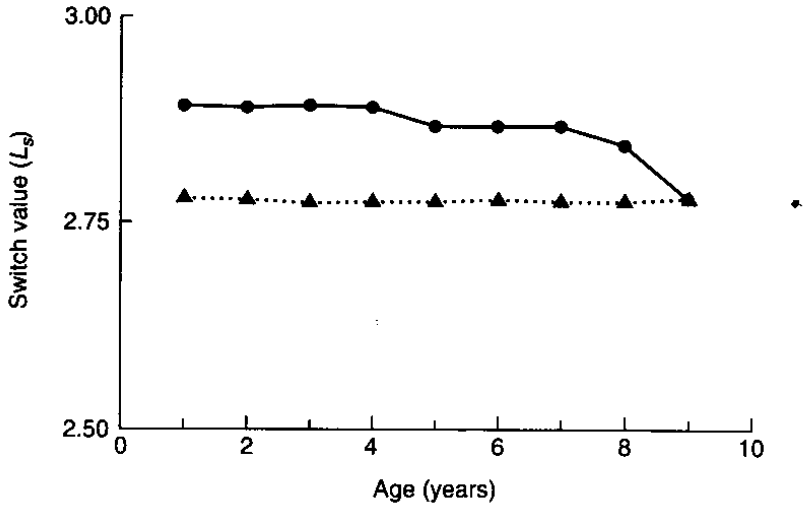

Figure 12.9 The predicted switching curve for Oenothera calculated using the DSV and one-year look-ahead models. Above the switching curve, individuals are predicted to reproduce; below it they are predicted to continue growing. The solid line is the DSV switching value; the dashed line is the one-year look-ahead switching value. As expected the two approaches give identical answers at time T-1 where there is only one year of growth possible. In this case T= 10, see text for other parameter values.

non-specific heterogeneity in growth, by setting $\varepsilon_{i,t}=0$ in equation (12.11), then both approaches predict a switch value of 1.97, which corresponds to an average size at flowering of 7.2 cm. This is close to the prediction based on the von Bertalanffy growth model (6.3 cm). We learn two things from these models:

1 Non-specific heterogeneity about the growth curve potentially has a large effect on the predicted flowering strategy, and as anticipated from the analytical models selects for larger sizes at flowering.

2 The combination of non-specific heterogeneity about the growth curve and an upper bound on longevity results in an age-dependent flowering strategy. This is a result of varying opportunities for growth as plants approach the terminal time, T. It is not a consequence of age-dependent mortality as demonstrated by the fact that the flowering strategy is not age-dependent when growth is deterministic.

In order to explore the generality of these approaches we developed an individual-based simulation, based on the flow diagram given in Kachi and Hirose (1985). We used the simulator to explore when and at what size a plant should flower. We did this by introducing a simple genetic algorithm (GA) into the model (Sumida *et al.* 1990). In the model, each individual is characterized by its size and age, but in addition to this also has a flowering strategy. Each seed inherits its parent's flowering strategy plus a small random deviation. In all the simulations, we assumed that offspring strategies were uniformly distributed about the parental strategy with a range of ± 0.05. The number of recruits next year is independent of the seed production this year, as demonstrated by Kachi (1983) see Fig. 12.5, but the flowering strategy of each recruit is determined by a fair lottery amongst seeds.

In this way, the flowering strategies of the recruits reflect the relative reproductive success of the different flowering strategies in the population. In the GA model, the intercept in equation (12.12), which describes how the probability of flowering varies with plant size, was allowed to evolve. We explored two different scenarios: in the first, we assumed there was no scatter about the growth equation (i.e. $\varepsilon_{i,t}=0$ in equation [12.11]), which means that all plants follow a deterministic growth curve, as in the simple growth models. In the second scenario, we incorporated the non-specific heterogeneity by using the estimated error variance about the growth equation.

In the first scenario the model evolved to an intercept of 1.5, which corresponds to an average diameter at flowering of 6.7 cm and an average age at flowering of 3.6 years (Fig. 12.10). These values agree well with the analytical predictions (von Bertalanffy 6.3 cm, DSV and one-year look-ahead 7.2 cm), but are considerably less than those observed in the field. In the second scenario the model evolved to an intercept of 2.5, which is close to the estimated value of 2.3, and the average diameter at flowering was 21.8 cm, which is close to the field value of ≈ 18 cm. The age at flowering was 4.7 years, which is within the range observed in the field (3–6 years) and exactly matches the value obtained in Kachi and Hirose (1985) simulation. Using the DSV results we can calculate the intercept predicted by the GA model; we do this by setting the probability of flowering, equation (12.12), equal to 0.5, L equal to L_s and solving for the intercept. This gives a predicted intercept of 2.55 while the GA gives 2.5; the agreement between the approaches is excellent.

Clearly, the non-specific heterogeneity about the growth curve is an important aspect of *Oenothera*'s demography and has substantial implications for the evolution of size at flowering in this species.

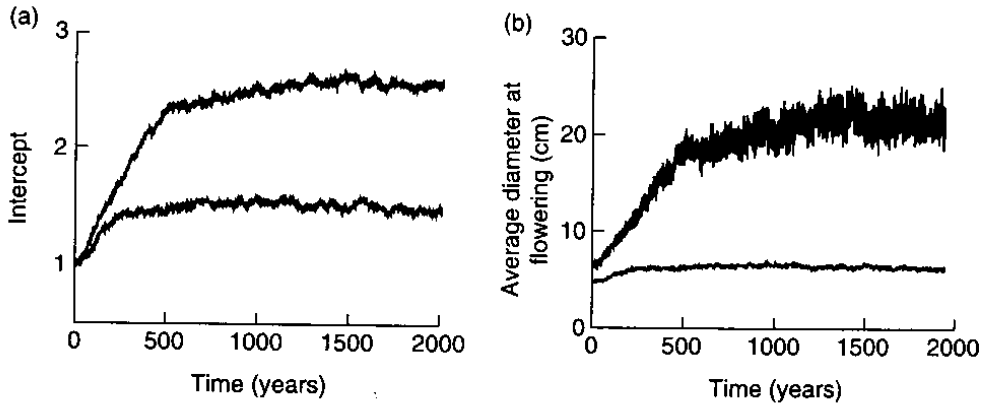

Figure 12.10 Evolutionary trajectories for *Oenothera* under two growth scenarios. (a) Evolution of the intercept of the probability of flowering equation and (b) the average size at flowering. In both panels the upper trajectory corresponds to scenario two, where there is non-specific heterogeneity in the growth equation, the lower trajectory is scenario one where there is no heterogeneity in the growth equation, see text for details. Note the non-specific heterogeneity in growth selects for substantially larger sizes at flowering, as predicted by the analytical models.

The size and age-dependent demography of *Onopordum illyricum* is described in Rees *et al.* (1999). As discussed earlier the simple growth model approach, equation (12.10), fails to describe the size-dependent flowering in this species, in fact this approach gives predictions that are 50% smaller than the average size observed in the field. Statistical analysis of the long-term population data indicated that:

1 recruitment was independent of the previous year's seed production;
2 mortality varied from year to year and was age and size-dependent; there was substantial individual-specific heterogeneity (Fig. 12.11);
3 flowering was age and size-dependent; there was little individual-specific heterogeneity, and growth varied from year to year and was age and size-dependent; there was little individual-specific heterogeneity but substantial non-specific heterogeneity.

Incorporating individual-specific and non-specific heterogeneity but excluding temporal heterogeneity into one-year look-ahead and DSV models lead to predicted sizes at flowering approximately double ($\approx 3600\,cm^2$) those observed. Surprisingly the substantial individual-specific heterogeneity in mortality had little impact on model predictions. This occurs because over the range of sizes that plants flower: (i) the individual-specific heterogeneity, in the intercepts of the mortality curve, translates into small changes in the probability of death; and (ii) the logistic mortality curve is approximately linear (Fig. 12.11). With approximate linearity and small changes in the probability of death between individuals, the effects of individual-specific heterogeneity in the intercepts of the mortality curve are small. Using an individual-based model incorporating a genetic algorithm, we

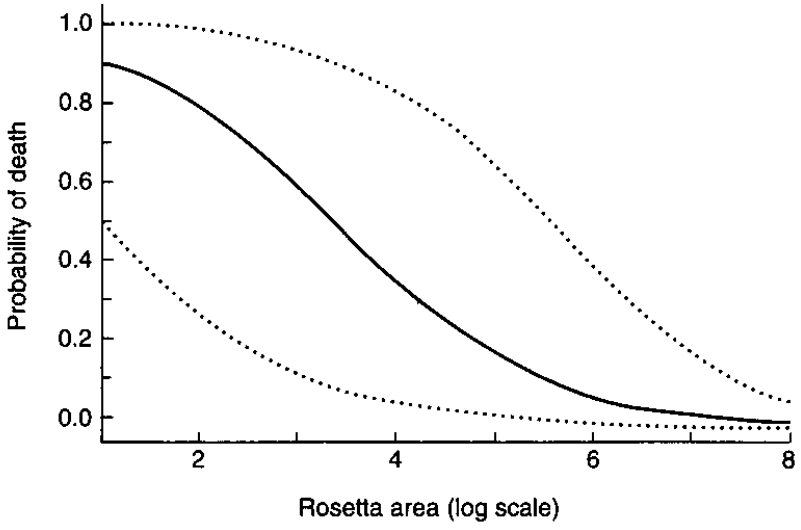

Figure 12.11 Probability of mortality in *Onopordum illyricum* for a two-year-old individual in the average environment (middle solid line) and ±3 standard deviations about the average (dotted lines about the central line). For an individual of size 4 the probability of mortality could be anything from 0.05 to 0.95, demonstrating substantial individual-specific heterogeneity. Redrawn from Rees *et al.* (1999).

studied the effects of temporal heterogeneity in growth. This model showed that temporal heterogeneity in growth selected for smaller sizes at flowering and gave predictions extremely close to the sizes at flowering observed in the field; the prediction error (predicted-observed/observed) was less than 2%. We can use this model to predict the distribution of age at flowering (Fig. 12.12). The predicted distributions are similar to those observed in the field (Fig. 12.4). The spread in the timing of reproduction is a direct consequence of the temporal and non-specific heterogeneity in growth.

In this system different forms of heterogeneity select for larger or smaller sizes at flowering or have little effect. How do the various forms of heterogeneity influence population size? We assessed this by running the model ignoring the different forms of heterogeneity in turn; the model predictions are given in Table 12.1. Clearly, the heterogeneities in this system have relatively little impact on the predicted population sizes. However, heterogeneity is critical in determining the average values of the model parameters through an evolutionary response. Therefore, although the direct effects of heterogeneity on population size are small, the indirect effects through evolutionary changes in model parameters, can be large.

Discussion

In this chapter we have explored how heterogeneity may be generated by colonization limitation, resulting in not all sites being colonized, and so allowing coexistence of species that otherwise would be unable to persist together. This heterogeneity can influence the conditions for coexistence; however, simple models based on the negative binomial distribution are potentially misleading. In

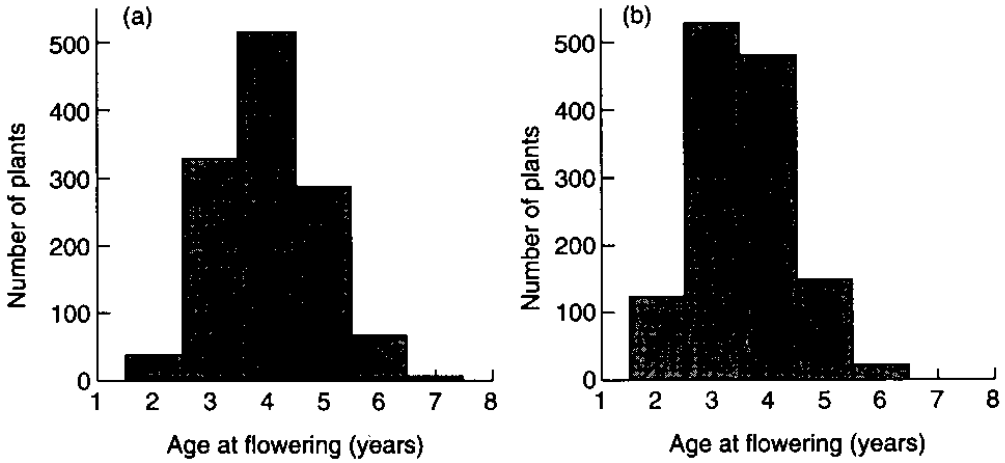

Figure 12.12 Predicted distributions of age at flowering in *Onopordum illyricum*, from an individual-based model incorporating all three types of heterogeneity. The predictions are for two sites in France, (a) La Crau and (b) Viols. In both cases, the models predict a wide range of ages at flowering. This is a consequence of the heterogeneity in growth combined with a size-dependent flowering strategy. See Rees *et al.* (1999) for details of the model.

Table 12.1 Effects of removing various forms of heterogeneity on the predicted population size based on an individual-based model of *Onopordum illyricum* at two sites. In each case, we removed the one form of heterogeneity at a time, leaving the others in the model, except where all forms of heterogeneity were removed

	La Crau	Viols
Data	176	240
Model	172	283
Temporal heterogeneity in growth	174	290
Temporal heterogeneity in mortality	148	219
Individual-specific heterogeneity in mortality	172	267
Individual-specific heterogeneity in growth	177	287
Non-specific heterogeneity in growth	179	296
All heterogeneity	152	217

these models, the condition for invasion of an inferior competitor does not depend on its spatial distribution, suggesting that dispersal does not influence community structure. This is a direct consequence of the way the invasion condition, which ensures that a species can increase when rare, is calculated. In more realistic models that consider the persistence of insects exploiting a patchy, ephemeral resource and explicitly include local movement, invasion depends on the foraging strategies of the competing species (Heard and Remer 1997; Remer and Heard 1998). These models assume that individuals have a fixed number of eggs that can be laid in clutches, and patches are visited at random (Remer and Heard 1998). If the inferior competitor lays eggs in larger clutches, its colonization potential is reduced and rapid exclusion occurs. However, if the inferior competitor lays eggs in smaller clutches than the superior competitor, then coexistence is possible. In this case, the inferior competitor has a colonization advantage that allows coexistence via the competition–colonization trade-off.

We then explored how heterogeneity can result in temporal dispersal in monocarpic plants. In these plants non-specific heterogeneity in growth results in a decoupling of age and size, and so makes size-dependent flowering strategies superior to age-dependent ones (Kachi and Hirose 1985; Rees *et al.* 1999). In agreement with this prediction, reproduction in monocarpic plants is strongly influenced by size, although in some species the flowering strategy does have an age-dependent component (Werner 1975; Baskin and Baskin 1979; van der Meijden and van de Waals-Kooi 1979; Gross 1981; Hirose and Kachi 1982; Gross and Werner 1983; Reinartz 1984b; Kachi and Hirose 1985; Klemow and Raynal 1985; de Jong *et al.* 1986; Lacey 1986; Klinkhamer *et al.* 1987a; Wesselingh *et al.* 1993; Bullock *et al.* 1994; Klinkhamer *et al.* 1996; Wesselingh and Klinkhamer 1996). However, strict biennials do occur and these species seem to have age-dependent flowering (Kelly 1985). In the strict biennial *Gentianella amarella* all surviving plants flowered in their second year, with the result that many plants flowered while very small and so failed to set seed (Kelly 1989a,b). It seems unlikely that such behaviour would be

adaptively superior to a size-based flowering strategy, and Kelly suggests that these species can be considered as 'extended annuals' that occur in habitats so infertile or densely vegetated that enough reserves cannot be accumulated in one year for successful flowering (Kelly 1985). In other species with age-dependent flowering, such as bamboo, delays in reproduction have been linked with mast seeding and predator satiation (Janzen 1976).

Non-specific heterogeneity in growth means that individuals of the same age can have very different sizes and so flowering is spread through time; resulting in a form of temporal dispersal. Heterogeneity here causes temporal dispersal although it does not directly select for it. In contrast to non-specific heterogeneity, temporal heterogeneity in growth makes waiting to flower more risky so selecting for smaller sizes at flowering. In *Onopordum illyricum* both these forms of heterogeneity dramatically influence the model predictions and accurate prediction is only possible when both forms of heterogeneity are included in the model Rees *et al.* (1999).

From the various examples presented, it should be clear that the potential effects of heterogeneity on ecological systems can be substantial, however, this is not always the case, and the best way of assessing the importance of various types of heterogeneity is through the use of parameterized mathematical models. In general, heterogeneity will be important when it interacts with any non-linearity in the system, this is essentially a consequence of Jensen's inequality (Ruel and Ayres 1999). For example, say heterogeneity acts on plant size, resulting in individuals having different sizes, and the probability of dying is an exponential function of plant size L, then:

$$\text{average probability of dying} = E[\exp(-dL)] \approx \exp(-d\bar{L}) + \frac{d^2\sigma^2 \exp(-d\bar{L})}{2} \tag{12.27}$$

where d is a parameter that determines how rapidly the probability of dying decreases with plant size, $\bar{L}$ is the average plant size and σ^2 the variance in plant size—a measure of heterogeneity. Now if heterogeneity was unimportant in the system, then we could ignore it, and work with mean plant size, $\bar{L}$. However, because the mortality function, $\exp(-dL)$, is non-linear, and has a positive second derivative, heterogeneity increases the average value of the probability of dying, as shown by equation (12.27). If the mortality function had a negative second derivative, then heterogeneity would decrease the average value. However, simply knowing there is substantial heterogeneity and that it influences demographic rates in a non-linear way does not mean that it will be important. For example, Pacala and Silander (1990) showed that plant performance was a non-linear function of the number of neighbours within a certain radius, and there was substantial variance in the number of neighbours around target plants in sown plots. But this spatial heterogeneity turned out to have little effect on the properties of this system because population size rapidly increased, and at high densities the relationship between plant performance and the number of neighbours was approximately

linear (Pacala and Silander 1990). A similar effect is seen in the influence of individual-specific heterogeneity in mortality on the evolution of flowering strategies in *Onopordum illyricum* (Fig. 12.11; Rees *et al.* 1999). General discussions of the effects of heterogeneity on life-history decisions can be found in a series of paper by Real and colleagues (Lacey *et al.* 1983; Caswell and Real 1987; Real and Ellner, 1992).

In summary, we have shown how dispersal may generate heterogeneity and conversely how heterogeneity can result in dispersal. Ecologists are only now starting to realize that the error terms used in their statistical analyses might be as important as the systematic parts of the model formulation (Pacala and Hassell 1991). We can no longer assume that error terms can be ignored as these provide quantitative estimates of the heterogeneity present in natural systems, and their consequences on model prediction can be substantial (Kachi and Hirose 1985; Pacala and Silander 1990; Pacala and Hassell 1991; Cain *et al.* 1995; Pacala *et al.* 1996; Rees *et al.* 1996; Wesselingh *et al.* 1997; Rees *et al.* 1999).

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