

## CHAPTER 18

# *Chance and Timing in Biological Invasions*

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### 18.1 INTRODUCTION

Both chance and timing play such a vital and obvious role in almost all biological invasions that any general analysis of these processes runs the risk of appearing somewhat banal. Despite (or perhaps because of) the importance of chance and timing, however, rather little has been written about them; their importance is taken for granted.

We can assess the relative importance of bad luck and bad timing in failures of establishment of an invading organism (N), by reference to the model presented by Crawley (1986a, 1987):

$$\begin{aligned} dN/dt = & \text{intrinsic rate of increase} \\ & - \text{exploitation competition effects} \\ & - \text{interference competition effects} \\ & - \text{natural enemy effects} \\ & - \text{effects of scarce mutualists} \\ & + \text{immigration and refuge effects} \end{aligned} \quad (1)$$

A necessary but not sufficient condition for successful invasion is that  $dN/dt$  is greater than 0 when N is small.

#### 18.1.1 Intrinsic rate of increase

While the theoretical notion of maximal intrinsic rate of increase is straightforward, there are formidable practical problems in its estimation. It is easy enough to estimate maximum fecundity, but it is hard to know what constitutes minimal mortality. The best practical solution is to take the maximum recorded value of the slope of a graph of  $\log_e$  numbers against time for a population thought to have an approximately stable age distribution, and to use this as the best estimate of  $r_{\max}$ . By this definition, the measure is unaffected by timing, but the *realized* rate of increase depends upon a wide variety of random variables (e.g. inclement weather

conditions) and may be extremely sensitive to the niceties of timing (e.g. synchrony of invasion with resource availability). Other random effects influencing the rate of increase include genetic founder effects, the age and life stage of the immigrant, and the chance of death between arrival and first breeding.

### 18.1.2 Exploitation competition

Whether or not exploitation competition has any influence on the population dynamics of an invading species is a moot point. In classical Volterra invasion models (Turelli, 1981) it is assumed that interspecific competition is the major structuring force in community dynamics. Invading species, however, may exploit resources that are not limiting (at least at the time of invasion), so that exploitation competition is not necessarily a force resisting invasion (Crawley, 1986a, 1987). Where it is important, then both the timing of resource supply and competitor phenology may be vital, and the luck of the year (whether it is a good year for the invader or a bad one) will influence resource productivity and competitor density.

### 18.1.3 Interference competition

This is virtually impossible to predict in advance of invasion (see Crawley, 1986a), unless the invading species is known to be exceptionally aggressive (e.g. the Argentine ant, *Iridomyrmex humilis*). However, if there are fierce, resident members of the invader's guild, then the phenology of their fierceness (whether it is continuous or seasonal, for example), could influence the probability of establishment. As with exploiting competitors, the luck of the year will influence competitor density and hence invasibility.

### 18.1.4 Natural enemies

Chance and timing are both likely to be important here. Timing of enemy abundance and foraging activity, coupled with luck of the year as it affects both enemy density and the abundance of alternative food species, will determine the death rate suffered by the invader. Other random elements affect enemy preferences, the synchrony between enemy and prey age-structures, and the relative logevities of enemies and prey.

### 18.1.5 Mutualisms

There is a substantial element of luck in having a full set of mutualists available for the invader on arrival. Clearly the most successful invaders are likely to be those with no obligate mutualists, or with only modest needs that can be met by

widespread, generalist mutualists. Timing is important in ensuring that the attentions of resident mutualists are not diverted by abundant, more preferred hosts.

### 18.1.6 Refuges

Both the availability and size of refuges will vary seasonally and from year to year. Luck will be important in determining whether or not there are reinforcing immigrations of the invading species (i.e. natural repeats of the invasion experiment), and this will depend upon the isolation of the habitat and the size of the nearest source of immigrants.

In short, chance and timing have the potential to affect every aspect of population dynamics relating to invasion. However, the relative importance of chance and timing is likely to vary from case to case and from process to process.

## 18.2 CHANCE

Changes are often said to be random when we do not understand what causes them. On other occasions, we may choose to ignore the complexity of causal factors, and refer to a change as random simply as a matter of convenience (i.e. as unexplained rather than inexplicable). Thus we have events which are, in practice, impossible to predict in anything but probabilistic terms (e.g. the precise location of lightning strikes), and events that we cannot (or have not planned to) explain. This latter kind of randomness is the statistical error familiar to experimentalists; it is the variation left over once we have explained all that we can, and, since analysis is retrospective, this residual variation can *never* be explained (even in principle). Thus, while random variation is not always unattributable in principle, it is frequently unattributed in practice.

Mathematical modellers refer to processes involving random elements as stochastic processes, a phrase only vaguely understood by many ecologists. To a mathematician, random events are those with a probability of occurrence that is determined by some probability distribution. A probability distribution is a mathematical relationship giving the probability of a given value,  $x$ , as a function of  $x$ . It may be derived empirically from a frequency distribution giving the observed frequencies of different values of  $x$ , or theoretically from a specified model of the process (like a Poisson or a negative binomial), which relates the probability of  $x$  occurring to the value of  $x$ . The phrase 'random event' is used to denote events that may or may not happen at a given trial (e.g. a six appears in a throw of a die), or an event that may or may not happen at a given time (e.g. an individual falls prey to a predator). A stochastic process is one where the system incorporates an element of randomness, and it is the opposite of a deterministic process (Kendall and Buckland, 1960).

A great deal has been written on the pros and cons of deterministic versus stochastic modelling (Bailey, 1957; Bartlett, 1966; May, 1973). While both sides have their fervent advocates, there does appear to be a consensus of opinion. Deterministic models of invasion are most likely to yield reliable approximations when the number of arriving individuals is large, or during the later stages of successful invasion, when population densities are high. However, deterministic models may exhibit patterns of dynamics that are qualitatively different from observed patterns, whereas stochastic models may describe observed patterns reasonably well (e.g. extinctions of apparently well-adapted species; see below).

In essence, the two kinds of models are best used to tackle different kinds of questions. Stochastic models are essential if one intends to address problems relating to the probability of extinction of small populations of invaders, to investigate the details of neighbour-dependent contact processes during the spread of invading species, or to estimate the variance of demographic parameters. Deterministic models, on the other hand, will give simpler, and usually clearer, insights into the equilibrium behaviour of large populations of invaders, and into whether or not a particular suite of demographic attributes equips a species for invasion into a specific community. These matters are discussed more fully below.

It is important to distinguish between two different kinds of randomness that are employed in ecological modelling, namely demographic stochasticity and environmental stochasticity (also called environmental noise). Ecological modelers have often referred to these very different kinds of randomness under the umbrella term of stochastic simulation models, frequently without making clear what kind of randomness is being modelled or why that kind of model is the most appropriate. Models containing environmental noise are actually deterministic models of population dynamics, in which the values of the (usually abiotic) driving variables are randomized at each time period, using pseudorandom numbers to select particular values from probability distributions that have specified means and variances. Even when variation in the demographic parameters themselves (e.g. fecundity) is simulated in this way, a given fecundity will uniquely predict the number of progeny born, and in this important sense the dynamics are deterministic.

Demographic stochasticity is quite different. Here, the fate of every individual member of the population is considered separately in every time period. For each individual, questions are asked as to whether it gives birth during the period, whether it emigrates, or whether it dies. Most simulation models of demographic stochasticity address these questions using 'Monte Carlo' techniques. The fate of individuals is resolved by generating a pseudorandom number between 0 and 1 for each demographic process; the random numbers are then compared with probabilities specified within the model, in order to determine the outcome. For example, if the probability of death is 0.1, then a random number between 0 and 1 is generated for every individual: if the number is less than or equal to 0.1, the

individual is assumed to have died; if the number is greater than 0.1 the individual lives to fight another day. Analytical models of demographic stochasticity have the advantage of showing unambiguously the consequences of their particular assumptions, an advantage they share with analytical deterministic models. However, as soon as the biological assumptions are made anywhere near realistic, the mathematics quickly become dauntingly complex, then completely insoluble.

Both environmental and demographic stochasticity are likely to be important in biological invasions. Environmental stochasticity encapsulates both bad luck and bad timing; it determines the good years and the bad years for invasion. Demographic stochasticity, however, is the luck of the draw; given that certain individuals will die or fail to reproduce, chance determines which individuals suffer which fates, and ensures that there will be a variable number of births and deaths, even under constant environmental conditions.

Deterministic invasion models like equation (1) define the set of conditions necessary for establishment (i.e. for initial increase following invasion). Whether or not these conditions are sufficient to explain persistence of a population depends upon the context. Crawley and May (1987) have recently proposed a simple stochastic model for competition between an annual and a perennial plant species. Briefly, the annual is assumed to have no effect on the demography of the perennial; the ramets of the perennial always win in competition with seedlings of the annual. The annual, if it persists at all, does so by germinating in the empty spaces that arise from the death of perennial ramets. The deterministic, necessary condition for persistence of the annual is that its fecundity ( $c$ ) must exceed the reciprocal of the equilibrium proportion of gaps ( $E^*$ ):

$$c > 1/E^* \quad (2)$$

Whether or not the annual persists in the face of competition in a stochastic model, however, depends upon the initial conditions. If an equilibrium population of annuals is invaded by the perennial, then stable coexistence is almost certain, because the annual is initially abundant and never becomes really scarce. If, on the other hand, the annual attempts to invade an equilibrium population of perennials, then there is a finite (and often substantial) probability that the invasion will fail, despite the fact that the fecundity is greater than the threshold defined by the deterministic criteria in equation (2). Figure 18.1 shows the probability that the annual will survive invasion by the perennial, or will itself persist as an invader of a perennial community. At a given fecundity the annual may be certain to survive invasion by the perennial, but have only a 25% chance of invading an established population of perennials. The mathematics of this beach-head effect are detailed by Crawley and May (1987). The present point, however, is that we must adopt stochastic models if answers to questions of this kind are required (e.g. how likely is it that an organism with the requisite deterministic demographic parameters will successfully invade a community?).

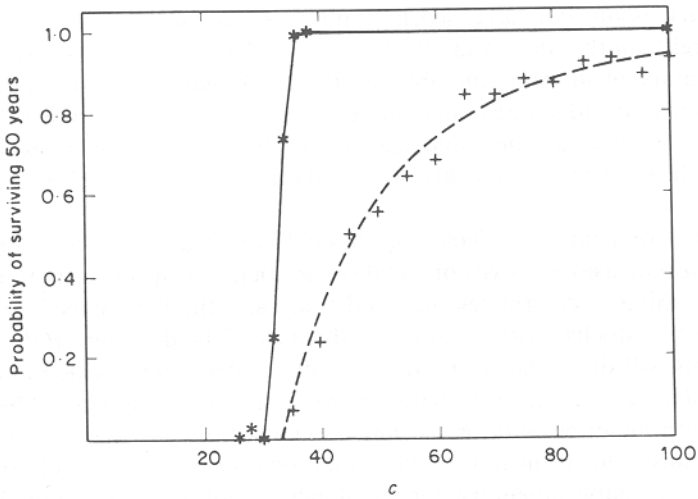


Figure 18.1. The probability that the annual will persist for at least 50 generations as a function of its fecundity,  $c$ . Solid curve: the annual is invaded by the perennial. Dashed line: the annual invades an established perennial community. Note that persistence is much less likely when the annual invades the perennial (from Crawley and May, 1987)

Other stochastic aspects of invasion are treated by Turelli (1981) and Chesson (1985). Successful invading species of plants and animals tend to exhibit one or more of a variety of mechanisms that buffer them from the full impact of environmental hazards or increase their performance relative to native species, in the aftermath of extreme conditions.

### 18.2.1 Buffering mechanisms exhibited by plants

Alien plants may be better buffered than natives for a variety of reasons: (1) because they tend to have fewer herbivores and seed predators, their fecundity may be higher; (2) this, in turn, may mean that they form larger seed banks; (3) because of this, there may be a greater likelihood of alien plants dominating gaps that appear in the canopy following disturbances; or (4) the alien's (preadapted) phenology may expose them to less risky periods of the season. This line of argument, of course, is entirely speculative at present.

Alien plants may themselves alter the risks they face. For instance, they may increase the likelihood of exceptionally severe fires occurring, either by accumulating inflammable fuel at a greater rate, or by burning with fiercer heat than native vegetation (G. J. Breytenbach, unpublished). Several alien plants appear to be more fire tolerant than natives (e.g. invaders of the South African fynbos such as *Hakea*), and a number of alien species may be more disturbance tolerant than

any of the natives (e.g. *Chamomilla suaveolens*, a virtually indestructible alien weed of gates and roadways).

The buffering ability of aliens in relation to rare events, however, is likely to be inferior to natives. Most native species of flora and fauna will have been exposed to extreme but rare environmental events (i.e. those occurring less frequently than, say, once per century). Alien species, on the other hand, are unlikely to have been exposed to the full range of different environmental extremes, and unusual weather conditions that might eliminate (or severely set back) an alien, might only cause temporary set-back to the natives. Indeed, it could be argued that if aliens had been around sufficiently long and had been exposed to these rare events, then we would probably not identify them as aliens in the first place. What appear, today, to be well-established, alien members of communities may simply not yet have been exposed to the particular environmental extremes that will eventually prove fatal to them. Unfortunately, this kind of optimism will be of little consolation to those who are charged with managing ecological communities dominated by alien species.

### 18.2.2 Buffering mechanisms exhibited by animals

I have argued elsewhere that probability of establishment should be positively correlated with the intrinsic rate of increase, and, therefore, negatively correlated with body size (Crawley 1986a, 1987), although the correlation may sometimes be reversed in comparisons within lower taxonomic groups (e.g. within certain genera; Williamson, this volume). Data on introduced species of weed biocontrol insects are consistent with two predicted patterns, with smaller species significantly more likely both to establish and to bring about substantial weed control. Given the central importance of the term for intrinsic rate of increase in invasion models like equation (1), this result is only to be expected.

There is a counterintuitive element to the argument, however. Consider the following correlations of body size: (1) bigger animals are more buffered against climatic extremes (especially for homeotherms); (2) bigger animals are more polyphagous and therefore less likely to starve in a foreign environment; (3) bigger animals have fewer predators; and (4) bigger animals may be able to disperse over greater distances if and when local conditions deteriorate. Weighted against these advantages, however, are all the problems associated with a low rate of increase, and it appears that, for most invaders, the ability to bounce back rapidly following disaster, and the ability to increase rapidly from a rare, initial bridge-head population, are of paramount importance compared with the attributes that buffer individual organisms against chance events. It is clear that there is a continuum of risk adaptation that runs parallel to (if not exactly coincidental with) the  $r$ - $K$  continuum, and along which there are a variety of trade-offs between risk spreading (high  $r$ ) and risk buffering (large size). Many of the successful large invaders are mammals associated with built-up and other

human-modified environments (e.g. rats, mice and cats), where the advantage of high buffering capacity is not at all clear. Others, like rabbits and goats on islands, are extremely polyphagous, but, considering their large size, have relatively high rates of increase.

For invading insects, high fecundity tends to be the main means of risk buffering. With species that show alternation of generations, chance may play a vastly different role in the two life stages, as in the two legs of the annual migration pattern of the alien gall wasp, *Andricus quercuscalicis*. Given the enormous difference in the relative abundance in southern England of the two host trees between which it migrates (about 100 *Quercus robur* to one *Q. cerris*), individual sexual females emerging from *Q. cerris* are much more likely to find a suitable *Q. robur*, than are agamic females emerging from *Q. robur* of finding a suitable tree of *Q. cerris*. This asymmetry in host abundance may have been the evolutionary cause of the differential fecundity exhibited by the two generations; each sexual female contains only 10 eggs on emergence, whereas each agamic female has over 1000.

### 18.3 DATA ON CHANCE IN INVASIONS

I shall illustrate this section on chance using data from the Silwood Project on Weed Biocontrol (see Crawley, 1987, for details), and the section on timing with data from the 130 years of experimental work on the Broadbalk Experiment at Rothamsted (see Crawley, 1986a, for details). I should have liked to draw information on both processes from both data sets, but the phenological data from weed biocontrol are too scanty, and we have no data at all on failures of invasion for the Broadbalk weeds.

#### 18.3.1 Chance in the weed biocontrol data

Several of the variables in the weeds data base allow us to assess the role of stochastic elements in the establishment of insects intentionally released as potential biocontrol agents.

#### 18.3.2 Number of releases

Other things being equal, the more releases that are made, the greater should be the chance of successful establishment. Indeed, the data do show that multiple releases are significantly more likely to establish than are single releases. Multiple releases are no guarantee of success, however, and the same proportion of species fails to establish following 13 years of introduction as fails following 2 years of introduction. The reason for this lies in the extraordinary persistence of the practitioners, who appear to be working on the rationale that 'this species worked somewhat else, so it had better work here, as well'.



If we take only those cases with well-documented releases, and calculate a figure for total release (the product of number of release-sites and the logarithm (base 10) of the number of insects released per site), we find that total release is significantly greater for introductions that succeeded in establishment (87.3, SE 23.1) than for those that failed (9.7, SE 1.9).

Release strategies were also important. Comparing single releases at one site with several releases at one site, single releases at several sites, and many releases at many sites, we obtain the expected increase in probability of establishment (see Table 18.1). Nevertheless, single releases were often effective, and multiple releases often failed. Redistribution of insects within the country of release following successful establishment further reduces the risk of extinction.

### 18.3.3 Previous experience

Agents are frequently introduced because they have been successful somewhere else against the same species of weed. Given information on prior performance of the agent, it might be expected that predictive ability would be improved. This expectation is only partially fulfilled. If it is known that the agent failed to establish in previous attempts, then it is significantly more likely to fail again. On the other hand, completely untried species are just as likely to establish as species which have successfully established elsewhere. In this context, therefore, the negative data are more valuable than the positive data in contributing to our predictive ability.

### 18.3.4 Taxonomic mistakes

Bringing together the wrong taxa by mistake introduces a stochastic element into the establishment probability. It might be expected that mismatched organisms

Table 18.1. Release strategy and probability of establishment for agents released against all weeds except *Opuntia* spp. and *Lantana camara*, the category of 'Other Weeds' in Crawley (1986b). Data show the number of releases in each category. Thirty-six species of agents were established accidentally. For 46 species the release strategy is unknown (26 of these failed to establish, 20 established successfully). Chi-squared = 12.15,  $v = 4$ ,  $P < 0.05$

Releases	Sites	Failed	Established
1	1	18	14
several	1	9	12
1	several	17	25
several	several	32	8
many	many	3	15

would stand a significantly lower chance of successful establishment, but this is not the case. There is no significant difference in the probability of establishment between those cases where the plant and animal were correctly identified. The reason for this is that the cases where genuinely mismatched species fail immediately just happen to be balanced by cases where the mismatch turns out, quite fortuitously, to benefit the agent. For example, the plant may be a suitable host for the insect even though (or perhaps because) the plant and the insect shared no evolutionary history of association (Crawley, 1986a).

### **18.3.5 Total effort**

Biocontrol effort consists of much more than just the scale of the individual releases. Energy is expended on geographical search for suitable agents, on collection, on taxonomic study, on screening, on specificity testing, and on pre-release rearing (Moran, personal communication). The relationship between total effort (a weighted sum of all these factors, each measured in scientist years) and the probability of establishment, suggests the biocontrol practitioners may well be wasting their time. The mean number of scientist years associated with successful establishment is 9.3 as against 6.9 for failures ( $t = 0.95$ ,  $v = 214$ , NS). This result is coloured, of course, by the fact that repeating successes is relatively cheap in terms of scientist years, an artefact that tends to reduce the mean effort associated with successful establishment. A less biased test would compare only the mean efforts associated with success or failure following the first introduction.

### **18.3.6 Spatial distribution of eggs**

One of the intriguing biological attributes of the agent which influences the probability of establishment is the pattern in which the female distributes her eggs. We compared species where the eggs are laid in batches, with species where the females lay their eggs singly, and found that batch-layers were significantly less likely to establish. This is presumably to do with risk-spreading; a single batch of 100 eggs is more likely to be completely lost to predators or to accidents than are all of 100 spaced-out eggs. Interestingly, once established, a good weed biocontrol is more likely with batch-laying species (Crawley, 1986a), since their impact on plant fitness is substantially greater.

### **18.3.7 Adult longevity**

The only other biological form of risk spreading that emerged from the weed biocontrol data concerned adult longevity. The introduction of species with relatively long-lived adult stages led to significantly increased probabilities of establishment, compared to species that had short-lived adults. The explanation of this involves a combination of good luck and good timing; the longer the adults

live, the more likely they are to encounter suitable conditions for successful reproduction.

### 18.3.8 Failure to establish

All of the factors identified in the data base as likely causes of failure to establish (climate, predators, parasitoids, disease, competition; see Crawley, 1986a) involve an element of chance. However, if they are ranked from most chancy to least chancy, there is a correlation between the importance of the factor (measured by the proportion of cases in which this was the major cause of failure) and the degree of chanciness involved with that factor. Thus bad weather is both the most frequent cause of failure, and the chanciest of the factors; competition is both the least common cause of failure and the most deterministic (it requires relatively high densities of the competing species, and when densities are high, competition is almost inevitable).

## 18.4 TIMING

In compiling his study on the phenology of British plants and animals, the 19th century naturalist, Leonard Blomefield, had occasion to correspond with Charles Darwin, about contributions that Darwin might make to his *Observations in Natural History*. In his reply, Darwin (see Francis Darwin, 1924) writes 'My work on the species question has impressed me very forcibly with the importance of ... [phenological works], containing what people are pleased generally to call trifling facts. These are the facts which make one understand the working or economy of nature.' Seventy-six years later, Francis Darwin (1924) was to write that phenology is 'a science which has suffered in two ways—viz. from incompleteness in observation, and a too bold style of theorizing'.

### 18.4.1 Seasonal phenology

Good timing is vital in all invasions. For example, matching an invading plant to its recruitment microsite often requires extremely precise timing (Harper, 1977). Similarly, matching the arrival of an invading animal species with the phenology of its food resources, mating and nesting requirements is crucial to successful establishment (Crawley, 1983). Synchrony of invasion with lows in the abundance of generalist natural enemies is also likely to increase the likelihood of successful establishment (Lawton, 1986).

Many of the best examples of the importance of phenology in animal population dynamics come from studies with herbivorous insects. For instance, a long-term study of English oak showed the key role played by the timing of bud burst in the population dynamics of the two principal herbivores, the winter moth, *Operophtera brumata*, and the green tortrix, *Tortrix viridana*. The tiny

hatchling larvae must penetrate between the expanding bud scales, or die. If bud burst is late, then massive insect mortality results (Varley and Gradwell, 1968). Unfortunately, we have little information on the phenology of invading insects, and virtually none on the phenological causes of failure in insect invasions. It may not be without significance, however, that two of the most recent alien additions to the British cynipid gall wasp community have rather extreme phenologies. The marble gall, *Andricus kollari*, lays its eggs in the buds of *Quercus cerris* in the autumn, at a time when most self-respecting gall wasps are already in their overwintering diapause. In contrast, the knopper gall, *A. quercuscalicis*, emerges exceptionally early in the spring (sometimes struggling through snow to get to the surface), and lays its eggs in buds of *Q. cerris* in March, long before the native species that gall male catkins of *Q. robur* (e.g. *Neuroterus quercus-baccarum*) have emerged from their overwintering galls.

With plants, phenological effects are much easier to study. For example, many of the alien herbaceous plants of Californian rangelands remain green longer into the summer than the native plants, a trait that may give them a competitive edge over some natives in years that are not unusually dry, if this increases their relative fecundity (Crawley, 1987). The precise seasonal timing of catastrophes such as fire determines the developmental stage of the plant that is exposed to hazard. A stage (like seedlings) may be killed by a disturbance that would barely set back a different stage (e.g. seeds or thick-barked, mature plants). The same disturbance might even be advantageous if it happened at different time, if, at that time, its effects were relatively more severe on the plant's competitors or natural enemies.

#### 18.4.2 Timing in the Broadbalk experiment

The effect of seasonal phenology on the composition of an invading guild is beautifully illustrated by the classic Broadbalk Experiment at Rothamsted. Every year since 1843, winter wheat has been cultivated in the same field. The experiment consists of 18 manurial treatments each crossed by seven weed control treatments. One block of the experiment has never been treated with chemical weed killers over this entire period. The dynamics of the community of weedy species on this plot provide an unparalleled source of data on plant invasions, as well as on questions relating to why competitive exclusion has failed to occur, even after more than 100 generations (Crawley, 1986a).

Two species of wild oat, *Avena fatua* and *A. ludoviciana*, are found in wheat fields in southern England. Both are aliens introduced from southern Europe, but only *A. ludoviciana* has become a serious pest in the Broadbalk Experiment (and this despite years of laborious, selective, hand-weeding). The reason is phenological. The autumnal cultivation which precedes sowing of winter wheat allows the autumn-germinating *A. ludoviciana* to establish free from competition with other weeds. Spring-germinating *A. fatua* is unable to compete in the shade cast by the well-established canopy of wheat and *A. ludoviciana*. In contrast, *A. ludoviciana* is

eliminated from fields where spring cereals are grown, because its autumn-germinated seedlings are killed by spring cultivation.

The Broadbalk data provide other insights on the importance of timing. In the 1920s and 30s, attempts were made to reduce weed problems on the field by fallowing for various lengths of time. This involves sowing no crop, and destroying the weeds as they germinate over the course of the year, timing the cultivations to ensure that none of the weeds set seed before they are cut down. Several successive years of fallow should run down the seed bank of species that possess dormancy, and should virtually eliminate annual weeds that exhibit no seed dormancy. It is interesting to compare the outcome of a 4 year fallow on two of the most important weeds, the poppy *Papaver rhoeas* (a relatively recent invader to this particular field) and the annual black grass *Alopecurus myosuroides*. Poppy has a vast seed bank (20000 seeds  $m^{-2}$  in the top 10cm of soil) and has moderate seed dormancy (it can survive for well over 4 years in the soil). Black grass, on the other hand, exhibits no seed dormancy at all. Given these life history traits, one might predict that fallowing would eliminate black grass, but that it would be ineffective in poppy control. As so often happens, detailed prediction is confounded. A 4 year fallow vastly reduced the poppy problem, but had no effect on black grass control. After fallowing, the wheat crop tends to grow particularly well because there is little competition from weeds, and nutrient levels are relatively high. Those weeds that do germinate after fallowing, therefore, tend to be suppressed by the crop and to set little seed, so the seed bank recovers only very slowly. Poppy is regarded as uncompetitive with winter wheat on Broadbalk soils (Brenchley and Warrington, 1930, 1945), and this is the likely reason that poppy stayed scarce during the 5 years after fallowing.

The case of black grass, however, illustrates the importance of chance and timing. It happened that in the first year of wheat cultivation following the fallow period, the crop was subject to heavy attack by wheat bulb fly, *Leptohylemyia coarctata*. Whether this was entirely coincidental, or whether fallowing in some way increased the probability of bulb fly attack, is unknown. In the large, competition-free gaps in the wheat crop caused by the pest, the few surviving seeds of black grass were able to produce highly fecund individuals, which, in the course of a single year, produced sufficient seed to bring the weed population back to its pre-fallow densities.

### 18.4.3 Successional timing

The importance of timing in the invasion of successional communities depends upon the kind of succession under consideration. In primary successions, where facilitation is a vital prerequisite for establishment, there are likely to be rather clearly defined windows of time in which invasion is possible; too early and the resources required by the invader may not be established, too late and generalist natural enemies may be too abundant (Crawley, 1986b; Gray *et al.*, 1987).

In secondary successions, where facilitation is usually less important, inhibition of invasion by established, native species may constitute more of a barrier to ill-timed invasions (Connell and Slatyer, 1977). Invasibility may also depend upon the details of the relative abundances of resident species of resources, competitors, mutualists and natural enemies, rather than simply upon which species are resident. In this case, rather detailed models of population dynamics (like equation (1)) for species in the trophic levels both above and below the invader may be necessary to predict success or failure of establishment. This vastly increases the complexity of the task of prediction. Unfortunately, we have no direct data on the importance of successional stage on invasibility, from any of our studies carried out so far. The natural history observation that aliens are more common in early successional communities, while intriguing, may reflect nothing more than the fact that rates of species introductions (and species' pool-sizes) are far higher for early successional communities. Hard data showing that with equal rates of species' immigration, late successional communities are harder to invade, are simply not available (Crawley, 1986b). If there is any evidence, it may actually point the other way; for instance, in southern Britain there are more alien 'late' than 'early' successional tree species.

If, indeed, it is true that late secondary successional communities are more difficult to invade, it is probably because their increased diversity (both structural and biotic) imposes extra constraints on community membership. The more rules that apply, and the more rigorous the selection process, the harder it is for a given species to invade. Because early successional communities are simpler, they tend to be more alike, so a species that is good at invading one kind of disturbed community is likely to be able to invade other communities created by the same agent of disturbance (be it fire, landslip, or urban dereliction). An excellent example is afforded by the African grass *Rhynchelytrum roseum* (= *repens*), that grows as an alien on dry, road-side verges all the way across Mexico from the Gulf to the Pacific, through countless different plant communities, up and down an elevational gradient of over 4000 m. Whether dominance throughout this extraordinary range of environments is due to tremendous phenotypic plasticity on the part of a few genotypes, or to wide genetic polymorphism, remains to be discovered.

## 18.5 CONCLUSIONS

What emerges most forcibly from this discussion is not that chance or timing are all-important, but that the *interaction* between chance and timing is the vital ingredient. Rare chance events that occur at just the right time may well be the cause of major, long-term structural and dynamic changes in ecological communities. However, exactly the same extreme event might lead to the development of a radically different community, if it occurred at a slightly different time (e.g. depending upon what propagules were abundant at the time of

the disturbance). Because of this, existing communities bear the marks of countless past contingencies. A good example is seen in oak woodlands in Silwood Park in southern England. This naturally regenerated forest owes its origin to the introduction of the myxoma virus to Britain in the mid-1950s. This brought about the complete collapse of the resident rabbit population and allowed a cohort of oaks to become established. Before the introduction of myxomatosis, the rabbits had maintained these sites as grasslands, selectively predated the seeds and seedlings of the trees. In recent years, rabbit numbers have risen again, as their resistance to myxoma has increased and the virulence of the virus has declined (Fenner, 1983). At present there is virtually no natural regeneration of oaks in rabbit-grazed areas. This dense oak woodland owes its existence to the chance event of the introduction of the virus. Had the timing been different, the low in rabbit numbers might not have coincided with any years of high acorn production, in which case the oak's many other seed predators might never have been satiated, and an entirely different kind of woodland would have developed (e.g. of *Betula*, *Acer* or *Tilia*; Crawley, 1983). Similarly, dramatic consequences of rare, chance events are described by Noble and Slatyer (1980) in relation to unusually severe fires, and Gleason (1927) in relation to the vagaries of plant immigration to newly created freshwater ponds.

The relative importance of deterministic elements of invasion, like those listed in equation (1), and the stochastic elements involved in good luck and good timing, are rather difficult to assess in practice. In principle, the deterministic model allows us to establish necessary conditions for invasion; values of the demographic parameters that ensure that  $dN/dt$  is greater than 0 when  $N$  is small. The stochastic elements should enable us to obtain estimates of how likely it is that a given set of (apparently suitable) demographic attributes will actually lead to establishment. Unfortunately, for untried species in new environments, we have virtually no idea of how to estimate these probabilities. Even for the deterministic models, many of the parameters are unknown, and some of them are even unknowable (e.g. the coefficients of interspecific interference between resident and invading species). In this sense, the condition that  $dN/dt$  be greater than 0 is not especially helpful, and, for the time being, we may have to accept that quantitative predictions on the probability of successful invasion may be impossible for most systems. This is not to say that deterministic criteria of invasion are inevitably unhelpful. Great steps have been made in quantitative epidemiology, for example, by analysing simple models for establishment (see the work of Anderson and May (1986) on  $R_0$ , the basic reproductive rate; see also Williamson, this volume). Can we learn anything about the importance of chance and timing from an examination of those cases where chance and timing appear to be relatively unimportant in determining the course of invasions? A list of the great invaders (cats and goats on oceanic islands, rats and mice in human settlements, human diseases in previously isolated populations, birds such as starling and partridge, mammals like rabbits and foxes from Europe, grey

squirrels and muskrats from North America, mongoose and axis deer from the Orient, and so on) is a list of species that can be confidently expected to invade successfully. There is a certain uniformity to the habitats involved (most are human-made or highly altered by people), to the physiological tolerances and buffering of the individual organisms (most are warm-blooded vertebrates) and to the population-level traits associated with high intrinsic rate of increase (relatively small size, rapid development and high fecundity). For the cold-blooded species, and for the insects in particular, it appears that great successes are less repeatable. The combination of higher climate-sensitivity, coupled with the small absolute size and low buffering capacity of the individuals, means that invasions are always going to be chancy. We know the attributes likely to increase the probability of establishment (Crawley 1986a, 1987), but we are not in a position to make accurate predictions about individual cases.

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