

## CHAPTER 19

# *Analysis of Risk for Invasions and Control Programs*

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### 19.1 INTRODUCTION

Dispersal, invasion, and range expansion are manifestations of some of the most fundamental aspects of life history evolution. The changing nature of the environment spells doom for the species that does not find some way to temper the mercy of a fluctuating local resource base, or soften the impact of a sudden increase in its natural enemies. Dispersal is a basic evolutionary response to such harsh or unpredictable aspects of environment; it allows bet-hedging in the absence of information concerning environmental change, or cued responses to direct or indirect hints of impending catastrophe. Even in a completely predictable and stable environment, competitive pressures may select for dispersal, because populations that do not at least occasionally send out propagules must ultimately be displaced by those that do (Hamilton and May, 1977).

Thus, dispersal and associated competitive displacement are inescapable features of the natural world, and powerful fundamental processes in the shaping of community patterns. The nature of the biosphere reflects a balance between the forces of local disturbance, reinvasion, and successional development; human activities have upset the balance, increasing the frequency of disturbance and invasion, and reducing biotic diversity.

Nearly 30 years ago, in his treatise on invasions, Elton (1958) wrote 'We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora.' The causes primarily are anthropogenic, as the activities of societies disturb natural areas, increasing their vulnerability to colonization by invaders, and as humans deliberately and accidentally serve as agents for transporting propagules from one habitat to another. What often is missed in much of the recent debate regarding the deliberate release of genetically engineered organisms is that it is the issue of the frequency and scale of introductions, as much as the nature of any particular introduction, that impels the concerns of ecologists. Our regulatory systems are not designed to deal with

the cumulative effects of multiple low probability events, and yet this is a primary challenge facing us in the case of introductions.

## 19.2 RISK ASSESSMENT AND RISK MANAGEMENT

Many of the most destructive biological invasions involved accidental introductions: epidemics of human diseases, plant pathogens such as asiatic chestnut blight (*Cryptonectria parasitica*), or disease vectors such as the malaria mosquito (*Anopheles gambiae*). A second major category, including such examples as the Africanized bee (*Apis mellifera scutellata*), the muskrat (*Ondatra zibethica*), and the gypsy moth (*Lymantria dispar*), involved species that were imported for very limited purposes, but escaped from inadequate biological or physical containment.

The third category of introductions includes those for which environmental release is deliberate. These sometimes can be carried out relatively safely provided the ecological characteristics receive adequate attention prior to the release. However, this is not to suggest that such deliberate introductions are somehow risk-free, since there have been numerous incidents arising from faulty assessments; rather, it says that care to ecological detail can minimize risk. Years of experience with plant breeding has led to a wealth of information concerning the hazards associated with introductions, and the ability to control risks. Biological control has had a number of spectacular successes with pests such as the cactus weed *Opuntia*, the European rabbit (*Oryctolagus cuniculus*) in Australia, the citrus mealy bug (*Cryptolaemus montrouzieri*), cottony cushiony scale (*Icerya purchasi*), and Klamath weed (*Hypericum perforatum*). In contrast, introduced fish species have driven many indigenous freshwater fish populations in the western United States and elsewhere to the brink of extinction; and more generally, huge shifts in species composition have occurred throughout subtropical areas of North America, where introduced cichlids largely have displaced centrarchids (Moyle, 1986). Thus, where ecological information has been lacking or faulty, deliberate introductions have led to major and sometimes catastrophic ecological occurrences.

The differences among these categories demonstrate the need to separate the various stages in the invasion process: introduction; escape from containment; the dispersion of individual propagules around the original source; the process of establishment, population growth and spread; and the manifestation of effects on other populations and on system processes. These will be discussed individually in the sections that follow. Depending on the nature of the proposed introduction, one or several of these aspects may assume paramount importance. For those species intended for contained uses, as is the case for many products of biotechnology, it is the escape from containment and survival in the external environment that is the key consideration. For deliberate releases, attention shifts to growth, spread, and ecological effects.

For practical purposes, it often is convenient to distinguish between the processes of risk assessment and risk management. In general, however, these are not cleanly separable. Levin and Harwell (1986) suggest that a regulatory program for the deliberate release of genetically engineered organisms must have four components.

1. Pre-release assessment of the likely fate and effects of the novel material.
2. Monitoring after release.
3. A plan for biological or physical containment.
4. A plan for mitigation of undesired side effects.

These elements are inextricably intertwined: the confidence that one can place upon prediction must influence the design of monitoring and containment programs, and in some instances the need for the latter will be minimal. Moreover, containment is not an absolute, and its evaluation is part of the initial assessment. Thus, although some parts of the above scheme assume primary importance in particular situations, the four are interrelated and essential elements in any generic management system.

Consideration of any of the above four points is influenced fundamentally by the category of introduction, in the sense of Levin and Harwell (1986). If the introduction involves a species that exists elsewhere in the natural environment, then it is critical to determine its characteristics in its natural environment, and how they might pertain to the target environment. Is the species absent from the target environment because it never previously has reached there in sufficient proportions to become established, or because it is incapable of competing against the native biota? Are there thresholds associated with local establishment? What are the natural mechanisms of population control in its native environment, and can they be transferred to the new environment if needed?

### 19.3 SPREAD OF PROPAGULES AND INDIVIDUALS

The first step in an assessment of the potential for spread of an introduced species is an identification of the primary modes of movement. It is essential to determine the relative importance of physical factors such as winds and currents, of biological vectors, and of active mechanisms of locomotion. The scales of movement differ by many orders of magnitude for different species, making it impossible to discuss risk assessment and management without a primary classification based on the scales of movement. For example, influenza virus and airborne fungal spores can traverse huge distances in short periods of time, while individual *Rhizobia* can move only very short distances, on the order of meters (Andow, 1986). The nature of risk and the potential for containment thus differ qualitatively among organisms with such different characteristics.

The basis for classification and extrapolation rests upon a clarification of the relationship between easily measurable parameters, such as those relating to

individual movements, and the patterns of spread of populations. The beginnings of appropriate theories exist, but are incomplete. For vertebrates, there have been isolated studies of individual movements, derived, for example, from radio-telemetry data; moreover, there is a vast and fascinating literature on orientation and migration. However, no general body of principles exists that allows one to proceed from the individual to the population. Similarly, for insects, information has been obtained regarding the responses of individuals to chemical cues, or regarding swarming behavior; but much of the most useful information has been derived from population level studies, from which inferences concerning the statistical distribution of the movements of individuals sometimes can be drawn. Most studies of this kind have been long-term, integrating over a large number of individual steps (e.g. Dobzhansky and Wright, 1943); but a number of recent studies (Kareiva, 1983) provide more detailed short-term information.

Phenomenological approaches to describing the distribution of distances traversed by individual spores are a well accepted part of the methodology of plant disease epidemiology (Gregory and Read, 1949; Gregory, 1968; Frampton *et al.*, 1942; Minogue, 1986; Fitt and McCartney, 1986), and can be extended to the distribution of seeds and pollen (Harper, 1977; Okubo and Levin, in press). The simplest models, the power law (Gregory, 1968):

$$y = ax^{-b}, \quad (1)$$

and the negative exponential (Kiyosawa and Shiyomi, 1972; Frampton *et al.*, 1942):

$$y = ae^{-bx}, \quad (2)$$

provide excellent agreement with observed data in a wide variety of situations. In these expressions,  $x$  is the distance from the release point, and  $y$  is the probability density.

Models of this form have the advantages of simplicity; they are linear respectively on logarithmic or semilogarithmic paper, facilitating parameter estimation. However, they do not explain the sometimes-observed displacement of the dispersal peak from the source. More importantly, because the parameters are derived from curve fits rather than from consideration of underlying physical properties such as wind velocity or height of release, there is no basis for extrapolation to new situations.

Gaussian plume models (Pasquill, 1962), which are the simplest of atmospheric dispersion models, relate the distribution of spores downwind from a source of a known height. These models are used widely in the air pollution literature to describe particulate distributions, but are valid only for very light particles. For heavier propagules, one must employ either a 'tilted plume' model, in which gravitational settling is included, or consider the full diffusion–advection–settling model with all forces considered explicitly, and with uptake kinetics at the surface of the earth also treated explicitly. The latter approach holds great

potential for the prediction of spread. Our investigations to date (Okubo and Levin, in press) indicate that such models can provide the basis for a useful classification system for seed and spore dispersal, one in which the critical parameters—settling velocity, wind velocity, and release height—are measurable directly.

Vectored organisms introduce another level of complexity, since one must consider both the movements of the vectors and the transfer kinetics by which organisms board and deplane. Treatment of such phenomena is central to the development of epidemiological models; usually the treatment is phenomenological, restricted to the calibration of standard models based on observed dynamics of outbreaks rather than on more mechanistic observations.

In the case of the release of genetically engineered organisms, an analogous set of considerations regarding infectious transfer via plasmids or viruses is recognized to be of major importance. Such transfers have been observed under laboratory conditions, and are known to occur in the field; but data on the frequency of occurrence under field conditions are in short supply.

#### 19.4 INTEGRATIVE MODELS OF POPULATION GROWTH AND SPREAD

The classical mathematical models for the spread of invading species were developed to represent the central aspects of spread in terms of a few measurable and biologically meaningful parameters, and to provide a basis for prediction. The most widely used models are based on a modified random walk or diffusion model, in which advective forces and growth terms are added. The diffusion term, as well as the other parameters, may be allowed to vary in space and time, or to depend upon population density. Depending on the context, diffusion may occur in one, two, or three dimensions, and not necessarily at the same rates; in two dimensions, the basic form (see Okubo, 1980) is

$$\partial n/\partial t = \partial^2(Dn)/\partial x^2 + \partial^2(Dn)/\partial y^2 - u \partial n/\partial x - v \partial n/\partial y + F(n, x, y, t) \quad (3)$$

where  $F$  represents the local growth term and  $n = n(x, y, t)$  is the population density. Here,  $D$  is the diffusion coefficient, which could be allowed to vary in the  $x$  and  $y$  directions, and  $u$  and  $v$  denote mean advective effects.

In this model, the means and variances of the lengths of individual steps are represented explicitly in the advection and diffusion coefficients, respectively; higher order moments are ignored. More general models incorporating higher order moments have been considered by Mollison (1977); these have the advantage of being able to account for a wider range of patterns of spread, but the disadvantage of being much more difficult to parameterize. As with any mathematical modeling, one must reach a compromise between detail and utility, and in general the resolution is to settle for the simplest possible model that can account for the major observed patterns.

A large literature, discussed in part by Williamson in this volume, concerns itself with the diffusive spread of species introduced into new environments, and interprets patterns of spread on the basis of equation (3). For the case of an invading organism, the form of the density dependence in equation (3) is of little importance at the front, where the population density is low. It is not surprising, therefore, that the asymptotic rate of advance of population fronts depends only upon the intrinsic rate of natural increase ( $r$ ), the diffusion coefficient, and advective effects. In the absence of advection, the speed of that front is  $2(rD)^{1/2}$ . This result was proposed originally by Fisher (1937) for the spread of advantageous alleles, and was demonstrated rigorously by Kolmogorov *et al.*, (1937) for a variety of forms  $F$  and initial distributions. Numerous authors since have perfected these results, and have applied them to particular case studies. Certainly the most important paper in this regard was that of Skellam (1951), who analyzed the case of the muskrat (*Ondatra zibethica*) that had been documented by Ulbrich (1930), and the spread of oaks. By relating observed patterns of spread to the distances covered by individual acorns, he concluded that the simple model was inadequate: active dispersal agents had to be involved in the spread of the oaks. On the other hand, the case of the muskrat remains of interest to theoreticians to this day (Williamson, this volume; Andow *et al.*, in press), and provides an excellent example of the usefulness of the basic approaches.

One can test such predictions at the coarsest level simply by seeing whether observed rates of advance are linear; but this is not a compelling test because the predicted constant rate does not apply for the early stages of spread, and it is impossible to specify how long that transient period should be. The stronger test of the model, and the situation in which useful predictions might be possible, occurs when independent estimates of  $r$  and  $D$  are available. We (Lubina and Levin, 1988) have done this for the linear spread of the California sea otter, and found excellent agreement with the theory. In related work (Andow *et al.*, in press), we have carried out similar studies for the muskrat, the cereal leaf beetle (*Oulema melanopus*), the rice water weevil (*Lissorhoptus oryzophilus*), and the small cabbage white butterfly (*Artogeia rapae*), with mixed success. It is clear that the framework provided by equation (3) is an excellent one for understanding observed rates of spread. It is equally clear that a more refined theory and much better data sets are needed before we have available a truly predictive theory. At the very least, however, the approach points the way to the essential data, and provides a basis for identifying the controlling factors.

For the cabbage white butterfly, the simple picture presented above is complicated by the fact that multiple invasions occurred, involving separate introductions and saltational movements. Such long jumps are demonstrated by Mollison (1977) for his more general model, and are treated in a somewhat different way by Moody and Mack (personal communication). When leaps of this kind can occur, one really must recognize that there are two scales of spread: the longer one on which new centers of spread are established, and the shorter one on

which diffusive spread from centers occurs. Patterns of this kind must be of fundamental concern for control programs, for it is the great leaps that are the least predictable and that can cause the major difficulties. One of the most interesting of such situations occurs for the great pandemics of influenza. For these, a most impressive model for the establishment of new centers has been put forth by Rvachev (see Rvachev and Longini, 1985), and is based largely on scheduled airline travel between major world cities. In general, this entire area of research is an extremely active one, and we should expect to see the development of more reliable empirically-based spread models for many species of interest. The major difficulty is that it is the tail of the distribution of dispersal distances that is most important for the questions of spread, but most difficult to deal with statistically.

### 19.5 ECOLOGICAL EFFECTS

Parallels exist between the evaluation of the consequences of species invasions, and the assessment of the effects of chemical releases. In the case of the environmental release of chemicals, the first step in assessment is the determination of the fate and transport of the material, as it is for the case of biological invasions. The determination of effects is much more problematical, for although it is possible to use laboratory bioassays to evaluate direct toxic effects on organisms, problems begin to multiply when one tries to extrapolate to field conditions, or to the population level. The reductionistic approach does not suffice for the evaluation of community and ecosystem effects, because of the multiplicity of pathways through which effects can be propagated. One cannot expect to gain very much information about indirect effects on community structure and system process without carrying out higher level studies in microcosms or in field situations, and the importance of such higher level effects has received increasing recognition in the ecotoxicological literature (Levin and Kimball, 1984; Kimball and Levin, 1985; Cairns, 1983, 1986).

Similar considerations apply to the introduction of biological material. The anecdotal literature is inconclusive on the effects of species introductions. As discussed earlier in this paper, and more completely in a variety of reviews (see, for example, the various papers in Mooney and Drake, 1986), the effects of a species introduction may range from benign to the elimination of major indigenous taxa. System processes in general are more buffered than are individual species, but even this generalization is debatable. Vitousek (1986) has documented the effects that invading species can have upon such system properties as productivity, soil structure, and nutrient cycling. Thus the need is clear for case by case consideration of introductions, using information derived from the experimental manipulation of whole systems where that is practicable.

Mathematical models may provide some guide to the assessment of effects on community structure and ecosystem processes, but these never will provide very

detailed information. Highly detailed and specific models cannot be adapted to contexts very different from those in which they were developed. Furthermore, they are limited in their predictive power because of the difficulty in obtaining reliable estimates of parameters, and because of the multiplicity of ways that error can arise and propagate. For environmental management in general, a compromise must be reached. No single model suffices, and one needs a combination of models at different levels of detail, and techniques for simplification and aggregation of the most complicated models.

One promising approach, still in its infancy, is the development of integrated models of disturbance, spread, colonization, and community interactions. We (Levin and Buttel, 1987) have begun the development of computer models of mosaic systems, in which recurrent disturbance is an essential feature and continually creates new opportunities for invaders. Our interests have been in gap phase systems in forests, grasslands, and the intertidal; but these models also can incorporate man-made disturbances such as logging or road construction. In such models, as patterns of disturbance change, competitive release may allow invasions by species that previously were suppressed. By coupling such models for community structure with those for dispersal and colonization, we hope to develop a method for relating disturbance to invasion (see also Crawley and May, 1987).

A fundamental difficulty regarding the assessment of ecological effects is the determination of which system level measures are of interest. Any ecosystem is valued differently by different people, and the multiple uses to which systems are put place different management objectives in conflict. A related but distinct issue, treated in much greater detail elsewhere (Levin, 1987, 1988; O'Neill *et al.*, 1986), is that of scale, neglected for too long in ecological studies. An ecosystem is not something that can be crisply defined, like the objects of study in molecular biology; rather, its characteristic patterns and responses to stress vary with the scale of investigation. For example, questions relating to how diverse and stable ecosystems are make no sense without reference to the scale of interest, and environmental management must not oversimplify this complexity and ambiguity in objectives.

## 19.6 CONCLUSIONS

Risk assessment and risk management are interrelated activities; the capability to do one eases the task in approaching the other. Because uncertainty is an ineluctable aspect of prediction, some potential for monitoring and adaptive management is essential.

Species invasions can result from deliberate or accidental introductions, or from disturbance of established biotic communities. In the case of the former perturbation, the considerations bear rough similarity to those that must be addressed in connection with the release of chemicals into the environment.



Principally, these involve the fate and transport of the released material, and their possible ecological effects. For the movement of organisms and propagules, a sound basis exists for the description of spread, and substantial theoretical advances are likely within the next few years. The issue of effects is much more problematical, and emphasizes the need for a general theory of the responses of ecosystems to stress. Such a theory can draw inspiration and generalization from mathematical models, but cannot rely exclusively upon them. To develop the understanding of process that is essential to a capability to extrapolate from one experience to another, we desperately need more information derived from the experimental manipulation of whole ecosystems.

Finally, as in any case of environmental management, we must deal explicitly with the recognition that ecosystems have vital characteristics on a multiplicity of spatial, temporal, and structural scales. The multiple uses that may pertain to a single ecosystem argue against any attempt to reduce all complexity to a minimum number of descriptors that somehow balance all societal interests. We must not cloak what should be societal decisions in the mantle of scientific objectivity when the determinations are not purely scientific. The scientist must consider the problem on multiple scales, making clear the conflicts and the levels of uncertainty, facilitating but not usurping the societal role in managing risks.

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