

MODELLING SPREAD IN INVASION ECOLOGY: A SYNTHESIS

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25.1 INTRODUCTION

Understanding the spatio-temporal dynamics of populations, their expansion and retraction, has always been one of the main pursuits in ecology and biogeography. Spread of invasive species, while posing real and escalating threats to biodiversity conservation and ecosystem functioning, also provides superb natural experiments for unravelling the mechanisms and factors behind the dynamics of species' geographical range. Studies of spread can be traced back to the dawn of mathematical ecology (Fisher 1937; Kolmogorov et al. 1937), with steady development on analysing species' dispersal using partial differential equations and other spatial modelling techniques (Skellam 1951). Spatial modelling currently forms a crucial part of invasion biology. A very wide range of methods, techniques and philosophies underpin modern spatial modelling and it seems worthwhile, five decades after Elton's (1958) pioneering book, to review the current status of the field of spatial modelling relating to biological invasions, to explore the emergence of different approaches and to identify the key challenges.

Organisms have an intrinsic drive to grow and expand. They must constantly be on the move, to alleviate intraspecific competition and inbreeding pressure, and to exploit opportunities provided by disturbances. Such movements of individuals, either through random-walk-like diffusion or directed dispersal, lead to a collective phenomenon of advancing frontiers in the geographic range of species, namely 'spread'. Classic examples of spreading organisms include the natural recolonization of Europe and North America by trees after the ice age, the spread of the European starling in America after its introduction to the region by humans and the expanding wave of the Canadian lynx in response to human-mediated environmental changes (see Hengeveld 1989). Although these examples of spread share some dynamic properties, in this chapter we focus on the spread of post-introduction alien species.

Mathematical modelling has been extremely valuable for uncovering the dynamics behind the spread of introduced species (see, for example, Okubo et al. 1989; van den Bosch et al. 1990; Shigesada & Kawasaki 1997; Caswell et al. 2003). However, most early mathematical ecologists lumped what we now call 'invasive' species (*sensu* Pyšek et al. 2004) with other spreading species, and were essentially interested

in general dispersal and colonization dynamics of organisms. As defined by Richardson et al. (2000a) and Lockwood et al. (2005), the invasion process includes the phases of arrival, establishment and naturalization of an alien species by breaking geographic, environmental and reproductive barriers. Breaching of dispersal barriers allows species to become 'invasive' (see also Wilson et al. 2009a). Spread models need to accommodate all parts of the invasion process.

Our synthesis of advances in spread modelling applied to biological invasions examines three components: the modelling core, environments and methods. Traditional spread models are classified into different categories according to their modelling core (e.g. those using differential equations). Theories about these models are briefly reviewed, and the rate of spread (i.e. the velocity of the travelling waves) is presented analytically where possible. Furthermore, to implement the modelling core in practice, it is necessary to consider other modelling environments and methodologies. Progress in modelling environments and methods (e.g. the neutral landscape model, niche modelling, and individual-based models) have enabled us to incorporate realistic habitat heterogeneity, stochasticity and more powerful algorithms for spatial realization in spread models.

25.2 SPREAD MODELS

A conceptual model

Higgins and Richardson (1996) provided a conceptual framework and a classification of models of alien plant spread. The number and types of models used in invasion ecology (not only for plants) has increased dramatically since this review was published. Models are now not only used to predict spread, but also to explore options for intervention (Jongejans et al. 2008). The essence of spread models has been broadened from a strictly mathematical orientation to a much more cohesive integration of data capture, mathematical analysis and modelling realization. Following these developments, we suggest a conceptual framework representing an 'optimal model' for studying the spatial spread of invasive species (Fig. 25.1).

This conceptual model comprises three components: modelling core, environment and method. The modelling core refers to dynamic models used to

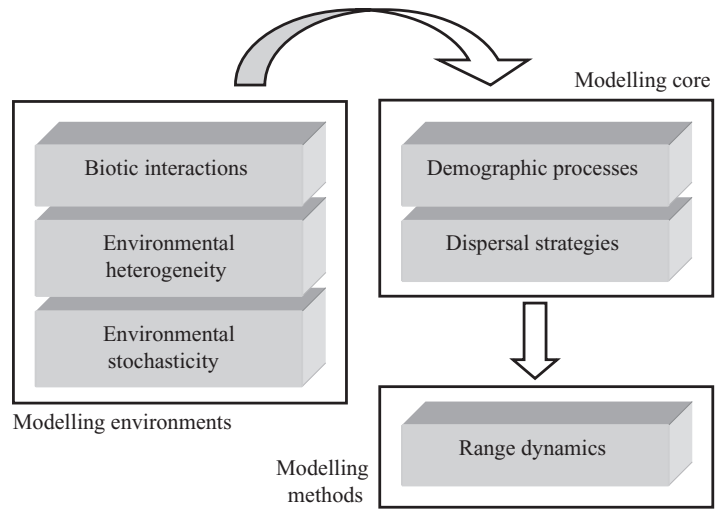


Fig. 25.1 A conceptual model for spread models for use in invasion biology.

describe the demography and spatial dynamics of species (Skellam 1951; Okubo 1980; van den Bosch et al. 1990, 1992). The use of a modelling core, such as differential and integrodifference equations, to analyse range expansions eventually evolved into a multidisciplinary endeavour drawing on dispersal ecology and invasion ecology, and focusing on identifying the ecological and evolutionary determinants and mechanisms of the spatio-temporal dynamics of invasive species, as well as designing the spatially optimal strategies for detection, control and eradication of focal species at different invasion phases.

Modelling environments are the factors that affect the rate of spread and the spatial distributions of invading species. They include biotic interactions, environmental heterogeneity and stochasticity (Hastings et al. 2005). The stage has been set for making real progress towards understanding the effect of environmental heterogeneity on the spread of introduced species, because (i) the potential distribution of a species, as reflected by its realized niche, can now be presented as a heterogeneous map using ecological niche modelling, and (ii) the spatial structure of habitats can now be simulated using, for instance, neutral landscape models.

There have been advances in modelling methods in recent years, especially because of advances in computer technology. Spatial modelling techniques such as individual-based models and cellular automata are fre-

quently incorporated into spatial spread models. Here we review only those methods that are most relevant to spatial spread and that have been most widely applied in invasion biology. Overall, a clear understanding of the assumptions, advantages and drawbacks behind each modelling core, environmental condition and technique enables us to present a clear synthetic view of our current challenges and trends in tackling the spatial spread of invasive species, not only as a theoretical question but also as a backbone for efficient management and control of problematic invasive species.

Modelling core

Ordinary differential equations

We start by considering a simple spatially implicit model that ignores population density: Levins' (1969) patchy occupancy model,

$$\frac{dP}{dt} = cP(1-P) - eP,$$

where P , c and e ($c > e$) denote the proportion of suitable habitat being occupied, the colonization rate and the local extinction rate, respectively. This has been widely applied to the study of metapopulation dynamics in spatial ecology and describes the dynamics of populations balanced by local extinction and recolonization

of empty habitat patches. Although the patchy occupancy model is spatially implicit, the occupancy dynamics can be easily interpreted as the spontaneous rate of spread, $v_t = 1/(2\pi^{1/2}P^{1/2})dP/dt$. This model describes the logistic dynamics of species occupancy, with an asymptotic equilibrium determined only by the colonization–extinction process, $\hat{P} = 1 - e/c$. The rate of spread initially depends on the difference between the colonization and extinction rates, as well as the initial range size (P_0), $v_0 \approx (c - e)\sqrt{P_0}/(2\sqrt{\pi})$, then reaches a maximum speed, $v_{\max} = (c - e)\sqrt{\hat{P}}/(3\sqrt{3\pi})$, and eventually slows down when the range size approaches its equilibrium.

Though simple, patchy occupancy models nonetheless infer several propositions that have been supported by the invasion biology literature: (i) the early phase of range expansion is often accompanied by an accelerating velocity of spread; (ii) stronger colonizers, indicated by the high colonization rate, are potentially good invaders with a high rate of spread; and (iii) high frequency or intensity of disturbance and a harsh environment result in high rates of local extinction and inhibit rapid spread. In practice, the spatial version of the model should be used and has been applied to reconstruct the spread of Argentine ants in Spain (Roura-Pascual et al. 2009a). One proposition from this model that has not been tested in invasion ecology is that, all else being equal, species with large potential distributions spread faster than those with small potential range. Because potential distribution can be extrapolated from ecological niche modelling (see ‘Modelling environments’ in section 25.2 for details), it should be possible to test this proposition empirically.

Partial differential equations

Most propositions about the rate of spread are derived using partial differential equations. Consequently, most modelling cores in the literature are based on partial differential equations, because of their advantage of incorporating spatial dimensions (see, for example, Holmes et al. 1994; Turchin 1998; Petrovskii & Li 2006). We focus largely on models with one spatial dimension (i.e. spread along a linear habitat, such as coastline, rivers and roads), although models with two spatial dimensions can easily be implied.

Two classical partial differential equations were first presented by Fisher (1937) and Skellam (1951) as the well-known reaction–diffusion models:

$$\frac{\partial n}{\partial t} = f(n) + D \frac{\partial^2 n}{\partial x^2},$$

where $f(n)$, D and n indicate the population growth rate, the diffusion rate and the population density. For Skellam’s (1951) model, the population follows the Malthusian growth $f(n) = r \cdot n$; for Fisher’s reaction–diffusion (1937) model, the population follows the logistic growth $f(n) = r \cdot n(1 - n/K)$, where r and K are the intrinsic growth rate and the carrying capacity. The model generates a travelling wave with an asymptotic velocity of $\hat{v} = 2\sqrt{f'(0)D}$. It is worth noting that this is the rate of spread caused by the Brownian-motion diffusion, and thus may not be suitable for representing realistic patterns of animal movement. Seed dispersal by different vectors defies random diffusion and is often studied by incorporating dispersal kernel into the integrodifference equations (Tsoar et al., Chapter 9 of this volume). Furthermore, when the reaction in the model is very fast, the asymptotic velocity can become arbitrarily large, and a solution to such an unrealistic property is to replace the above model by an integrodifferential equation, often known as the generalized Fisher–Kolmogorov–Petrovskii–Piskunov equation (Branco et al. 2007).

It is clear that any effects causing changes to the linear approximation of population growth function at the initial point of invasion $f'(0)$ will have an impact on the rate of spread. For instance, Lewis and Kareiva (1993) examined the rate of spread of the reaction–diffusion model when the population dynamics is subjected to the Allee effect, $f(n) = r \cdot n(n - a)(1 - n)$, and found the asymptotic rate of spread to be sensitive to the intensity of the Allee effect: $\hat{v} = \sqrt{2rD}(0.5 - a)$ if $a < 1/2$ and $\hat{v} = 0$ if $a \geq 1/2$. Furthermore, in a two-dimensional landscape, the expanding wave can only start if the initial radius of the beachhead is greater than a threshold ($\sqrt{D/2r}(0.5 - a)$), i.e. there exists a minimum initial population size for the range expansion (Lewis & Kareiva 1993).

Besides the random-walk diffusion, if species dispersal is biased due to, say, air and water currents, a drift (or convection) term can be added to the reaction–diffusion model; it is then called an advection–diffusion model:

$$\frac{\partial n}{\partial t} = f(n) - v_x \frac{\partial n}{\partial x} + D \frac{\partial^2 n}{\partial x^2},$$

where v_x is the drift velocity along the x -axis direction. The travelling wave of the advection–diffusion model

is a simple overlap between the travelling wave of the diffusion model and the convection velocity (van den Bosch et al. 1990).

Another extension to the basic reaction–diffusion model was made because of the realization that animals do not follow strictly random walks in their movements, but tend to move with persistence. This correlated random walk can be depicted by the reaction–telegraph equation (Holmes 1993):

$$\frac{\partial n}{\partial t} = f(n) + \frac{1}{2\lambda} \frac{\partial f}{\partial t} - \frac{1}{2\lambda} \frac{\partial^2 n}{\partial t^2} + \frac{\gamma^2 n}{2\lambda} \frac{\partial^2 n}{\partial x^2},$$

where γ is the velocity of the individual and λ is the rate of changing direction. For logistic growth, $f(n) = r \cdot n(1 - n/K)$, Holmes (1993) found that the rate of spread (i.e. the speed of the travelling wave) is $v = \gamma\sqrt{8r\lambda}/(r + 2\lambda)$ if $0 < \sqrt{r/2\lambda} \leq 1$, and $v = \gamma$ if $\sqrt{r/2\lambda} \geq 1$. Furthermore, if we let $D = \gamma^2/2\lambda$, the comparison of the rate of spread from diffusion and telegraph models is made possible, which often predict relatively similar rates of spread in reality (Holmes 1993).

A general density-dependent diffusion model is presented by Okubo (1980) as the crowding-induced diffusion. Aronson (1980) investigated one such general reaction–diffusion (crowding-induced) model:

$$\frac{\partial n}{\partial t} = f(n) + \frac{\partial^2 n^m}{\partial x^2},$$

where $f(n) = n(1 - n)$. This model has been rescaled so that the equation only has one parameter m . Obviously, if $m = 1$, this model is essentially Fisher's reaction–diffusion model. Individual movement only responds to overcrowding when $m > 1$, and the rate of spread thus significantly slows down. For instance, if $m = 2$, the rate of spread drops by half, and the population density also becomes zero at a certain distance ahead of the wave. Individuals tend to avoid crowded areas when $m < 1$, suggesting a potentially high rate of spread. The crowding-induced diffusion comes from a biased random-walk, instead of a pure or correlated random-walk, and thus differs from the diffusion and the telegraph models (Aronson 1980; Turchin 1998).

Dispersal kernel models

The differential equation models discussed above do not take into account two measurements that are often obtained from ecological surveys: the stage structure

of the organism (e.g. age structure or egg–larvae–adult stages of insects) and the different forms of dispersal kernel (i.e. the probability density function with respect to the distance away from the original location after dispersal; a Gaussian dispersal kernel is assumed in diffusion models). A group of models enables us to incorporate both the demographic factors and the dispersal characteristics: the discrete-time dispersal kernel model (also called the *integrodifference equations*) and the continuous-time dispersal kernel model (also called the reproduction-and-dispersal kernel model; R&D kernel model for short).

Integrodifference equations are further discretization of integrodifferential models, and can be used to estimate the rate of spread based on any specific dispersal kernels (Weinberger 1982; Kot et al. 1996; Lewis et al. 2006). Let $k(x, y)$ denote the probability density function for the location x to which an individual at y disperses, we have the following integrodifference equation for calculating the population density in locality x at time $t + 1$ (Kot et al. 1996; Neubert & Caswell 2000):

$$n(x, t + 1) = \int_{-\infty}^{\infty} k(x, y) b[n(y, t)] n(y, t) dy,$$

where $b[n]n$ gives the size of the growing population at locality y . The asymptotic rate of spread exists $\hat{v} = \min_{s>0} \ln[b(0)\Phi(s)]$ provided that $b[n]n$ increases monotonically with the population density n (also with no Allee effect) and that the dispersal kernel has a moment-generating function:

$$\Phi(s) = \int_0^{\infty} k(z) e^{sz} dz,$$

where z indicates the distance between x and y . The integrodifference equation can also further incorporate the stage-structured population growth and dispersal, resulting in the stage-structured (matrix) model and enabling us to estimate the elasticity and sensitivity of different demographic stages (Neubert & Caswell 2000). Recently, a special focus of using integrodifference equations, which deserves continuous attention, is to estimate the rate of spread for fat-tailed long-distance dispersal (Higgins & Richardson 1999; Clark et al. 2003; Tsoar et al., Chapter 9 of this volume).

A closely related dispersal kernel model is the continuous-time R&D kernel model (van den Bosch et al. 1992):

$$n(x, t) = \int_{-\infty}^{\infty} \int_0^{\infty} k(z, a) l(a) b(x - s, t - a) da \cdot ds,$$

where $l(a)$ is the probability that an individual is still alive at age a . This leads to a rather similar rate of

spread as the reaction–diffusion model, suggesting that $\hat{v} = 2\sqrt{f'(0)D}$ is a robust measure of the rate of spread (van den Bosch et al. 1992; Grosholz 1996; Turchin 1998). An important area for future work is to explore the relationship between the rate of spread and different forms of dispersal kernels (e.g. the general power-law function for the long-distance jump dispersal) under different modelling environments (see discussion below).

Modelling environments

Biotic interactions

The relationship between species richness of a community and its invasibility was raised by Elton (1958) and has been one of the most persistent debates in the invasion biology literature ever since (Richardson & Pyšek 2007; Fridley, Chapter 10 of this volume; see also Stohlgren et al. 2003; Tilman 2004). Although recent studies suggest that the impact of biological invasions on native species richness is strongly scale dependent (Gaertner et al. 2009), theoretical studies have confirmed that biotic resistance does have an effect on the rate of spread (Okubo et al. 1989; Dunbar 1983, 1984). For interspecific competition between invaders and native competitors, Okubo et al. (1989) considered a diffusion model of two competing species:

$$\begin{aligned}\frac{\partial n_1}{\partial t} &= D_1 \frac{\partial^2 n_1}{\partial x^2} + r_1 n_1 (1 - \alpha_{11} n_1 - \alpha_{12} n_2) \\ \frac{\partial n_2}{\partial t} &= D_2 \frac{\partial^2 n_2}{\partial x^2} + r_2 n_2 (1 - \alpha_{21} n_1 - \alpha_{22} n_2)\end{aligned}$$

where α is the coefficient of intra- and interspecific competition. Okubo et al. (1989) found that the rate of spread for the invader (species 1) can be slowed down by its native competitor: $\hat{v} = 2\sqrt{r_1 D_1 (1 - \alpha_{12}/\alpha_{11})}$. Dunbar (1983, 1984) examined the effect of predation on the rate of spread in a Lotka–Volterra model:

$$\begin{aligned}\frac{\partial n_1}{\partial t} &= D_1 \frac{\partial^2 n_1}{\partial x^2} + r \cdot n_1 (1 - n_1/K) - a \cdot n_1 n_2 \\ \frac{\partial n_2}{\partial t} &= D_2 \frac{\partial^2 n_2}{\partial x^2} + \gamma \cdot a \cdot n_1 n_2 - \delta \cdot n_2\end{aligned}$$

where a , γ and δ are the rate of predation, the conversion rate of captured preys and the death rate of the predators, respectively. If the predator is the invader, then it spreads according to the rate $\hat{v} = 2\sqrt{(\gamma \cdot aK - \delta)D_2}$.

Both studies suggest that biotic interactions such as competition and predation can inhibit the fast spread of invasive species.

Besides the confirmation from such theoretical studies, real evidence is limited. Ferrer et al. (1991) reported that the range expansion of the European starling and the spotless starling in Spain slowed down due to their interspecific competition. Similar evidence has also been reported for other bird species (e.g. the red-whiskered bulbul (Clergeau & Mandon-Dalger 2001)). However, such competitive resistance may not to be important for insects (ants and wasps) (Holway 1998; Walker et al. 2002; Roura-Pascual et al. 2010a), and shows mixed effects on the spread of plants (Higgins et al. 2008). Other interspecific relationships, such as pollination mutualisms and predation, have also been suggested to affect the rate of spread (Lonsdale 1993; Richardson et al. 2000b). Overall, biotic interactions can clearly affect the rate of spread, and such impacts are taxon- and scale-dependent (Traveset & Richardson, Chapter 12 of this volume).

Environmental heterogeneity

Niche theory in ecology posits that the performance of organisms, such as the growth rate and mobility, changes along environmental gradients. Spatial spread of invasive species is also affected by environmental heterogeneity, and this can be incorporated in the modelling core of differential equations and dispersal kernel models using spatially dependent diffusion. Two frequently used methods for this are replacing the diffusion term in the model by the Fokker–Planck equation $\partial n/\partial t = \partial^2(\mu(x)n)/\partial x^2$ or the Fickian diffusion equation $\partial n/\partial t = \partial(D(x)\partial n/\partial x)/\partial x$, where $\mu(x)$ and $D(x)$ are motility and diffusivity at locality x that determine the rate of spread (Turchin 1998). For instance, Shigesada et al. (1986) studied a Fickian diffusion model in a spatial heterogeneous landscape. Clearly, it is difficult to arrive at an analytical solution to the rate of spread. However, numerical simulations can be easily obtained for studying the spread of invasive species in heterogeneous environments. Recently, Dewhurst and Lutscher (2009) have derived an approximate rate of spread in heterogeneous habitats using integrodifference equations, thereby making significant progress in the field (see also Higgins et al. 2003; Kawasaki & Shigesada 2007).

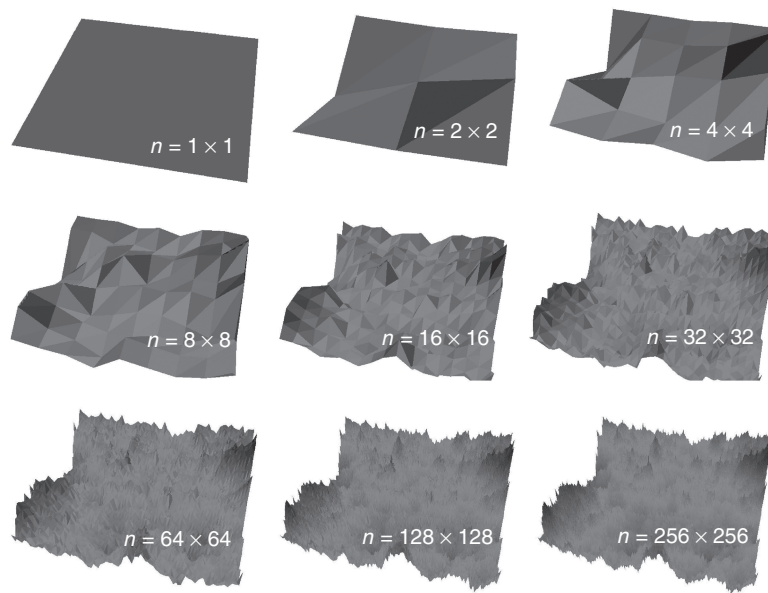


Fig. 25.2 The procedure of generating a spatially heterogeneous fractal landscape using the midpoint displacement algorithm (Fournier et al. 1982).

In theoretical studies of spread in heterogeneous landscapes, spatial heterogeneity is often generated by neutral landscape models, which can be broadly categorized into random, hierarchical and fractal types (With & King 1997). Random neutral landscape is the first-generation model that seeks the critical scales in detecting or comparing ecological processes based on the prediction of percolation theory (see, for example, Gardner et al. 1987; Wiens et al. 1997). The clumped neutral landscape model that incorporates spatial autocorrelation between different localities has been proposed as an improvement (Hiebeler 2000). The second generation of neutral landscape models are hierarchical (Lavorel et al. 1994). Because landscape processes are more or less assembled in a hierarchical structure, such neutral landscape models perform reasonably well in predicting dispersal patterns of species in heterogeneous landscapes (Lavorel et al. 1995). The most realistic neutral landscape models are those of fractal nature (Palmer 1992). Algorithms, such as the midpoint replacement (Fig. 25.2), are often used to generate artificial landscapes for examining species' distributional patterns (Leung et al. 2010). Furthermore, fractal neutral landscape models are clearly consistent with the fractal and self-similar

structure of species' distribution and assemblage (With 2002; Hui & McGeoch 2008; Storch et al. 2008), and the effect of the fractal structure of the landscape on the rate of spread is expected to be clarified soon.

For investigating the effect of environmental heterogeneity on spread, ecological niche modelling (also called species distribution modelling or (bio)climatic/environmental envelope modelling), in its general sense, has become a standard approach for transforming environmental variables into suitability maps that can describe species' fundamental (bottom-up approach) and realized niche (top-down approach) (Fig. 25.3). The bottom-up ecological niche modelling translates species physiological limits into the fundamental niche using fine-scale microclimate data by measuring the survival rate of the organism (see, for example, Kearney & Porter 2009). It thus projects the suitable habitat of focal species in the spatial landscape. The top-down ecological niche modelling, on the other hand, translates the broad-scale presence-absence (and even abundance) records and macroclimate data into the realized niche and, as a result, projects the potential distribution of the species (see, for example, Kriticos et al. 2003; Peterson & Vieglais 2001; Franklin 2010).

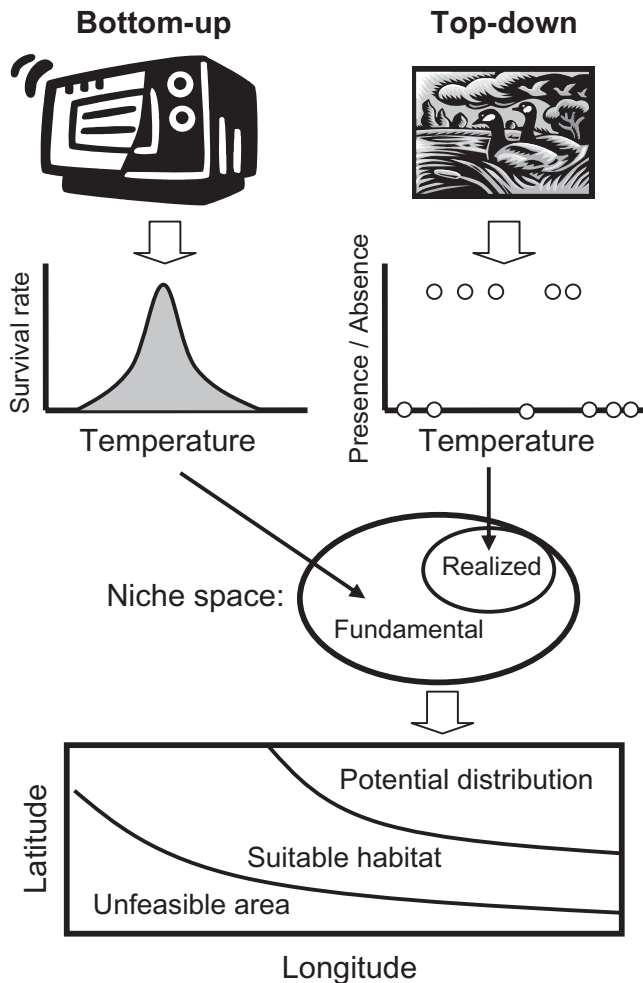


Fig. 25.3 A schematic illustration of the bottom-up and the top-down ecological niche modelling.

Because invasive species experience novel combinations of environmental variables and biotic interactions, the top-down ecological niche modelling for generating the realized niche and projecting the potential distribution of invasive species could be biased (Guisan & Thuiller 2005; Pearson et al. 2006). In contrast, the bottom-up niche modelling can often identify a reliable suitable habitat in the invaded area due to niche conservatism (Wiens & Graham 2005). Furthermore, ecological niche models have been criticized for the low-sensitivity of their prediction (Heikkinen et al. 2006) and the lack of efficiency in the evaluation method, *Area Under Curve* (AUC (Lobo et al.

2008)). Therefore two key challenges in this research are the following: to (i) design (hybrid) models that can encompass population dynamics (see, for example, Gallien et al. 2010) and predict the realized niche shift within its fundamental niche when encountering a new environment; and (ii) design a more sensitive measure than the AUC index to evaluate models that can incorporate spatial information of the input data.

Environmental stochasticity

Even if a spread model is mechanistically correct, its predictive power can still be hindered by the determin-

istic chaos potentially inherent in the system, and also by the stochasticity of population dynamics. Indeed, no populations can avoid demographic and environmental stochasticity in the real world. Demographic stochasticity refers to the variability in population size caused by the birth–death–dispersal process and could be responsible for the slow rate of spread at initial stage when the population size is small (Hastings 1996). Environmental stochasticity refers to the variability in population size caused by the variations in the life-history parameters from other environmental heterogeneity and disturbances (e.g. the birth rate can be seasonal and locational dependent and further influenced by fire and floods). In general, Mollison (1977, 1991) suggests that stochastic models predict the same rate of spread for density-independent populations as the rate of spread in deterministic models, but could alter the rate of spread in density-dependent populations. Although recent work on modelling the spread of invasive species often includes environmental stochasticity, or uses stochastic models (Schreiber & Lloyd-Smith 2009), further attention needs to be given to clarifying measures of stochasticity and the relationship between the stochasticity and rates of spread. Questions that need to be addressed include the follow-

ing. (i) Do invasive species experience higher variability in their population dynamics in novel environments? (ii) Do invasive species that encounter high variability spread faster? Clearly, stochasticity and variability require special attention in future studies, not only with reference to rates of spread, but also at all stages of biological invasions.

Spatial modelling methods

Spatially explicit modelling techniques in invasion ecology have advanced gradually (Box 25.1), and involve complex rule-based programming under the scope of agent-based models, often with an intractable analytical solution. The classification of modelling techniques can be based on the way that the population, space and time are considered (e.g. whether discrete or continuous) (Berec 2002).

In general, nearly all techniques for modelling spread belong to the family of individual-based models (IBMs). These simulation techniques treat individuals as unique and discrete entities that often have at least one property that changes during the life cycle (Grimm & Railsback 2005). When modelling spread in a

Box 25.1 The development of modelling methods

Methods for the spatial modelling of spread have been developed since the 1950s, with the advance of electronic computers. Cellular automata (CA) were first developed in 1950s by John von Neumann in a failed attempt to prove the emergence of self-reproduction in life by discretizing partial differential equations in lattices. Numerous attempts followed, seeking transition rules in CA to imitate life phenomena (e.g. ‘the game of life’ (Conway 1970)). The development of CA were also accompanied by the design of parallel computers and digital image processing. In the 1960s, CA began to be used to study neural networks, reaction–diffusion processes of active media as in heart and muscles, and the Ising model in physics (CA with randomness). By the end of 1970s, when computers became widely available, research on CAs accelerated rapidly. In invasion ecology, the spread of invasive species is often simulated by CAs (often called lattice models) with continuous cell state on heterogeneous landscapes (Roura-Pascual et al. 2009a).

The earliest work using individual-based models (IBMs) can be traced back to the 1960s in a doctoral dissertation on the dynamics of Douglas-fir (Newnham 1964). One of earliest papers that brought individual-based models (IBMs) into the ecological literature was by Michael Huston et al. (1988). This visionary work separated IBMs from other types of model and called the development of IBMs ‘a self-conscious discipline’. Several reviews have traced the history of IBMs for animals, plants and in general (DeAngelis & Mooij 2005; Grimm & Railsback 2005). IBMs quantify differences between individuals both biologically and spatially (Huston et al. 1988), consistent with the reality in spread models. Given this advantage and increasing computational power, the use of IBMs has grown continuously (DeAngelis & Mooij 2005). Although IBMs are unlikely to lead to any general theories in ecology (DeAngelis & Mooij 2005), they are contributing substantially to predicting case-specific spread in invasion ecology.

spatially explicit context, all individuals need to be assigned a location which may be static in the case of plants, or variable in the case of animals. The 'individual' in IBMs need not be a real individual, but can also represent a group of individuals that share a common entity, for example a colony of insects.

Another class of models are (classical and extended) cellular automata (CA; also termed 'lattice models'). CAs are an idealized 'system in which space and time are discrete' in which the cells have a finite number of possible states (Chopard & Droz 1998). Classical CAs are also deterministic, and the state of a cell at the next time step is defined by the state of the cell and its neighbours in the previous time step (Conway 1970). As these conditions are quite limiting, the stochasticity condition can be relaxed and an infinite number of states for each cell allowed, resulting in the extended CA. CA modelling faces the modifiable areal unit problem (Openshaw 1984) giving that the cell size is often artificially chosen. As a result, the linear dimension of the cell for any spread models should be less than the median of the dispersal kernel.

Given the different units of IBMs and CAs (individuals versus cells), CAs can use IBMs internally by defining the state of a cell as a collaborative measure of all dwelling individuals that are governed by IBM rules. This hybrid is actually the case for spatially and temporally discrete IBMs. Bithell and MacMillan (2006) provide an overview over the problems associated with this approach, and suggest several approaches for the 'escape from the cell'. In contrast to spatially discrete models (CAs), such spatially continuous models do not use an underlying grid to define the location, but store the location as coordinates. This removes the modifiable areal unit problem when using a CA (Hui et al. 2010). Although the spatially continuous model avoids using an artificially chosen cell size, it creates computational challenges: the intensity of interactions between individuals has to be defined as a distance-dependent function (e.g. the dispersal kernel). Furthermore, complications also arise in the construction of these models, as discrete time steps are inherent in the modelling. Even though this is not a problem for species with synchronized life-history events (e.g. breeding and migration), it poses problems for species with no coherence. This problem can be mitigated by either choosing small time steps or using random process to determine the exact time for each event (e.g. the background Poisson process with density dependent rate (Berec 2002)).

In general, IBMs are more computationally intensive than CAs and other formula-based models. Consequently, a major constraint in the use of IBMs is the number of individuals expected, rather than the size of the area simulated. In contrast, CAs are limited by the number of cells simulated (i.e. spatial extent). As a rule of thumb, in cases where large areas need to be simulated, CAs are more suitable than IBMs, unless the number of individuals is expected to be relatively small. However, with recent advances in high-performance computing (e.g. parallel computing), computational requirements have become less restrictive. It is becoming feasible to construct and run advanced simulations that were impossible previously (Bolker et al. 2000).

In cases where the behaviour of the individual is important for predicting the spread of the species, IBMs have to be used, as they can incorporate detailed information about the individual (Jongejans et al. 2008). As outlined by Jongejans et al. (2008), the complexity of spread models varies considerably, depending on (i) the dispersal mode of the species of concern, (ii) the type of model selected and (iii) the required level of realism of the model. CAs are preferred to IBMs when the data related to the spread is limited given that CAs are less data hungry. For programming, we need to specify the initial and boundary conditions and transition rules for CAs and rules governing individual's life-cycle process for IBMs (Grimm & Railsback 2005).

In contrast to data- and computationally intensive dynamic models of spread, other methods exist which can be summarized as non-simulation based static spread models. These models provide no temporal sequence of predictions, but rather use knowledge gained from experts or from statistical models (e.g. regression-trees and multi-criteria decision models) to identify areas likely to be occupied by invading species (see Rouget et al. 2003), prioritize areas for conservation management (Roura-Pascual et al. 2009b, 2010b), or to define integrated strategies to reduce the threat of ecosystem dysfunction and species extinction due to climate- and land use changes and biological invasions (Richardson et al. 2009). These static models are relatively easy to construct and are a good way of capturing expert knowledge, but can be applied only to the area for which they were constructed.

25.3 SYNTHESIS

Although substantial progress has been made in understanding the mechanisms and factors that drive

the spatial spread of invasive species in novel environments in the past 50 years, we must acknowledge that the dynamics and management of biological invasions is a multi-stage and multidisciplinary field. From the early work on invasion dynamics (Hengeveld 1989) to the recent emphasis of biological invasions as a multi-stage process, the focus of modelling studies has changed, from an initial preoccupation with only 'spread' to the current interest in parameterizing and simulating dynamics at all stages of the naturalization–invasion continuum. Particular modelling approaches and philosophies are emerging for each stage; these are increasingly linked to management requirements. For instance, human and cargo transportation by ships and aircrafts have been strongly correlated with the number of species introduced to different places across the globe (Drake & Lodge 2004; Tatem 2009). An important theoretical issue at this stage is the estimation of the introduction rate from the discovery records (Solow & Costello 2004). Prevention is clearly the best (most cost-effective) strategy for reducing rates of introduction. Once introduced, only a fraction of alien species establish in the novel environment. The outcome of an introduction event depends on numerous factors associated with the introduction pathway (Wilson et al. 2009b), as well as many other factors, including environmental suitability, resource availability and the ability to adapt and naturalize. The combined influence of many post-introduction factors often causes a time lag before fast spread, during which time eradication may be feasible. Once established, the spatial spread of an invasive species can be modelled in different ways, by stochastic modelling in a heterogeneous landscape, as reviewed in this chapter. Once a species reaches this stage, eradication becomes expensive, and often impractical or impossible, leaving only various options for reducing population sizes or growth rates. The whole process of biological invasion can be incorporated into a probability transition model (see an attempt by Jerde & Lewis (2007)). Advances in the modelling core, environment and methods, as reviewed here, have brought fundamental insights in facilitating the management and control of invasive species, for example identifying crucial demographic stage for fast spread (Neubert & Caswell 2000) and determining optimal control and clearing strategy (Moody & Mack 1988; Moilanen et al. 2009).

Spread dynamics is the collective behaviour of individuals in an expanding population. Obviously, this becomes possible only through dispersal. This leads to a joint focus between dispersal ecology and invasion

biology: the dispersal kernel (Porter & Dooley 1993; Bullock & Clarke 2000; Tsoar et al., Chapter 9 of this volume). The forms of dispersal kernels are diverse, depending on the life forms of the species, dispersal pathways and landscape structure (Greene & Calogeropoulos 2001). Importantly, individuals tend to follow different dispersal types, even within species (Williamson 2001): natal versus breeding dispersal in vertebrates, pollen versus seed dispersal in plants, walking versus flying in insects, within and outside habitat patches, genetic and morphologic difference (e.g. sexual and age difference). Such multi-type dispersal within one species has been suggested to be able to explain the long-distance jump dispersal in fast expanding species (see Clark et al. 1999; Higgins & Richardson 1999). Although a robust conclusion has been reached regarding the rate of spread under the Gaussian dispersal curve (i.e. $\hat{v} = 2\sqrt{f'(0)D}$), a clear deduction of the spreading rate from other forms of dispersal curves is expected to foster a synthesis between invasion biology and dispersal ecology (see, for example, Dewhurst & Lutscher 2009). Furthermore, we have to realize that the evolutionary and genetic identity of a population is constantly changing, causing variations and uncertainties of the rate of spread at different invasion stages (Phillips et al. 2008; Williamson 2009).

Although dispersal kernel and the rate of spread are two main focuses about the spreading dynamics in invasion ecology, it is necessary to link these focuses with other concepts in invasion biology, especially invasiveness and the impact of invasive species. The invasiveness (the ability for alien species to establish in a new environment) has to be stated in the context of the invasibility of the native community and often refers to the ability to cross strong environmental barriers (high stress tolerance and adaptation rate) and suffer no Allee or other founder effect. It is unclear whether species with high invasiveness should have a fat-tail dispersal kernel or a high rate of spread; yet, in general we would expect this, because high dispersability could reflect the life-history strategy for mitigating risks and uncertainty when facing new environments (Trakhtenbrot et al. 2005). However, a fast-expanding species does not necessarily have major impact in the receiving community. In fact, the impacts of such species may be lower, owing to the potential life-history trade-off between 'win stay' and 'lose shift' strategies. This proposition has a clear management implication for prioritizing for eradication of slow-expanding species first. The test of this hypothesis would require a clear understanding of the

physiological, genetic and evolutionary background of the species.

Integration within invasion biology is necessary, especially between the application of the type of spread models reviewed in this chapter and the risk assessment framework that is increasingly driving management of biological invasions. Possible applications include the identification of sites threatened by the spread of alien invasive species, testing management strategies and budgets, motivation and justification of budget requirements (Moilanen et al. 2009). In addition, as the need of spread models in management increases, the development of new spread models has to pay more attention to the management demand. This requires new ways to simulate spread and more transparent interpretation of modelling results, as well as problem-driven modelling with targets identified by managers. Web-based technologies have potential to deliver such a user-friendly interface for managers to provide input data and for modellers to deliver the results. In all, the spread of invasive species provides an ideal natural experiment for ecologists to examine the biotic and abiotic factors behind species spatio-temporal dynamics, and poses challenges to managers and modellers for simulating and assessing the trend and impact of the invasion with sufficient accuracy.

ACKNOWLEDGEMENTS

We thank Steven Higgins, Nanako Shigesada, John Wilson and Aziz Ouahinou for helpful comments on the chapter. Our work was largely funded by the DST-NRF Centre of Excellence for Invasion Biology. C.H. acknowledges support from the NRF Blue Sky Programme; R.M.K. and D.M.R. acknowledge support from the Global Environmental Facility (GEF) through the Cape Action for People and the Environment (CAPE) programme.

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