Dispersal, demography and spatial population models for conservation and control management

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Abstract

Spatial population dynamics can seldom be ignored in management aimed at conserving or controlling plant species in a spatial context. Therefore, spatial population models, that bring together knowledge about a species' local demography and dispersal behavior, are of growing applied importance. Here, we survey increasingly complex analytical and simulation models that are being developed to describe both demography and dispersal in applied studies. Local population dynamics can be modeled in an unstructured way, by specifying age- or stage-structure or by modeling each individual. Dispersal is often summarized in population-spread models with descriptive and simple statistical models. Mechanistic models that incorporate the physical or behavioral dynamics of dispersal vectors, however, provide more insight and can more readily be applied to novel situations. Importantly, mechanistic models provide a tool for linking variation in species traits and environments to dispersal and population spread.

Spatial population models span a wide range: from diffusion models, metapopulation models, integrodifference equation models, and Neubert–Caswell models, to spatially explicit individual-based models. The complexity (and biological realism) of such models often trades off with tractability: for instance, individual-based simulation models allow for unlimited incorporation of biological detail, but rarely for analytical exploration of the model dynamics. We discuss the advantages and disadvantages of these various spatial population models; the choice of the most appropriate model will depend on the management objective, the biological complexity, available data and the principle of parsimony. We present five case studies of endangered and invasive species for which spatial population models have been developed to inform management, for instance to decrease the spread rate of invasive species or to improve the regional persistence of endangered species. We also anticipate exciting new developments in both spatial analytical and spatial simulation models with increasing demographic, dispersal and spatial sophistication.
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Introduction

Population models are frequently used in species management studies. Often the central question of

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managers is how to control plant populations effectively and efficiently (Shea et al., 1998): which component of the life cycle of the focal plant species should be targeted? However, the spatial component (e.g. long-distance dispersal) of species dynamics in a landscape cannot be ignored when management problems are investigated (With, 2002; Trakhtenbrot et al., 2005). For instance, it is sometimes more important to target the dispersal process rather than the local population dynamics to control an invasion (Caswell et al., 2003). Similarly in conservation management, it may not be sufficient to conserve an endangered native plant locally since, for a persistent and dynamic metapopulation structure, management needs to enable successful colonization between habitat patches (Nicholson et al., 2006). Therefore, spatial population models have been developed that bring together knowledge about a species' local demography and dispersal behavior (see also Jeltsch et al., 2008). Spatial population models can be applied in studies with a large range of

management problems, for instance: conservation and reintroduction of endangered species, plant response to range shifts due to climate change, and control of invasive plants or genetically modified organisms. Currently, scientists are investigating how management recommendations based on spatial population models differ from those based on non-spatial models (Shea, 2004).

In this review, we will focus on how the dispersal process is incorporated into spatial population models for management problems. We will first provide an overview of methodologies for modeling demography and dispersal, and then look at the various ways demography and dispersal are linked in spatial population models. Such models can differ considerably in complexity due to the different levels of biological realism that is described in the demography and dispersal components. We will discuss the model selection process using five case studies (Table 1) from the conservation and control literature.

Table 1. The five case studies that are used throughout the text

Study system	Management	Seed dispersal	Spatial population dynamics
Rhinanthus minor[a]	Reintroduction and subsequent grassland management	Dispersal by wind, sheep, and mowing machinery measured with traps	NCMs with empirical MGFs derived from the seed trap data directly
Cytisus scoparius[b]	Traditional and biological control	Ballistic dispersal measured with traps around isolated plants; dispersal by ants inferred from seedling distributions	NCMs with empirical MGFs derived directly from the dispersal data
Carduus nutans[c]	Mowing, herbicides, and biological control	Dispersal by wind measured with traps and by tracking individual seeds; seed release studied in a wind tunnel	Integrodifference equation models for spatial spread with unstructured local dynamics; NCM; empirical MGF generated with a mechanistic WALD model
Succisa pratensis[d]	Mowing and hay removal; reducing landscape fragmentation for conservation	Seed tracking experiments and mechanistic models: short-distance dispersal by wind	Cellular automaton based on habitat maps with good, poor and non-habitat. Matrix models with density-dependent correction within cells
Heracleum mantegazzianum[e]	Integrated management: mechanical control, grazing, herbicides	Fruits can disperse long distances by water and humans, short distances by wind	Cellular automaton based on aerial photographs; individual-based demography model within cells; assumptions: short-distance dispersal to neighboring cells only, random long-distance dispersal

The case studies were selected to exemplify the range of modeling approaches used in spatial conservation and control studies.
NCM = Neubert–Caswell model: integrodifference equation for spatial spread, including a structured matrix model for local population dynamics.
MGF = moment-generating function, which describes the mean, variance and higher moments of a dispersal kernel.

[a]Coulson et al. (2001), Bullock et al. (2002, 2003).
[b]Parker (2000), Neubert and Parker (2004).
[c]Jongejans et al. (2007b), Skarpaas and Shea (2007).
[d]Jongejans and de Kroon (2005), Soons et al. (2005), Herben et al. (2006), Mildén et al. (2006).
[e]Müllerová et al. (2005), Nehrbass et al. (2006, 2007), Nehrbass and Winkler (2007).

Local demography

Local population processes can be as important for the spatial dynamics of plants as dispersal. However, because demographic modeling techniques are more well-known than dispersal models, we will only briefly summarize key demographic models. Excellent and detailed treatises do exist on local population models (e.g. Edelstein-Keshet, 1988; Begon et al., 1996; Roughgarden, 1998; Gotelli, 2001). Their localized nature means that spatial heterogeneity is not usually incorporated.

The simplest population models assume exponential growth, and potentially density-dependent asymptotic convergence to a carrying capacity. Matrix models can harbor more biological detail by defining the survival, growth and reproduction rates of different life cycle stages, while still allowing for a full analysis of, for instance, the projected population growth rate, and its sensitivity to small perturbations in the model parameters (Caswell, 2001). Unfortunately, however, matrix models require the imposition of discrete categories even if such categories do not exist. The position of category boundaries can make large differences to predictions (Enright et al., 1995). Ignoring the individual variation within these artificial categories can also lead to quantitative, and even qualitative differences in predictions (Easterling et al., 2000; Pfister and Stevens, 2003; Shea et al., 2006). One solution is to use individual-based models (IBMs). These models allow individuals to be tracked (DeAngelis and Gross, 1992; Grimm and Railsback, 2005), but normally sacrifice analytic results (but see Dieckmann et al., 2000).

Recently, a new approach has been developed, that incorporates much of the flexibility of IBMs with the technical arsenal of tools developed for matrix models in an analytic framework: integral projection models (Easterling et al., 2000; Ellner and Rees, 2006). Instead of discretizing continuous state variables into representative categories, the continuous function itself is used in the model. This exciting technique is rapidly gaining in popularity because of its obvious utility (Rees and Rose, 2002; Childs et al., 2003; Metcalf et al., 2003). Reanalysis of data previously used in matrix models provides additional ecological insights (e.g. Easterling et al., 2000), and has greatly improved our understanding of how complex local demographic processes, and the associated individual variation, affect population growth and the evolution of life history strategies (Rees and Rose, 2002; Childs et al., 2003; Ellner and Rees, 2006).

Dispersal

The shape of the dispersal kernel (the probability distribution of dispersal distances) has been found to be a crucial determinant of spatial population dynamics

(Kot et al., 1996; Ruckelshaus et al., 1997; South, 1999; Neubert and Caswell, 2000). There are several ways in which dispersal data is acquired (Bullock et al., 2006): e.g. by tracking seeds during dispersal (e.g. Jongejans and Telenius, 2001; Soons et al., 2004), by trapping seeds at different distances from a seed source (e.g. Skarpaas and Shea, 2007), or by reconstructing dispersal, based on distances between seedlings and potential parental plants (e.g. with genetic markers, García et al., 2005). These approaches differ importantly in which parts of the dispersal process they include. For instance, natural seed release dynamics are included in experimental designs that use natural seed sources such as some trapping studies, but are either ignored or are mimicked in a highly artificial fashion in seed tracking studies. Ignoring those processes may lead to incorrect estimation of dispersal distances (Jongejans and Telenius, 2001). Similarly, true dispersal kernels may differ from colonization (i.e. dispersal and establishment) kernels if secondary dispersal occurs, if establishment probabilities vary throughout the landscape, or if the dispersal ability of seeds trades off with their colonization potential (e.g. through seed weight; Strykstra et al., 1998; Jakobsson and Eriksson, 2003). Studies in which dispersal kernels are reconstructed from seedlings may overestimate dispersal distances for a particular mechanism if secondary dispersal is ignored or if, for example, local conditions at the seed source are less favorable for early life history stages (cf. the Janzen–Connell hypothesis; Janzen, 1970; Hyatt et al., 2003), and underestimate dispersal distances if local conditions are more favorable.

Dispersal models differ strongly in their complexity, depending on the level of realism that is included and on whether the dispersal processes are modeled mechanistically or not (Nathan and Muller-Landau, 2000; Greene and Calogeropoulos, 2002; Kuparinen, 2006). Empirical, phenomenological or parametric models, in the form of probability density functions, describe the dispersal kernels that are the outcome of dispersal events, rather than modeling the mechanisms underlying the observed patterns. Such phenomenological models can be very useful in simulations, as most simulation programs allow random numbers to be drawn from well-known distributions. However, when dispersal distances are strongly affected by environmental factors (such as wind or height of release), that vary considerably at the spatial and temporal scale of interest, mechanistic models are a better alternative. In contrast to empirical models, mechanistic models can contain information on how dispersal is affected by environmental or species-specific factors, and hence they can be used to predict dispersal distances under a range of different conditions. In Table 2, we present an overview of the variety of empirical and mechanistic dispersal models currently in use.

Table 2. A selection of dispersal models

Dispersal models	Formulas	Notes
Empirical/phenomenological models		
Exponential power[a,b,c]	$f_R(r) = \dfrac{a^{2/b}br}{\Gamma(2/b)}\exp(-ar^b)$	Exponential distribution if $b = 1$, normal (Gaussian) if $b = 2$. Thin tail if $b > 1$, fat tail if $b < 1$. No peak possible away from source
Gamma[a]	$f_R(r) = \dfrac{a^b r^b}{\Gamma(a)}\exp(-ar)$	Fat tail
Generalized logistic[a]	$f_R(r) = \dfrac{c'\Gamma(c)r}{a^{2/c'}\Gamma(2/c')\Gamma(c-(2/c'))}\left(1+\dfrac{r^{c'}}{a}\right)^{-c}$	Fat tail
Geometric[a]	$f_R(r) = \dfrac{(b-2)(b-1)r}{a^2}\left(1+\dfrac{r}{a}\right)^{-b}$	Linear, elliptic or sinusoidal. Fat tail. No peak possible away from source
Half-Cauchy[d]	$f_X(x) = \left\{\pi b\left(1+\left[\dfrac{x-a}{b}\right]^2\right)\right\}^{-1}$	Fat tail. No peak possible away from source
Laplace[e]	$f_X(x) = \dfrac{1}{2b}\exp\left(-\dfrac{|x-a|}{b}\right)$	Also called double exponential (two exponentials back-to-back at $x = a$). Thin tail
Lognormal[d,e,f]	$f_R(r) = \dfrac{1}{br(2\pi)^{1/2}}\exp\left(\dfrac{-[\log r - a]^2}{2b^2}\right)$	Peak away from source possible. Fat tail
Weibull (including Normal/Gaussian)[a,b,c,e]	$f_R(r) = abr^{b-1}\exp(-ar^b)$	Normal (Gaussian) distribution if $b = 2$
2Dt[a,c,e,g]	$f_{R2}(r) = \dfrac{b}{\pi a}\left(1+\dfrac{r^2}{a}\right)^{-(b+1)}$	In density per square meter rather than per meter. Tends to a normal distribution as b becomes large and to a Cauchy as b tends to zero. Peak away from source possible. Fat tail
Quasi-mechanistic model		
WALD (inverse Gaussian) for dispersal in air[d,e,h,i]	$f_R(r) = \left(\dfrac{b}{2\pi r^3}\right)^{1/2}\exp\left(\dfrac{-b[r-a]^2}{2a^2 r}\right)$	The parameters are related to species and environmental variables by $a = HU/F$ and $b = (H/\sigma)^2$. Peak away from source possible. Tail can be fat or thin. H is the seed release height, F the falling speed of a seed in still air, U the hourly mean wind speed and σ is a turbulent flow parameter that reflects wind variation due to vegetation structure and weather conditions
Mechanistic models		
Behavior of animal dispersers with retention time[j]	$f_R(r) = \displaystyle\int_0^\infty n(r,t)g(t)\,\mathrm{d}t$	Duration (g) of a seed in an animal's gut or on its fur, and the animal's displacement distance (n) determine the dispersal kernel
Behavior of animal dispersers with post-foraging behavior[k]	$E[D(n)^2] = nE[L]^2 - (1+[n-1]x)d^2$	Animal movement distances are feeding-dependent. $E[D(n)^2]$ is the expected squared distance moved after n trees have been visited. $E[L]$ is the expected mean flight distance between trees. $(1+[n-1]x)d^2$ is a correction for the shorter flight distances upon leaving feeding trees compared to when leaving non-feeding trees
Simple ballistic in air[l,m]	$x_m = \dfrac{H\bar{u}}{F}$	Mean dispersal distance (x_m) determined by the mean wind ($\bar{u}$) speed, release height (H) and falling speed (F)
Ballistic in air with Brownian motion[n,o,p]	$\mathrm{d}Z = (\tfrac{1}{2}ku_*t - F)\,\mathrm{d}t + (2ku_*Zt)^{1/2}\,\mathrm{d}W$	Brownian motion is used to mimic the effect of eddies on the seed or pollen in the vertical direction (Z). k is the Von Karman constant. u_* is the friction velocity. F is the falling speed of the seed or pollen in still air. W is Gaussian white noise

Table 2. (*continued*)

Dispersal models	Formulas	Notes
Ballistic in air with horizontal wind speed variation (wind profile)[o,q,r]	$u_Z = \left(\dfrac{u_*}{k}\right) \log\left(\dfrac{z-d}{z_0}\right)$	Logarithmic wind profile: the wind speed at a certain height (u_z) depends on the friction velocity (u_*), the von Karman constant (k), a vegetation roughness parameters (z_o) and the height below which the wind speed is zero ($d+z_o$)
Ballistic in air with 3D wind speed autocorrelations[r,s]	$du_i = a(x_i, u_i, t)\,dt + b(x_i, u_i, t)\,d\Omega$	The change in instantaneous wind speed (u_i) in direction x_i is a function of a drift coefficient (a) and a stochastic acceleration coefficient (b). $d\Omega$ is a Gaussian random variable with zero mean and variance dt
Seed release dynamics from flower heads[t]	$R(t) = R_i - D(t - t_r)$	Release threshold wind speed (R) decreases at rate D over time. R_i is the initial threshold
Seed release from the fur of animal vectors[u]	$\dfrac{-S_F}{dt} = \dfrac{S_F}{T_R\,dt}$	The proportion of seeds detaching is modeled to be constant over time. S_F is the number of seeds in the fur. T_R is the average time a seed remains on a dispersal vector
Seed release from snow[v]	$p \propto \dfrac{u}{(m/A)^{0.5}}$	Probability of dispersal initiation (p) depends on a threshold wind speed (u) and seed wing loading (seed mass/planform area) (m/A)
Seed release from sand[w]	$\|\vec{U}\| > U_{\text{lift}} = \dfrac{2mg}{\rho A(C_L + (C_D/\mu_s))}$	Dispersal initiation depends on the wind velocity at the location of the seed ($\vec{U}$) and a threshold lift-off velocity (U_{lift}). mg is the weight force on the seed. ρ is air density. A is the planform area of the seed. C_L is the seed's coefficient of lift. C_D is the seed's coefficient of drag. μ_s is a coefficient of static friction
Secondary dispersal on snow[v]	$x_s \propto \dfrac{Tu}{(m/A)^{0.5}}$	Dispersal distance depends (x) on wind speed (u), wing loading (m/A) and traveling time (T)

The *empirical/phenomenological* models $f_R(r)$ give the probability density of dispersal distances R from a point source, assuming R is independent of direction Θ. The distribution $f_R(r)$ is related to the bivariate distribution $f_{X,Y}(x, y)$ in Cartesian coordinates (X, Y) by $f_{X,Y}(x, y) = f_R(r)\, f_\Theta(\theta)/r$ (Tufto et al., 1997). In the special case when Θ is uniformly distributed $f_{X,Y}(x, y) = f_R(r)/2\pi r = f_{R2}(r)$. Note that the form of the empirical model equations given in the table may be different than in the cited reference. The parameters a and b are also not comparable among models. These parameters are usually estimated by fitting the models to dispersal data, but note that the parameters of several of the models can be interpreted and estimated (quasi-)mechanistically, as illustrated by the WALD model (see footnote references). The moment-generating functions for several empirical functions can be found in e.g. Evans et al. (2000) or Klein et al. (2006).

Only the characteristic equations are given for the *mechanistic* models: some equations describe dispersal distance, whereas others describe vector behavior or the initiation of dispersal. This table provides an overview to illustrate the breadth of models currently available. Again, the parameters are not comparable among models.

Different dispersal models (both empirical and mechanistic) can be combined to construct mixed models in order to acknowledge common scenarios in which the total dispersal kernel involves multiple vectors and processes.

[a]Klein et al. (2006).
[b]Tufto et al. (1997).
[c]Austerlitz et al (2004).
[d]Skarpaas et al. (2005).
[e]Bullock et al. (2006).
[f]Greene and Johnson (1989).
[g]Clark et al. (1999).
[h]Katul et al. (2005).
[i]Skarpaas and Shea (2007).
[j]Morales and Carlo (2006).
[k]Sun et al. (1997).
[l]Okubo and Levin (1989).
[m]Dauer et al. (2006).
[n]Andersen (1991).
[o]Jongejans and Schippers (1999).
[p]Klein et al. (2003).
[q]Goudriaan (1977).
[r]Nathan et al. 2002.
[s]Soons et al. (2004).
[t]Schippers and Jongejans (2005).
[u]Mouissie et al. (2005).
[v]Greene and Johnson (1997).
[w]Schurr et al. (2005).

Empirical dispersal models

A classical problem in empirical dispersal modeling is to obtain the right shape of the dispersal kernel both near and far from the source (Clark et al., 1999; Nathan and Muller-Landau, 2000). The most commonly used parametric distributions (Table 2) differ in two important aspects: (1) they decrease monotonically with distance from the source or they are peaked, and (2) their tails are thinner or thicker than that of the negative exponential distribution. Which distributions fit best differs between studies. For instance, observed dispersal patterns for a number of trees and forbs seem to be well approximated by the lognormal or 2Dt, which are both peaked and fat-tailed (Clark et al., 1999; Greene and Calogeropoulos, 2002; Skarpaas et al., 2004; Dauer et al., 2006). Bi- and multi-modal patterns of dispersal are less frequently modeled, but they can conveniently be represented using compound distributions, either as a weighted sum of distributions for alternative mechanisms or conditions (Bullock and Clarke, 2000; Higgins et al., 2003), or as a convolution of different dispersal distributions (Neubert and Parker, 2004; Bullock et al., 2006).

Dispersal distances can be measured in various settings: from a point source in one-dimensional (e.g. coast line or river, Johansson and Nilsson, 1993), or two-dimensional landscapes (e.g. grassland, Skarpaas and Shea, 2007), from multiple point sources (e.g. within a forest, Ribbens et al., 1994) or from a front source (e.g. away from a forest edge, Nuttle and Haefner, 2005). The dimensionality of the resulting kernels can therefore differ; for example the number of seeds per unit length in one dimension or per unit area in two dimensions. A further distinction is whether polar or Cartesian coordinates are used. These distinctions are critical for correct spread rate estimation (Lewis et al., 2006; Pielaat et al., 2006).

From empirical models to mechanistic dispersal models

Several empirical models for dispersal patterns are derived from mechanistic models of the process. For instance, the exponential distribution of dispersal distances arises from organisms moving in straight lines with a constant deposition (stopping) rate (Tufto et al., 1997). Diffusion models can lead to normal (Gaussian) kernels (Turchin, 1998), the 2Dt (Clark et al., 1999), the inverse Gaussian (Klein et al., 2003) or the Cauchy distribution (Stockmarr, 2002), and others, depending on the specific assumptions regarding the dispersal process.

Quasi-mechanistic models are functions in which some parameters are directly informative about the dispersal mechanism, while the functions can still be fitted to dispersal data (Klein et al., 2003). A promising mechanism-based distribution model for dispersal by wind is the Wald analytical long-distance (WALD) model (Katul et al., 2005). This model is derived from well-established models in fluid mechanics and predicts an inverse Gaussian (Wald) distribution of dispersal distances and can be fitted to empirical data sets (Evans et al., 2000; Katul et al., 2005). In contrast to empirical/phenomenological models of dispersal, WALD has the desirable property that its parameters are directly linked to characteristics of the species and the environment. Skarpaas and Shea (2007) found that the WALD model, even with independent parameter estimates, performed as well as or better than a range of commonly used empirical dispersal models (exponential, lognormal, and half-Cauchy) that were fitted to seed trap data for invasive *Carduus* thistles. An important point to note is that when inferences are made about mechanisms by fitting a quasi-mechanistic distribution, the time scale of the assumed mechanism and the pattern should match. The same is true when predictions of mechanistic models are tested with an observed dispersal pattern. This is well illustrated by the WALD model, which is built for hourly wind data: it can be used directly for seed release studies on this time scale, but must be integrated over the dispersal season to match seasonal trapping data.

Mechanistic dispersal models

Mechanistic dispersal models are normally parameterized with independent data and can therefore predict dispersal distances rather than being fitted to distance data like empirical dispersal models (Levin et al., 2003). Mechanistic dispersal models can be used to explicitly incorporate biotic and abiotic variation. For instance, seed characteristics like seed weight and plume size can strongly affect dispersal capacity among wind-dispersed plants (Burrows, 1973; Andersen, 1993). Variation in abiotic variables also contributes considerably to spatiotemporal variation in dispersal distances of trees (Nathan et al., 2001) and invasive thistles (Skarpaas and Shea, 2007). Mechanistic pollen and seed dispersal models can be subdivided into models that keep track of the movement of individual propagules (a Lagrangian approach) and models that formulate the probability density of propagules in space (a Eulerian approach).

Most progress seems to have been made with mechanistic trajectory models of seed dispersal in passive mediums such as water and wind (see also Table 2). For instance, wind speed in the boundary layer is easily incorporated using simple wind profiles that are a function of vegetation height and the position above the soil (Burrows, 1973; Nathan et al., 2001; Skarpaas et al., 2004). Vertical movement, often from turbulence and updrafts, seems to be a major component in dispersal by wind (Nurminiemi et al., 1998; Nathan et al., 2002;

Tackenberg, 2003) and water (Gaylord et al., 2002). Turbulence can be simulated as a source of random variation (Andersen, 1991; Tufto et al., 1997; Jongejans and Schippers, 1999), though it is actually auto-correlated in space and time (Greene and Johnson, 1995). Nathan et al. (2002) explicitly modeled spatial and temporal coherency of eddies in air flows. Soons et al. (2004) found that such simulation models with autocorrelated eddies performed better than uncorrelated variation models.

For plant management, it may be important to understand the movement of other organisms as well, for instance when animals move seeds (Russo et al., 2006; Vellend et al., 2006; Jordano et al., 2007) or when herbivores coinvade (Fagan et al., 2005) or have specifically been introduced for biocontrol (Fagan et al., 2002) or when plant diseases spread through landscapes (Thrall and Burdon, 2002; Isard et al., 2005). This also applies when we consider how humans move endangered species to assist with conservation efforts (Hodder and Bullock, 1997). Mechanistic models of animal-vectored dispersal consider the duration of seed retention in or on animals, and the speed of the seed-carrying animals. Russo et al. (2006) used observed behavioral differences in their seed dispersal model: spider monkeys aggregated seeds at their sleeping sites while seeds were scattered more during foraging. Animal behavior has also been mimicked with random walks (Sun et al., 1997; Mouissie et al., 2005; Morales and Carlo, 2006).

There are several aspects of the dispersal process that need better mechanistic understanding and mechanistic modeling. For instance, incorporation of realistic dispersal initiation and cessation in mechanistic models that include all relevant dispersal vectors is still an open challenge in dispersal modeling (Buckley et al., 2006; Kuparinen, 2006). The few but growing number of studies that have investigated the release of seeds or pollen show patterns of high significance for the dispersal process (e.g. Tufto et al., 1997; Nurminiemi et al., 1998). For example, Skarpaas et al. (2006) and Jongejans et al. (2007a) found that more seeds of invasive *Carduus* species were released in turbulent than in laminar airflows, which may increase dispersal distances even though seeds are released at lower wind speeds in turbulent air. Differential seed release has a strong impact on mechanistically modeled dispersal distances (Schippers and Jongejans, 2005). It is therefore critical to know whether or not natural seed release is included in the dispersal data that is used for model fitting or validation.

So far, almost all mechanistic dispersal modeling studies have assumed homogeneous landscapes. Only a few attempts have been made to include transitions from one habitat type to another (Nathan et al., 2005; Nuttle and Haefner, 2005), or to include encounters with objects (Schurr et al., 2005). It will be interesting to see how much the inclusion of edge dynamics (e.g. turbulence caused by hedgerows) improves the performance of mechanistic dispersal models, since landscapes are rarely homogeneous. Another aspect of dispersal that sometimes can not be ignored is secondary dispersal, especially when seeds fall on water or relatively smooth surfaces like snow or sand, or when seed predators have access to dispersed seeds (Matlack, 1989; Redbo-Torstensson and Telenius, 1995). In such cases, different serial dispersal processes need to be modeled in order of occurrence.

Different seeds from the same plant can be dispersed by different dispersal vectors such as wind, water, various animals, or vehicles like cars or mowing machinery, resulting potentially in bi- or multimodal distributions. The combined dispersal kernel, resulting from different dispersal vectors, has been coined the 'total dispersal kernel' (Nathan, 2006). Horvitz and Schemske (1986) for instance found that one ant species dispersed *Calathea ovandensis* seeds one or two orders of magnitude further than other ant species. It is also possible that scatter hoarding animals disperse individual seeds several times (Jansen et al., 2004). Long-distance dispersers are expected to have a disproportionately large effect on population spread, but how the effects of different parallel or serial dispersal agents relate needs more investigation, perhaps with a Neubert–Caswell (2006) modeling approach like that used by Le Corff and Horvitz (2005) who investigated the effect of differential dispersal of seeds from different flower types. Analyses of how different parallel and serial dispersal vectors shape the total dispersal kernel (Nathan, 2006), and what their relative importance is for spatial population dynamics, promise to be very informative.

Spatial population dynamics

Spatial dynamics result from a combination of local demographic processes (which determine how many propagules are produced) and dispersal processes (which determine how far those propagules move). Simple statistical models (e.g. regression models) do not assume prior knowledge of the mechanisms involved in spatial dynamics, and may be useful when such knowledge is scarce. However, this also means that their predictive power is limited. Models that include information on processes (e.g. reaction–diffusion models, dispersal – including matrix population, metapopulation and IBMs) have a much greater predictive power (Higgins and Richardson, 1996). Thus, these latter models are recommended whenever sufficient data and adequate understanding of the mechanisms of the system are

available. Here, we will discuss spatial population models with increasing spatial and demographic complexity (Table 3).

A null model: population diffusion

Spatial spread has been studied in the context of reaction–diffusion models (i.e. assuming a random walk by individuals) for some time (Fisher, 1937; Skellam, 1951; Okubo and Levin, 2001; Morales and Carlo, 2006). The simplest version of Skellam's spread model (for exponential growth; Table 3) includes the population density (N) at location x at time t, the intrinsic rate of population increase (α) and the diffusion coefficient (D). As t becomes large, the rate of spread reaches an asymptote, which can be compared with observed spread rates. Advection by wind or water can readily be incorporated in the dispersal component of diffusion

Table 3. Mechanistic population spread models with increasingly complex demographic and spatial model structure

Spatial model structure	Demography model structure		
	Unstructured	Discrete stage	Continuous
One population, no spatial dimension (no spread)	Exponential or logistic growth $$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$	Matrix population models[a] $$\begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \end{pmatrix} = \begin{pmatrix} 0 & a_{12} & a_{13} \\ a_{21} & 0 & 0 \\ 0 & a_{32} & 0 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}$$	Individual-based models Integral projection models[b] $$n(y, t+1) = \int_{\Omega} [p(x,y) + f(x,y)]n(x,t)\,dx$$ p represents survival and growth, f reproduction.
One population, spatially explicit	Reaction–diffusion models[c] $$\frac{\partial n(x,t)}{\partial t} = rn\left(1 - \frac{n}{K}\right) + D\frac{\partial^2 n(x,t)}{\partial x^2}$$ *Dispersal is part of the diffusion coefficient, D*	Integrodifference equation models for the spread of structured populations (NCM)[d] $$n(x, t+1) = \int_{-\infty}^{\infty} [K(x,y) \circ B_n(y)]n(y,t)\,dy$$ *Dispersal is included as the MGF of a dispersal kernel. K is a stage-specific dispersal kernel, B_n is a local transition matrix.*	Spatial integral projection models[e] *Dispersal is included as the MGF of a dispersal kernel*
Multiple populations, spatially implicit	Metapopulation, incidence models[f] $$J_i = \frac{C_i}{C_i + E_i + C_i E_i}$$ *Dispersal is part of the colonization parameter C. E represents extinction*	Multiple-patch, stage-structured megamatrix models[g] $$A = \begin{pmatrix} 0 & f_1 & 0 & 0 \\ (1-d)p_1 & q_1 & dp_1 & 0 \\ 0 & 0 & 0 & f_2 \\ dp_2 & 0 & (1-d)p_2 & q_2 \end{pmatrix}$$ *Dispersal is given by the proportion (d) of individuals that disperses to another patch*	No examples known at this time
Multiple populations, spatially explicit	Metapopulation models with specific distances between locations[h] $$M_i = \beta \sum_{j=1}^{n} p_j e^{-\alpha d_{ij}} A_j$$ *Dispersal is a function of distance, d* Unstructured individual-based models[k]	Cellular automaton models with matrix population models within cells[i] *Dispersal can be modeled with various dispersal kernels or decision models*	Spatially explicit individual-based models[j] *Dispersal can be modeled with various dispersal kernels or decision models*

Examples are given where possible. The outcomes of all models in the first three rows and the metapopulation models can be analytical, whereas spatially explicit individual-based models (including cellular automaton models, which span the entire bottom row) require simulations to generate results. The formulae in the table are intended to illustrate the different (non-)spatial models. The number of individuals is often denoted by N or n, but the parameters in the formulae are not generally exchangeable between models. Please see the accompanying references for parameter definitions. MGF = moment-generating function.

[a] Leslie (1945), Lefkovitch (1965), Caswell (2001).
[b] Easterling et al. (2000), Ellner and Rees (2006).
[c] Fisher (1937), Skellam (1951), Shigesada and Kawasaki (1997), Okubo and Levin (2001).
[d] Neubert and Caswell (2000), Neubert and Parker (2004).
[e] E. Jongejans et al. (unpublished model).
[f] Hanski (1994).
[g] Hunter and Caswell (2005).
[h] Hanski et al. (1996).
[i] van Dorp et al. (1997), Herben et al. (2006).
[j] Nehrbass et al. (2007).
[k] Wadsworth et al. (2000).

models (Andersen, 1991; James et al., 2002). However, diffusion models tend to greatly oversimplify demographic and dispersal processes; Skellam's model has only one parameter for demography and one for dispersal. Diffusion models also usually assume homogeneous environments (Pachepsky et al., 2005) or very simple spatial heterogeneity (Shigesada and Kawasaki, 1997).

Adding demographic complexity to spatial population models

Recent advances have greatly improved our understanding of how local demographic details can affect spatial spread. By linking age- or stage-structured matrix models with integrodifference equations, Neubert and Caswell (2000) combined demographic and dispersal dynamics into a single response variable, the invasion wave speed. They then developed measures for the sensitivity and elasticity of wave speeds to demographic parameters. These Neubert–Caswell models (NCMs) express the population structure and density at location x at time $t+1$ as a sum of inputs (through survival, reproduction and dispersal) from all plants at locations y at time t. Importantly, different stage-specific dispersal kernels can be utilized. Under the assumption of spatial homogeneity (i.e. that vital rates do not depend on location), the model can be simplified and rates of spread can be analyzed in terms of sensitivity and elasticity to changes in vital rates (see Neubert and Caswell, 2000 for further details). For thin-tailed dispersal kernels (i.e. where long-distance dispersal is not more likely than in the negative exponential function) these models yield finite spread rate estimates. Fat-tailed parametric functions result in accelerating invasion speeds (Kot et al., 1996). Dispersal is incorporated in NCMs by the moment-generating functions (MGFs) of dispersal kernels. These moments describe the shape of the kernel: the first moment is the mean, and the next higher-order moments are the variance, skewness, and kurtosis around that mean (Evans et al., 2000). The MGFs for several empirical functions can be found in e.g. Evans et al. (2000) or Klein et al. (2006).

Buckley et al. (2005) used the NCM approach to show that the invasion speed of *Pinus nigra* in ungrazed grassland was mostly determined by long-distance dispersal, as well as by seedling survival and growth. They concluded that targeting these processes will therefore reduce the invasion most effectively, for instance by grazing or by removing trees from exposed sites where long-distance dispersal is likely. In another example, Jacquemyn et al. (2005) constructed NCMs for *Molinia caerulea* to study if fire affects the ability of this problematic grass species to invade heathlands. Invasion wave speeds were three times higher in recently burned

plots, which, in this case, could be attributed (with variance decomposition techniques, Caswell et al., 2003) to increased growth and reproduction, while dispersal was unaffected.

A point of concern is that dispersal probability density functions are continuous, whereas only discrete seeds are really dispersed. The far tail of the kernel has only a slim chance of representing a real seed but can have a significant effect and hence result in overestimation of the spread rate (Clark et al., 2003). A useful alternative approach is to directly use empirical dispersal data (Clark et al., 2001; Lewis et al., 2006). However, this only works well when sufficiently large data sets are available (Bullock et al., 2002). For example, Skarpaas and Shea (2007) showed that less trap data would have severely reduced spread rate estimates. Therefore, they estimated the parameters of the quasi-mechanistic WALD function using independent measurements of wind, vegetation and species traits for their invasive *Carduus* spp. dispersal data, and then used the function to simulate large dispersal data sets which were used in an empirical MGF, while integrating wind speeds over the entire dispersal season.

Obviously, these are technical points that remain to be resolved. Similarly, the assumption of traveling waves in homogeneous landscapes will be violated in many instances. Nonetheless, the NCM approach is proving to be very useful and has opened up a wealth of analytical possibilities.

Adding spatial complexity to spatial population models

Although spatial homogeneity is a convenient assumption that may be justified in some cases, it is unlikely to hold for most real, heterogeneous landscapes. Theoretical and empirical studies in landscape ecology and metapopulation biology suggest that spatial structure plays a crucial role in population dynamics (Tilman and Kareiva, 1997; Hutchings et al., 2000; Hanski and Gaggiotti, 2004). Spatial structure has been added to population models in a number of ways.

Patch-based metapopulation models ignore local demography and population dynamics and only consider the (dynamic) presence or absence of local populations in habitat patches. In stochastic patch occupancy models (SPOMs; Moilanen, 1999) a habitat patch can be in one of two states (occupied or unoccupied) at any time t and the pattern of patch occupancy at time $t+1$ is assumed to depend on the pattern of occupancy at time t. Hanski's (1994) incidence function model is a SPOM that has become very popular (e.g. Quintana-Ascencio and Menges, 1996; Kindvall, 2000; Sjögren-Gulve and Hanski, 2000) in particular because it is useful in conservation

management (Hanski, 1994; Hanski and Ovaskainen, 2000). These functions can be modified in several ways to suit different situations (Hanski, 1994). Hanski's original approach assumes that the population is at a colonization-extinction equilibrium – clearly an unrealistic assumption for invading or declining species. However, a more recent technique using implicit statistical inference allows parameter estimation under the assumption of a trend (Moilanen, 1999, 2003), which is useful in applied situations.

Space can also be modeled realistically based on geographic maps. One approach is cellular automaton models, where groups of individuals or single plants are located explicitly in a spatial array (e.g. Tews et al., 2004). Cellular automaton or lattice models divide space into discrete cells within a regular grid. Such models have been used to study, for instance, stochasticity and the evolution of dispersal (Travis and Dytham, 2002; Kawasaki et al., 2006). This spatially explicit approach can be especially useful if management questions are explicitly being asked about a species' dynamics in a particular landscape with a particular landscape configuration. However, this approach does require detailed information about which patches on the landscape map constitute suitable habitat (currently occupied or not). Recently, such detailed maps have been made for protected grassland herbs (e.g. *Succisa pratensis*), including information on both present and historical habitat distributions (e.g. Soons et al., 2005; Herben et al., 2006). When the dispersal capacity of these plant species is included, these studies alarmingly show that the surviving plant populations have become isolated in an increasingly fragmented landscape, and that present patch occupancy levels are better explained by historical species distributions than by current metapopulation dynamics (Lindborg and Eriksson, 2004; Soons et al., 2005). Such models can now be used to investigate whether efforts to restore old and to create new habitat (e.g. corridors; van Dorp et al., 1997) will improve the metapopulation dynamics of these plant species (Westphal et al., 2003). This will contribute to the theoretical SLOSS debate (i.e. whether single large or several small but connected habitat patches will preserve an endangered species best; Etienne, 2004; Pearson and Dawson, 2005). The downside of these tailor-made, detailed spatial models is that they are no longer analytical and that the results and sensitivity analyses are not standardized and therefore harder to compare among studies.

Combining demographic and spatial complexity in spatial population models

Cellular automaton models can also incorporate demographic complexity (e.g. van Dorp et al., 1997; Herben et al., 2006; van Mourik et al., in press). However, where these two extensions (spatial and demographic) really coincide is in the realm of IBMs; DeAngelis and Gross, 1992; Grimm and Railsback, 2005), which allow researchers to combine detailed life history information and the realism of heterogeneous landscapes. The defining characteristic of IBMs is that they contain information about each individual in the population. This may be a particularly useful approach when individual variation is important, e.g. when populations are small. Although individual variation has always been an issue in biology, modeling approaches considering each and every individual were practically impossible until recently. The development of IBMs has been greatly enhanced by increases in computer power and by the rise of object-oriented programming (Congleton et al., 1997). The parallel development in digital representation of landscape structures in geographical information systems (GIS; e.g. Haines-Young et al., 1993) facilitates the simulation of spatial spread in realistic landscapes. Goslee et al. (2006) used an individual-based GIS to predict where in Colorado the problematic herb *Acroptilon repens* is likely to invade. In their study seeds were assumed to be uniformly distributed over the landscape, which clearly can be made more realistic when the relevant dispersal mechanisms are included. Similarly, Nehrbass et al. (2007) used a spatially realistic IBM to reconstruct an invasion of *Heracleum mantegazzianum* and to show how rare long-distance dispersal events drive the spatial spread.

Model selection

It is a good practice to test if each level of complexity that is added to a spread model really contributes to our understanding of the spatial population dynamics for management (Higgins and Cain, 2002). If this is not the case, simpler models are usually preferable (the principle of parsimony). Comparison between matrix population models and NCMs has shown that interesting differences in the elasticity patterns may occur, which suggests that different management strategies are optimal for controlling either local populations or population spread (Shea, 2004; Le Corff and Horvitz, 2005). Agreement of model predictions and data suggests (but is not proof) that models incorporate all necessary complexity, and are somehow realistic depictions of the main processes involved in spatial spread. If model predictions and data do not concur, it is likely that spread rates are dominated by demographic and dispersal processes other than those incorporated in the model.

In reality, researchers have to select model components from a range of demographic models and from a

range of dispersal models, which together can combine to an even larger variety of spatial population models. These choices are mostly motivated by a combination of the complexity of the species life history, the research or management goals and the available data. For instance, for annual species a non-structured population model may suffice, while a more detailed population structure may need to be modeled as soon as a substantial seed bank is present, or if plants live longer. If little dispersal data are available, the simplest dispersal models seem most parsimonious. However, if data on dispersal is available, that data can be used to fit empirical or mechanistic dispersal models or can be used directly in developing an empirical probability density function or empirical moment generating function (MGF). Sometimes the research objective is to understand the role of a particular demographic or dispersal process within a species' spatial population dynamics. In such cases, mechanistic approaches seem essential. However, if the research is more descriptive than focused on processes, phenomenological model components may suffice. Below we will illustrate these issues with five case studies (see also Table 1) in which different model choices are made: three examples with invasive plants (*Cytisus scoparius*, *Carduus* spp. and *H. mantegazzianum*) and two examples with conservation management (*Rhinanthus minor* and *S. pratensis*).

Case study: *Rhinanthus minor* (Yellow rattle)

Considering spatial spread is important in restoration projects, where plants need to spread out over the restored habitat after their initial reintroduction. Coulson et al. (2001) and Bullock et al. (2003) investigated which management practices promote dispersal and spread of the hemi-parasitic summer-annual *R. minor* after initial sowing. They measured seed dispersal with seed traps up to 25 m from a seed source and found that dispersal distances were small when the grasslands were unmanaged or grazed. Mowing, especially during seed set, increased dispersal distances considerably. Bullock et al. (2002) then used NCMs to calculate wave speeds for the expanding *R. minor* populations in the different management scenarios. Bullock et al. (2002) directly used their seed trap data in an empirical MGF. The populations were estimated to expand at rates of 0.66 and 6.11 m year^{-1} in the grazed and hay-cut fields, respectively. This illustrates how these models can be used to evaluate the efficacy of different restoration practices and management timing. Excitingly, the projected wave speeds closely match observed spread rates in experimental *R. minor* populations. In the *R. minor* case study spatial complexity was correctly ignored because the aim was to evaluate management options within more or less homogeneous fields.

Modeling demography and management-specific dispersal therefore not only suffices but also seems to be exactly the right level of detail in this case study.

Case study: *Cytisus scoparius* (Scotch broom)

The invasion speed of *C. scoparius* was modeled by Neubert and Parker (2004). This European bush has successfully invaded many parts of the world. On the west coast of North America, for instance, this invader threatens native prairie communities and causes economic losses in forestry. Parker (2000) studied the demography of *C. scoparius* at the edge and in the center of six populations with matrix models. The edges of these stands showed particularly large increases in population size. Using the population dynamics at the edges – where density dependency is much less important – Neubert and Parker (2004) applied NCMs. They included two modes of dispersal: first seeds dispersed ballistically from the pods, then secondary dispersal by ants that are attracted by the elaiosomes of the seeds. Although these authors present possible mechanistic models for both processes, they use empirical data to generate the necessary MGFs. Ballistic dispersal was measured with sticky seed traps around isolated plants and by counting seeds that landed in each trap (Parker 1996 in Neubert and Parker, 2004). The resulting dispersal kernel was marginalized in one dimension and used to obtain an empirical MGF. Seed dispersal by ants was studied by placing seeds out in the field and inferring dispersal distances from resulting seedling distributions. This approach of course relies on the assumption that there are no spatial differences in seedling establishment probabilities. The radial distances from the seedlings to where the seeds were placed on the soil were then used to parameterize an analytical MGF. Given that the two dispersal processes occur in series rather than parallel, the two MGFs could be convolved to get the MGF of the total dispersal kernel. This approach, combining different dispersal vectors into a total dispersal kernel, is a really promising development since it incorporates important biological realism. The resulting wave speed estimations were rather low, 0.46 m year^{-1}, forcing the authors to conclude that these local population expansion processes are not responsible for spreading this species across a landscape. Seed dispersal by humans is a more likely suspect, and it would be very interesting if that dispersal vector could also be included in future studies. However, with this local expansion model, Neubert and Parker (2004) were able to investigate the interesting question of what effect seed predators would have on the invasion speed. They found that such biological control agents would reduce the spread more and more (non-linearly) when seed losses increase.

Case study: *Carduus nutans* (Musk or Nodding thistle) and *Carduus acanthoides* (Plumeless thistle)

Carduus nutans thistles have successfully invaded Australia, New Zealand and the Americas, where they are an economic problem in pastures. Skarpaas and Shea (2007) measured their seed dispersal by wind with seed traps. As was found for *R. minor* the integrodifference models for spatial spread are very sensitive to the maximal distance at which traps are placed. However, this problem was solved by using the mechanistic WALD model to simulate dispersal distances, which subsequently were used to generate empirical MGFs (Skarpaas and Shea, 2007). The mechanistic dispersal model predicted the seed trap data well, justifying the *a posteriori* conclusion that such seed trap studies would be redundant in the future. This mechanistic approach allowed for an investigation of the roles of environmental factors like wind speed and turbulence and biotic parameters like plant height and seed terminal velocity in spread. This mechanistic spread model was extended with demographic complexity into NCMs in a study in which the spatial population dynamics of *C. nutans* were compared among three invaded ranges and with the native range (E. Jongejans et al., unpublished analysis). Increased spread rates in the invaded ranges were caused by both dispersal and demographic differences with the native range. Interestingly, however, the contribution of changes in parameters like seed production, plant height and seed terminal velocity to the increase in invasion spread varied among the invaded ranges. This may well mean that optimal management strategies to reduce the spread of this invasive plant will differ among the invaded ranges. A suite of local and spatial population models with different levels of complexity (local matrix models, IBMs, unstructured integrodifference equation models and NCMs) have now been developed for *C. nutans*, and it will be highly informative to compare their performances in order to find out which complexities can be omitted without jeopardizing the quality of management recommendations.

Skarpaas and Shea (2007) also modeled the spread of the related invasive thistle *Carduus acanthoides*, and found spread rates of about $10 \, \text{m year}^{-1}$. This seems consistent with a study that shows that this species is not ubiquitous but has a regionally aggregated distribution (Allen and Shea, 2006). However, the modeled spread rate is considerably higher than is found for this species in small, $64 \, \text{m}^2$ experimental plots ($<1 \, \text{m year}^{-1}$, Jongejans et al., 2007b), while $10 \, \text{m year}^{-1}$ is still orders of magnitude lower than what is necessary to explain the spread of this species across North America in the last 150 years. These discrepancies again show that datasets and model predictions can be governed by different dispersal processes depending on the spatial scales that are studied (Pauchard and Shea, 2006); here short- and long-distance dispersal by wind and extreme long-distance dispersal by humans. Similar comparisons have been made to investigate which dispersal mechanisms can explain post-glacial spread of tree species (Cain et al., 1998; Clark, 1998).

Case study: *Succisa pratensis* (Devil's-bit scabious)

In the previous case studies with analytical models, the convenient but limiting assumption was made that landscapes are homogeneous and that an invasion starts from a small focal point. However, more detailed models are useful when specific management questions are asked for specific systems. For example, for declining herbs in highly fragmented landscapes, policy makers and managers want to know if costly new restoration areas will decrease fragmentation in such a way that the spatial dynamics of these target species will be revived. For the endangered grassland perennial *S. pratensis*, information is available on the spatiotemporal variation in demography (Jongejans and de Kroon, 2005), as well as on habitat maps and the fragmentation process itself (Soons et al., 2005; Herben et al., 2006). The grassland habitat of *S. pratensis* was strongly reduced during the 20th century, both in area (by 99.8%) and in connectivity (Soons et al., 2005). Mildén et al. (2006) constructed a spatially realistic model using transition matrices for stage-structured population dynamics within each $5 \, \text{m} \times 5 \, \text{m}$ grid cell. They included unassisted, short-distance dispersal (ranging from 0.46 to 2.35 m) but also assumed that a small fraction of seeds (e.g. 10^{-5}) were broadly dispersed by sheep in a distance-independent fashion. Patch occupancy was most sensitive to the parameter that determined the proportion dispersed by either dispersal mode, and also to parameters associated with short-distance dispersal. With these simulations they showed that it takes thousands of years to reach an equilibrium situation.

It will be interesting to investigate if increasing demographic and dispersal complexity in the model will improve the predictions of such simulations. For *S. pratensis* detailed information is also available on multiple interactions between habitat isolation, habitat quality, population size, inbreeding depression and gene flow through seed dispersal (Soons and Heil, 2002; Vergeer et al., 2003; Jongejans et al., 2006; Mix et al., 2006). Combining these insights in a spatially realistic IBM may answer the pertinent management questions with more accuracy. Ruckelshaus et al. (1999) pointed out that the accuracy of such spatially explicit population models is more likely to suffer from uncertainty in natural history than from geographic uncertainty.

A comparison of predictions with those from both simple and spatially explicit metapopulation models would allow us to assess the necessity for the extreme model complexity inherent in the IBMs.

Case study: *Heracleum mantegazzianum* (Giant hogweed)

One of the most problematic invasive species in Europe is *H. mantegazzianum* (native to the Caucasus). This very tall (up to 5 m) herb is able to outcompete other plant species and to form monocultures in many habitats. Furthermore, its phototoxic sap can injure humans. Müllerová et al. (2005) studied the historical spread of this species in a 60 ha area in the Czech Republic. They quantified the distribution of potential habitat on aerial photographs from 11 sampling dates from before the start of the invasion (1947) till 2000. Large individual *H. mantegazzianum* plants could be distinguished on these photos. Nehrbass et al. (2007) reconstructed the historical spread in this landscape with an IBM and the spatiotemporal distribution maps of suitable habitats. The choice for an IBM over a matrix model (for *H. mantegazzianum* see e.g. Hüls, 2005) was made because the demography that was observed in an established population resulted in a deterministic projection of declining population sizes. Nehrbass and Winkler (2007) showed that their IBM (based on the same data) resulted in more stable population dynamics due to the individual variation that was included. In contrast to this demographic complexity, dispersal was included very simplistically in their cellular automaton (Nehrbass et al., 2006, 2007): an arbitrary number of the seeds were modeled to disperse to neighboring cells, while a certain percentage was randomly distributed over the landscape irrespective of distance (i.e. uniformly). The model predictions fitted the observed occupied area best when this random uniform long-distance dispersal percentage was set to 2.5%. Although long-distance dispersal is very important for the spread of *H. mantegazzianum* and many other species, a better understanding of the mechanisms underlying spatial spread may be gained if detailed dispersal kernels are used based on empirical data or mechanistic models. Detailed knowledge of the dispersal dynamics seems especially important for assessing the efficacy of local management practices (e.g. manual and mechanical control, grazing, herbicides or combinations thereof, Nielsen et al., 2005) for controlling the spatial spread of invaders.

Conclusion

Any management topic that has a spatial component requires a spatial model. Spatial models will therefore be vital for developing optimal management strategies, for instance for controlling invaders (including GMOs), or for the translocation and conservation of endangered plant species. The studies reviewed in this paper strongly suggest that local population dynamics and dispersal are both important contributors to spatial dynamics. As we have seen, a large variety of demographic and dispersal models have been developed. This array of models can be combined to form many different types of spatial population models (as illustrated in Table 3). The choice of exactly which demographic and dispersal components should be combined can appear daunting.

Such choices will depend on the data available, on the life cycle of the plant species concerned, and on management objectives. Highly sophisticated mechanistic dispersal models will not be possible in the absence of appropriate data, complex demographic models are not necessary for species with simple life cycles, and simple metapopulation models will be unhelpful if spatially detailed management recommendations are required. In general, the identification of conditions under which the spatial population dynamics are affected will immediately suggest appropriate management strategies (e.g. Fagan et al., 2002). We have used case studies to demonstrate how different spatial population models can be used to inform conservation and control management. We also identified useful extensions and comparisons that would importantly increase the value of these models for management.

The trend in spatial population models is that both non-analytical models and analytical models are becoming increasingly complex (Table 3). Analytical models can now include demographic processes and their variation in a continuous way (Easterling et al., 2000; Ellner and Rees, 2006), combine dispersal functions and stage-structured population matrices (Neubert and Caswell, 2000), and to some extent approximate spatial IBMs (Dieckmann et al., 2000; Ovaskainen and Cornell, 2006). Analytical models are very appealing because it is almost always possible to formulate exactly how much any underlying parameter contributes to the population growth or spread rate or the variation therein. These standardized features of analytical models also allow for important comparisons of model outputs between study systems. At the present time less biological and geographic realism can be included in analytical spread models than in spatially explicit IBMs. IBMs are therefore still more suitable for answering very specific questions and for studying the spatial implications of a myriad of interacting factors that influence plant performance in a landscape. However, increasingly complex analytical models will undoubtedly be developed in the near future. For instance, megamatrix models (see Table 3) and integral projection models can theoretically be combined to investigate continuous

demographic functions and their variation in spatially implicit metapopulations. Another novel approach will be to construct spatially explicit integral projection spread models by combining integrodifference equation models for spatial spread with integral projection demographic models. Such developments will create new opportunities to determine analytically the potential role of, for example, phenotypic variation in spatial population dynamics with all the consequent management implications.

An important opportunity to learn about the value of increased model complexity for management recommendations is the comparison of suites of models. For instance, in the *C. nutans* case study, a wide variety of local and spatial population models have now been constructed. A preliminary comparison among matrix models and NCMs already suggested that importantly different management options may be suggested by these models (Shea, 2004). However, more comparisons are needed to find out in which cases biological realism of demographic and dispersal processes are essential and in which cases they can be safely omitted without altering management recommendations.

In conclusion, we reiterate that the overall goal of these applied spatial modeling approaches is to plan effective management. Modeling efforts should therefore be linked with field-testing, to demonstrate that the theoretical conclusions based on the model assumptions and input parameters hold in reality. As was seen in the successful case study of *R. minor*, model-experiment comparison can thus point to whether the main biological processes are included in the model, or whether further complexity is required for the model to be an appropriate management tool.

Acknowledgments

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