ESSAY REVIEW

Forecasting plant migration rates: managing uncertainty for risk assessment

S. I. HIGGINS, J. S. CLARK*, R. NATHAN†, T. HOVESTADT‡, F. SCHURR, J. M. V. FRAGOSO§, M. R. AGUIAR¶, E. RIBBENS** and S. LAVOREL††

*UFZ Umweltforschungszentrum, Leipzig-Halle, Sektion Ökosystemanalyse, Permoserstrasse 15, 04318 Leipzig, Germany, *Department of Botany, Duke University, Durham, NC 27708, USA, †Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel, ‡Ecological Field Station, University of Würtzburg, Glashüttenstrasse 5, 96181, Rauhenebrach, Germany, §Environmental and Forest Biology, College of Environmental Science and Forestry-State University of New York, 1 Forestry Drive, Syracuse, NY, 13210–2778, USA, ¶IFEVA, School of Agronomy, Universidad de Buenos Aires, Avenue San Martin 4453, Buenos Aires 1417, Argentina, **Western Illinois University, Department of Biological Sciences, 1 University Circle, Macomb, IL 61455, USA, ††Centre d'Ecologie Fonctionnelle & Evolutive, UPR 9056 du CNRS, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France*

Summary

1 Anthropogenic changes in the global climate are shifting the potential ranges of many plant species.
2 Changing climates will allow some species the opportunity to expand their range, others may experience a contraction in their potential range, while the current and future ranges of some species may not overlap. Our capacity to generalize about the threat these range shifts pose to plant diversity is limited by many sources of uncertainty.
3 In this paper we summarize sources of uncertainty for migration forecasts and suggest a research protocol for making forecasts in the context of uncertainty.

Key-words: spread rate, climate change, range shift, seed dispersal, long-distance dispersal.

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Introduction

Although the migration of populations has been of interest to biologists for centuries, it was Darwin (1859) who emphasized the role that it plays in influencing the distribution and diversity of organisms. Climate change is redefining the potential distribution of organisms at an unprecedented rate. The capacity of plant species to fill redefined ranges will be strongly influenced by their migration rates. Hence it has been argued that migration rates will play a pivotal role in defining future patterns of plant diversity (Pitelka *et al*. 1997).

Fisher (1937), Kolmogorov *et al*. (1937) and Skellam (1951) first developed mathematical techniques for predicting rates of population spread. These early models were able to translate assumptions concerning life history and dispersal into estimates of rates of population spread. Within the context of simple models, it was demonstrated how reproduction and dispersal might influence rates of spread. The underlying assumption, that seed dispersal followed a diffusion process that could be described by a Gaussian distribution, led to the apparent paradox that the migration rates predicted by these models were very much slower than much of the evidence suggested (Reid 1899; Clark *et al*. 1998). This paradox was 'resolved' by using seed shadows that could describe occasional long-distance dispersal events in migration models. Such 'fat-tailed' dispersal distributions describe the dispersal data better than Gaussian distributions (Clark 1998). Moreover, migration models that used fat-tailed descriptions of seed shadows generate migration rates that are easy to reconcile with palaeo-evidence for Holocene migration (Cain *et al*. 1998; Clark 1998; Clark *et al*. 1998; Higgins & Richardson 1999).

While the resolution of the paradox was a break-through for the way in which ecologists think about migration, it exposed many more inadequacies in our capacity to predict migration rates (Clark *et al*. 2003). These inadequacies suggest that there is a need for a re-evaluation of the role of uncertainty in models and data of plant migration. We examine this uncertainty in the context of the main application of such models – forecasting which species are most likely to be threatened by changing climate.

Correspondence: S. I. Higgins (e-mail higgins@oesa.ufz.de).

The elements of migration modelling

Clark *et al.* (2001b) presented a minimal model for spread rate. The model contains parameters and functions that describe the net reproductive rate, the generation time and the dispersal of offspring. The net reproductive rate (R_0) is the number of offspring expected from a female and is calculated as the product of survivorship and fecundity integrated over age. Generation time (T) can be calculated in several different ways, depending on precisely how it is defined. Perhaps the most common definition is the average age of mothers of individuals in the population, calculated as the 'centre of mass' of the fecundity × survival function (Pielou 1977). Generation time (T) and the net reproductive rate (R_0) together define the finite rate of increase (λ) of a population ($\lambda = R_0/T$). The dispersal kernel f(x) describes the distribution of offspring as a function of the distance and, in more complicated cases, the direction from the parent. It must be emphasized that the dispersal kernel describes the distribution of offspring, and not merely the distribution of seeds around the parent plant. Hence the dispersal kernel integrates the effects of seed dispersal, seedling germination and survivorship. In many cases, decomposition of the dispersal kernel into a seed to seedling survivorship kernel and seed dispersal kernel may generate further insight.

Traditional models of spread are based on diffusion. Diffusion occurs when dispersal is 'bounded', in the sense that the dispersal kernel has a tail that decays at least as fast as an exponential. In this case, simple models of spread that represent population density as a continuous variable (i.e. with non-integer 'individuals'), match empirical observations. They predict a coherent 'travelling wave' that eventually moves with constant velocity. The travelling wave prediction is based on an 'expected density' approach and represents the progress of the leading front of a spreading population (Skellam 1951; Weinberger 1982; Neubert & Caswell 2000). Such models predict that migration rate is weakly dependent on R_0 (it is proportional to sqrt(log(R_0))), and it is proportional to mean dispersal distance, which is an adequate summary of f(x). These models have been successfully applied to a number of cases of animal spread (Skellam 1951; Lubina & Levin 1988; Andow *et al.* 1990; van den Bosch *et al.* 1992).

Traditional diffusion models cannot be used to estimate spread of populations with dispersal kernels that are fat-tailed. The velocity of spread for populations characterized by fat-tailed dispersal is highly sensitive to R_0 and f(x). In fact, when the kernel is fat-tailed (i.e. the variance of the kernel is infinite), an expected density approach does not provide a finite estimate of spread (Mollison 1977; Kot *et al.* 1996), because the continuous tail of such kernels predicts that fractions of individuals can arrive at locations unrealistically far from the population front. For kernels with infinite variances the expected density models make the impossible prediction that spread accelerates indefinitely as time passes (Kot *et al.* 1996; Turchin 1998).

The problems that thwart efforts to predict potential spread rates from populations described by fat-tailed dispersal can be avoided by recognizing the discrete nature of seeds. An 'expected density' approach provides estimates of spread for discrete dispersal kernels that can be empirical (Clark *et al.* 2001a). In these cases, there is no assumption regarding the shape of the kernel tail, but the estimate does depend on the distribution of the data. A 'furthest forward' approach can be used to estimate spread by using dispersal information to determine a distribution of extreme dispersal events (Clark *et al.* 2001b). Similarly, simulation models of migration typically simulate dispersal as a discrete process and consequently generate finite rates of spread (e.g. Higgins & Richardson 1999). Both the furthest-forward and simulation approaches can be applied with either parametric or non-parametric dispersal kernels, including continuous kernels that have infinite variances.

Sources of uncertainty in model forecasts

A forecast or prediction is a future probability distribution of a variable of interest. The forecast is contingent on initial conditions, model type and parameter estimates. Uncertainty is a measure of our confidence in a statement or forecast. Three types of uncertainty are particularly relevant to our discussion of migration forecasts. *Model uncertainty* is caused by uncertainty in the representation of ecological processes. *Parameter uncertainty* is uncertainty in parameter estimates derived from data and is consequently a function of sample size. *Inherent uncertainty* results when, even when the model and parameter estimate are perfect, the processes under investigation are so fundamentally influenced by stochastic processes that the mean forecast is uninformative. The consequences of these sources of uncertainty are evaluated by Clark *et al.* (in press); here we review these consequences with emphasis on forecasting migration rates.

MODEL UNCERTAINTY

All models are caricatures – there is no correct model. But useful models can be parameterized to capture the important features of a process within a restricted domain. Deficient models miss key processes, and may consequently yield misleading forecasts. In the context of migration, sub-models used to define the life history and dispersal parameters are uncertain, because the many processes that affect seed dispersal, establishment, survival, growth and reproduction might be poorly understood. For example, a deficient model might miss the fact that the life history involves a seed bank with an extended dormancy phase. Migration model uncertainty can be reduced by research into the processes influencing demographic rates and dispersal

distances and by ensuring that our understanding of these processes is adequately translated into the model.

The potential for migration model deficiency is high in the dispersal sub-model. A dispersal kernel might be wrong due to failure to recognize an important dispersal process. This is an acute problem when one considers that the seeds of most plant species are moved by multiple dispersal processes (Ridley 1930). For instance, seeds with morphologies that suggest they are wind dispersed are occasionally moved long distances by animals, and seeds with morphologies that suggest animal dispersal can be moved long distances by wind (Wilkinson 1997; Higgins *et al*. in press). The level of detail in dispersal models depends on available information and on the goals of the analysis. Rare long distance dispersal events are difficult, but not impossible, to study systematically (Cain *et al*. 2000; Higgins *et al*. in press). However, even detailed study of rare dispersal events often only marginally narrows the confidence intervals of rate of spread predictions (Clark *et al*. in press).

Nonetheless, some types of large scale dispersal processes have yielded to systematic study and in recent years significant advances have been made in both phenomenological (describing patterns) and mechanistic (describing processes) models for long distance dispersal. For wind dispersed seeds, phenomenological studies have observed and described the tail of the dispersal distribution (Greene & Johnson 1995; Bullock & Clarke 2000), and mechanistic studies have successfully simulated the effects of updrafts that influence long distance dispersal (examples are Nathan *et al*. 2002b; Tackenberg in press). These more recent mechanistic studies have shown that long distance dispersal is most strongly influenced by wind properties (particularly updrafts). Plant traits such as propagule morphology and height of seed release are of lesser importance. For dispersal by animals, the outcome of animal movement, seed retention and seed deposition are difficult to observe (Fragoso 1997). Hence few phenomenological studies exist (examples are Yumoto *et al*. 1998; Wenny 2000). Mechanistic models of animal dispersal are also poorly developed, perhaps because the environmental and behavioural factors influencing animal movement are so varied that these models are often case-specific (examples are Sun *et al*. 1997; Hickey *et al*. 1999; Westcott & Graham 2000). However, combining information on the scale of animal movement and seed retention (e.g. Higgins *et al*. in press; Powell & Zimmermann in press) could provide a general way to generate dispersal kernels for animal dispersed seeds. Molecular methods also provide a promising avenue for estimating long-distance dispersal (Cain *et al*. 2000; Godoy & Jordano 2001) although how widely applicable such methods are remains unclear (Rousset 2001).

An important aspect of model uncertainty is how we combine the dispersal and demographic sub-models. In this context it is worth repeating that the dispersal kernel in migration models is the distribution of surviving recruits and not merely the distribution of seed dispersal distances. Most migration models are based on seed dispersal data and assume that seed germination and seedling survivorship do not change with distance from the parent plant. However, seed germination and survivorship rates can be higher further away from the parent plant – the 'Janzen–Connell' effect (Janzen 1970; Connell 1971; Clark & Clark 1984). Hence in a Janzen–Connell world, where seedling survivorship increases with distance from the parent, we would expect fatter-tailed dispersal kernels. Janzen–Connell effects may also operate at a biogeographical scale. For instance, in some plant invasions seed production in the novel environment is orders of magnitude higher than in the home environment. This phenomenon is often attributed to predator release (Honig *et al*. 1992). Another source of model uncertainty that may counteract Janzen–Connell effects are Allee effects. Individuals in small isolated populations may have lower reproductive rates than those in larger populations, due, for instance to the lower likelihood of receiving out-crossed pollen (Groom 1998). Although most migration models ignore Allee effects, these may act to retard spread rates when migration rate is driven by occasional long distance dispersal events (Keitt *et al*. 2001).

Establishment success may also vary as a function of environmental variables that are not correlated with distance from the parent plant. This may be due to microsite quality, or to habitat changes that occur within a plant's seed shadow. Similarly, directed and anisotropic dispersal may obscure the relationship between distance and recruitment rates. Most migration models do not consider variation in environmental conditions, directed dispersal or anisotropic dispersal effects. Accounting for environmental factors that are not correlated with distance from the parent plant may often necessitate the use of spatially explicit models.

PARAMETER UNCERTAINTY

Parameter uncertainty is a measure of how sensitive the likelihood of a parameter estimate is to changes in the parameter estimate. Parameter estimates are uncertain when sampling is limited. Moreover, parameter estimates are only as good as the statistical models used to estimate them – that is, parameter estimation cannot be divorced from model uncertainty. Statistical models require appropriate specification of the ecological processes, sources of error in these processes, and observation error. Provided the statistical model is adequate, parameter uncertainty is reduced by more sampling.

Statistical modelling of empirical data typically provides a limited amount of information on dispersal parameters. This is because dispersal sampling is often limited to short distances. When sampling strategies include long distances, the high variance in the processes generating long distance dispersal means that

parameter estimates remain uncertain, even for very large sample sizes. Parameter estimates can be improved by designing sampling strategies geared towards sampling the variance in dispersal processes (Higgins *et al*. 2003). Such a sampling strategy may involve sampling dispersal distances in many different environmental contexts. Stratifying sampling effort in this way can reduce the overall sampling effort significantly (Greene & Calogeropoulos 2002). In mechanistic models parameter uncertainty in the driving variables (e.g. release height, wind velocity or gut retention time) can be considerable. While the effort required to estimate parameters for mechanistic models may seem prohibitive, new techniques for tracking animal movement (Webster *et al*. 2002) or recording wind behaviour (Nathan *et al*. 2002b; Tackenberg in press) provide cause for optimism that difficulties can be overcome.

Dispersal studies do not routinely include information on how survivorship varies with distance from the seed source (e.g. Augspurger & Kitajima 1992; Wenny 2000). Our almost complete ignorance in this regard suggests that this may be the overwhelming component of parameter uncertainty. Migration forecasts are also constrained by uncertainty in parameters that describe demographic processes. Fecundity is the demographic parameter that is particularly uncertain. For example, Clark *et al*. (1999) have shown that 10 years of fecundity data may be needed for parameter estimates of fecundity to stabilize.

INHERENT UNCERTAINTY

Inherent uncertainty can be expected to be large when stochastic processes with high variance influence the response variable. Inherent uncertainty cannot be reduced by improving model or parameter uncertainty. For migration rate, inherent uncertainty is particularly large for populations with fat-tailed dispersal kernels. This problem is compounded when R_0 is large. Large R_0 and fat-tailed kernels together result in uncertain forecasts that cannot be appreciably improved by improving parameter estimates or model structure (Clark *et al*. in press).

Managing uncertainty in forecasts of spread rates

Forecasts of required migration rates are needed to address questions such as: will this species be able to spread fast enough to avoid extinction? Or, what proportion of this species' climatically defined range will it occupy? These questions in turn assume that we know the current range of a species and have a forecast of its future range. Forecasting future ranges has its own set of assumptions and uncertainties (Huntley *et al*. 1995; Rutherford *et al*. 1995; Schwartz *et al*. 2001; Bakkenes *et al*. 2002; Hannah *et al*. 2002), the discussion of which is beyond the scope of this paper. However, forecasts of range shifts provide essential context for interpreting forecasts of migration rates. To be useful to migration

modellers, however, range shift forecasts need to be translated into required migration rates (RMR). RMR can be defined in various ways; for instance, as the migration rate required by a species to be present in its future climatic range under a changing climate, or alternatively as the migration rate required by a species to occupy its entire future climatic range. The first definition may be more appropriate for assessments of biodiversity change, whereas the second definition may be more appropriate for assessments of carbon balances. Currently very few studies that use climate change scenarios to forecast climatically defined ranges of species report required migration rates, something that could be easily remedied.

Once we have an estimate of the required migration rate we can attempt to forecast a potential migration rate. As an example we consider three species invasive to South Africa. Using data on the distribution of parent plants and seedlings collected by Higgins *et al*. (2001) we use an inverse method (Ribbens *et al*. 1994) to estimate the parameters of a log-normal kernel and R_0. Using these parameter estimates and assuming a generation time of 12 years, which corresponds to the return interval of mortality-inducing fires, we use computer simulations to forecast migration rates for these three populations. Figure 1 shows how uncertainty in the parameter estimates propagates through to the forecasts. For *Acacia saligna* there is very high uncertainty in R_0. This translates into excessive uncertainty in the forecast migration rates. This high parameter uncertainty may be interpreted as evidence of model uncertainty. For instance, the sampling design assumed that seeds do not persist between generations. However *Acacia saligna* is known to form seedbanks, and some sampled sites may have had intergenerational seedbanks. For *Pinus pinaster* there is less uncertainty in the estimates of R_0, but considerable uncertainty in the estimated kernel. In particular, the location of the modal dispersal distance is uncertain. The sample included both closed and open stands of *Pinus pinaster* – it is plausible that the mode is closer to the source in closed stands than in open stands. This uncertainty in the kernel results in high parameter uncertainty in the forecast migration rate, while the fact that the kernel is relatively fat-tailed produces considerable inherent uncertainty in the forecast migration rate. For *Acacia cyclops* there is low uncertainty in the dispersal kernel and moderate uncertainty in R_0. The kernel is also not fat-tailed, hence inherent uncertainty in the forecast migration rates is low. Uncertainty in R_0, however, means that uncertainty in the migration rate due to parameter uncertainty is significant.

In these examples (Fig. 1) we have assumed that inherent uncertainty can be calculated as uncertainty in the forecasts made using the maximum likelihood parameter estimates. If our maximum likelihood estimate (MLE) suggests a fat-tailed kernel we will forecast high inherent uncertainty. However if the MLE suggests a kernel with a rapidly decaying tail we will
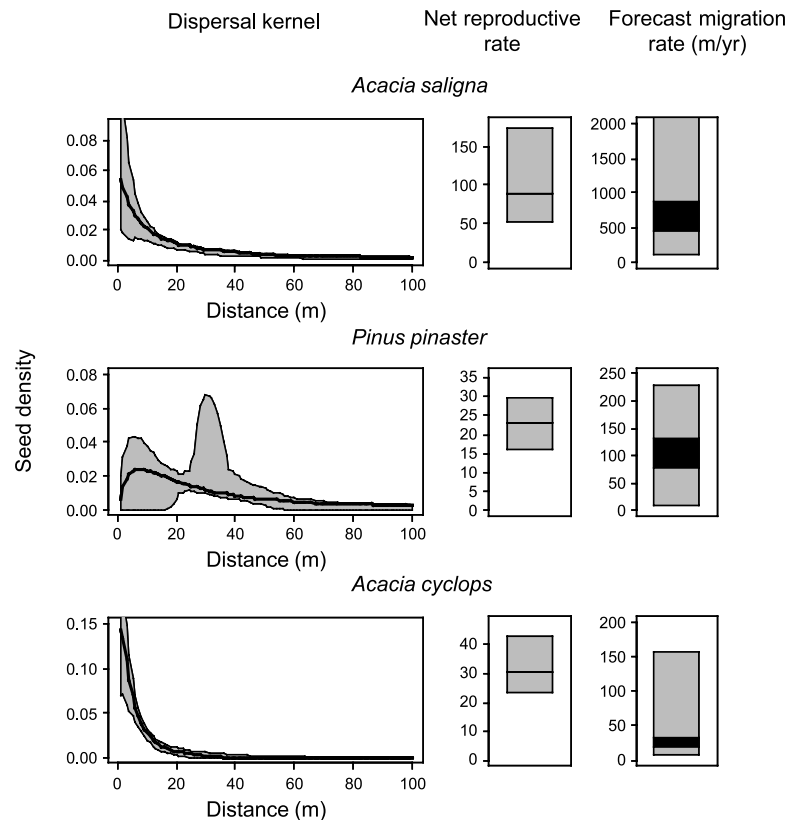
Fig. 1 Error propagation for estimates of migration rates for three species invasive to South Africa (data from Higgins *et al.* 2001). Inverse methods (Ribbens *et al.* 1994) were used to estimate the parameters of a log-normal kernel and R_0. Non-parametric bootstrap was used to estimate the confidence intervals of these parameters. Using these parameter estimates and assuming a generation time of 12 years, which corresponds to the return interval of mortality-inducing fires, we use computer simulation to forecast migration rates for these three populations. The left panels show the maximum likelihood estimates (MLE) of the dispersal kernels (solid lines) and their 90% confidence intervals (shaded areas). The central panels show the MLE estimates of R_0 (horizontal lines) and their 90% confidence intervals (shaded boxes). The right panels show the forecast migrate rates. The black-shaded areas represent the inherent uncertainty in the migration forecast, assumed to be the 90% confidence intervals of forecasts made using the maximum likelihood parameter estimates. The grey-shaded areas represent the parameter uncertainty in the migration forecasts, assumed to be the 90% confidence intervals of forecasts made using the bootstrapped parameter estimates.

forecast no inherent uncertainty. Hence the estimate of inherent uncertainty is conditional on the MLE being true. Although the MLE should move towards the true value as sample size increases, when dispersal is fat-tailed even large sample sizes will not eliminate parameter uncertainty.

Few estimates of plant migration rates exist and even fewer estimates include an assessment of how uncertainty in model selection and parameter estimates influences the forecasts (Clark *et al.* in press). Moreover, because of rapid developments in theory and techniques for forecasting migration rates, the few estimates that do exist are developed using different approaches. This makes comparison and synthesis difficult. Synthesis and comparison could be improved by using a standard model to report spread rates. However, because studies differ in their objectives and available information we cannot expect that one 'standard' model is universally appropriate. Nonetheless, we believe that almost all migration models can be reduced to the special case where the migration rate is defined by the aggregate parameters f(x), R_0, T or merely by f(x) and

λ (the finite rate of increase). In more realistic models that explore the interactive effects of demographic processes, disturbance, resource supply, and habitat distribution on migration rates , R_0, T and f(x) can be estimated from the model's outputs. Many functional forms of f(x) are appropriate for describing dispersal, these cannot be accommodated by a single analytical framework, suggesting that computer simulations will often be necessary to generate migration rates.

Future challenges

The models we have described make many simplifying assumptions. We think it prudent to draw attention to the potential implications of some of these assumptions. Perhaps most notably, our discussion has ignored the importance of the density and distribution of suitable habitat. Because the behaviours of dispersal agents are strongly influenced by landscape structure, dispersal distances can be highly variable in different landscapes. For example, wind dispersal in a forest yields much shorter dispersal distances than wind dispersal in a

grassland (Nathan *et al.* 2002a). Also, the arrangement of barriers to dispersal processes influences dispersal distances and migration rates. However techniques for describing such effects are not well established (Pitelka *et al.* 1997; Collingham & Huntley 2000; Higgins *et al.* 2003).

We also assumed that plant traits affecting fecundity and dispersal mechanisms will not change over time. However, evolutionary responses may be quick, e.g. species arriving on islands have been observed to rapidly reduce their ability to disperse (Cody & Overton 1996). Because the current wave of climate change is combined with habitat loss and fragmentation, selection may be against long-distance dispersal, because in fragmented landscapes the risk of dispersal to unsuitable habitat increases with increasing dispersal distance (Cody & Overton 1996; Hovestadt *et al.* 2001). In addition, we cannot exclude the possibility that local adaptation to new climatic conditions may reduce the need to spread, or that plant pests may respond independently to climate change.

Conclusions

Forecasting migration rates for plants is fraught with many uncertainties. We have argued that we can coherently acknowledge many of these uncertainties. Such acknowledgement is an important first step for defining a research agenda that directs effort to processes where uncertainty can be reduced. We advocate caution when devoting effort to studying long-distance dispersal, as the uncertainties involved may be inherently overwhelming. We also advocate closer co-operation between researchers forecasting changes in climatic ranges and researchers forecasting migration rates. Such co-operation will allow us to direct migration research towards species that are threatened by climate change and species that have expanding climatic ranges.

Acknowledgements

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